

PROSPECTS OF CONTROLLING FIRE ANTS WITH PARASITOID FLIES: THE PERSPECTIVE FROM RESEARCH BASED AT BRACKENRIDGE FIELD LABORATORY

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Abstract: Because imported fire ants, *Solenopsis invicta*, arrived in the U.S. free of the specific parasites and pathogens that infect them in their native South America, they have enjoyed a dramatic competitive advantage over indigenous ants as they spread through southern North America. In Brazil these ants exist as low-density single-queen colonies and are not generally viewed as pests. Up to five species of *Pseudacteon* phorid fly parasitoids can be observed attacking *S. invicta* in any given location in their homeland. A similar situation holds for native fire ants, *S. geminata*, in Texas, where two host-specific *Pseudacteon* attack them but not their invading cousin. Like *S. invicta*, *S. geminata* becomes a pest when introduced to other regions free of biological controls. Experiments on the interaction of *Pseudacteon* and their *Solenopsis* hosts suggest that these flies have the capacity to reduce the dominance and ecological impact of introduced fire ants. Several species of *Pseudacteon* demonstrate specificity to the imported fire ant and are now permitted for release in Texas.

Introduction

Pest insects and weeds are typically organisms introduced between continents free of their co-evolved predators, pathogens and parasites. Without natural biological controls, such species often dominate the native communities which they have invaded. Any disturbance of the native biotic system may promote these introduced pests since they tend to be opportunistic colonists. In the case of imported fire ants in the United States (IFAs), topsoil disruption and pesticides constitute disturbances to native ant communities which help spread the IFA.

In 1981 the IFA invasion reached Brackenridge Field Laboratory (BFL) in Austin, Texas. Fortunately, Feener (1978) had completed a biological survey of ants for the area and therefore we had a baseline condition against which to measure change. Starting with undergraduate honors student Bill Van Eimeren and finishing with Postdoctoral Associate Sanford Porter, we mapped the course of the invasion from 1983 to 1987 (Porter et al. 1988).

We were surprised by the pattern of the invasion. In most ants, including fire ants,

winged virgin queens leave their colony, mate high in the air and land to establish a new colony alone. At first, such airborne invasions would be predicted to lead to new colonies patchily distributed across a landscape still dominated by dozens of species of native ants. This is not what we found. We found a continuous carpet of *S. invicta* spreading like a large amoeba across the area (Fig. 1). At the edge of the amoeba we found native ants on one side and dense IFAs on the other. For every mound of native fire ant lost, seven mounds of the imported species were gained. All native ants declined dramatically, and arthropod diversity was reduced by over 40% (Porter and Savignano 1990).

As the study proceeded at BFL, we noted that all *S. invicta* colonies in the IFA amoeba were of the multiple-queen or polygyne variety. This form of the fire ant first appeared in the 1970s and is now the predominant form in much of Texas (Fig. 2). The more typical single-queen or monogyne form does not reach the extreme colony densities seen in Texas polygyne populations because monogyne colonies defend intra specific territories, attacking and killing workers from other colonies. Conversely, the lack of territorial defense in polygyne colonies allows them to build to vast numbers with densities of over 1000 colonies per acre not uncommon in parts of Texas (Porter et al. 1991).

What accounts for the pattern of spread observed at BFL? We noted two aspects which required explanation. First, in the zone not yet occupied, there were no *S. invicta* colonies, large or small, in spite of thousands of mated queens raining down over the area. Second, large colonies appeared along the boundary as it spread. Ed Vargo's work showed how both of these observations are related to polygyny. First, he found that polygyne queens are smaller, lay fewer eggs and are less capable of initiating a colony alone than are their monogyne counterparts (Vargo and Fletcher 1989). Apparently, such queens do not stand a chance of surviving and reproducing in areas occupied by native ants. Teaming up with Porter, Vargo demonstrated that polygyne colonies reproduce by budding, i.e. queens may leave with a group of workers and establish new colonies nearby (Vargo and Porter 1989). This explains the pattern of spread observed at BFL.

Exceptions to the pattern of spread and distribution I have described further support the role of polygyny and interaction with native ants. The one patch of *S. invicta* separate from the continuous front appeared in a cultivated area treated with pesticides (Fig. 1, top). We assume that lone polygyne queens were able to colonize in the absence of native ant resistance. Conversely, the only two isolated colonies of *S. invicta* discovered in the survey were both monogyne. It is relevant to note that the last open habitat to succumb to the invasion was a patch of little bluestem which dates back to the 1920's as an open grassland. Do the native ants occupying undisturbed native grassland provide better resistance to the invasion? Everything we know about fire ant ecology would support this assumption.

Surprisingly, until Porter and co-workers (Porter et al. 1992) surveyed fire ant densities in Brazil, no substantial studies had been carried out to test whether imported *Solenopsis* species are relatively less dominant in their home regions. Comparable transects between Texas and Florida and in Matto Grosso revealed striking differences (Fig. 3). Brazilian roadsides have 10% of the fire ant density seen in the U.S., and comparisons with multiple-queen populations in Texas are even more extreme (Fig. 4). While there are occasional reports of local fire ant problems in Brazil, these are probably related to severe habitat disruption. Our native *S. geminata*, while generally sparse like *S. invicta* in South America, can be locally abundant to the point of being a nuisance.

In my own experience in Brazil, mounds are not so easy to find while driving cross country. Even along fields and roadsides in suitable habitat, it is not uncommon to walk 100 - 200 yards between adjacent mounds. In urban lawns in Campinas, Sao Paulo state, *S. invicta* densities may rival those seen here in Texas. Remarkably, these mounds are virtually ignored by Brazilians, and dozen of other ant species--large and small--coexist with the fire ants. It is possible to have a picnic next to a fire ant mound in Brazil. Furthermore, if one disturbs a mound in Brazil, workers pour out in defense, as we see here in Texas. But in Brazil, workers run back underground to avoid the attack of parasitoid flies in the genus *Pseudacteon* (Phoridae). The same can be said for *S. geminata* in Texas, if you can find them.

Phorid Flies as a Biological Control of Fire Ants

From a large family (Phoridae) of typically scavenging flies, a few genera of ant parasitoids have evolved, including species which specialize on fire ants (see Disney, 1994). Some of the first natural history studies of ant specialist phorid flies were conducted by C.T. Brues (1901, 1907) around Austin, Texas, early this century. Taxonomic descriptions and host associations for ant-attacking phorid genera appeared in the literature during that time. In the early 1970s during a general search for biological control agents, USDA researchers noted that *Pseudacteon* species frequently associated with fire ants in South America (Williams et al. 1973, Jouvenaz 1983). At that time (as now) the focus was on biotic agents that would inflict high rates of direct mortality on hosts. Interest in phorid flies diminished when it became obvious that only a tiny fraction of ants are infected and killed (1- 3%) by these parasitoids.

A conceptual breakthrough with other species of ants and phorid flies led us to reassess the potential of phorids in controlling ants. As part of his dissertation in the (pre-invasion) ant community at BFL in the late 1970s, Feener (1978) conducted experiments to determine species dominance at food baits. He noted that the outcome of competition between *Pheidole dentata* and *Solenopsis texana* was always victory by *P. dentata* (which

mobilizes large-headed soldiers specifically against ants of the genus *Solenopsis*) unless phorid flies arrived to attack the *P. dentata* soldiers. At that point, the latter retreated to hide, and the food was taken by *S. texana* (Feener 1981). Feener and I saw immediately that his work revealed the importance of indirect effects (through behavior rather than mortality) and indicated that the presence or absence of host-specific phorids could explain why imported fire ants (without phorids) dominate not only native fire ants (with phorids) but other native ants as well (many with phorids or other biological controls).

From the early 1980s to the early 1990s, I talked and wrote proposals about the prospects for phorids in IFA biocontrol, but we got nowhere with funding for appropriate research. Porter went to the USDA in Gainesville in 1990 and later began to focus on the phorid question there. In February 1994, I traveled to Campinas, Brazil, on an NSF travel grant obtained in collaboration with BFL postdoc Michael Kaspari to establish a project with colleague W.W. Benson at the State University of Campinas (UNICAMP). Porter, meanwhile, was just starting work nearby at Rio Claro with Harry Fowler. Dr. Matt Orr joined the BFL group in March 1994 and went to Brazil May through June to conduct (with the help of Sergio Seike) our first experiments on the impact of phorids on fire ants in Brazil. I should say that the \$10,000 required for this work was arranged by an avid quail hunter, rancher and conservationist, who helped "prime the pump" for everything to follow as far as our work on the phorid question is concerned.

The results of our initial observations and experiments indicated a dramatic impact of phorid flies on foraging by fire ant workers during the day in Brazil (Orr, et al. 1995). We found that by removing flies, we could induce a rapid increase in foraging *S. invicta* at any time of day (Fig. 5). However, with flies present, other ants always manage to win competition for food. Independently, Porter and colleagues obtained similar results with different species (*S. saevissima*) and somewhat different techniques (Porter et al. 1995a).

Recently, Orr, Seike and I have expanded our field study to examine the ways that different species of *Pseudacteon* might impact host ants. We have observed nine of the fourteen species known to be associated with *Solenopsis* in Brazil and Argentina. We find that some *Pseudacteon* species are primarily found around disturbed mounds with thousands of workers milling about releasing alarm pheromones. Others are primarily associated with quiet foraging trails, such as supply lines connecting a dead grasshopper with the mound (Fig. 6). Some approach victims from the head first; some approach from the rear of the victim. Some pursue a single ant for over a minute before attempting to oviposit while others make frequent but possibly inefficient attempts. Some are more likely to attack larger workers, others less likely, and sizes of phorid species differ substantially. Our current goal is to determine which species or combination of *Pseudacteon* species will be the most effective in reducing the competitive dominance of *S. invicta* in its introduced range. Further basic studies on interactions between *S. invicta*, ant competitors and *Pseudacteon* in Brazil will be initiated in collaboration with Don Feener (Now at the University of Utah), Matt Orr and our Brazilian colleagues as

soon as the Washington gridlock frees up our three-year NSF grant.

A parallel line of research, spearheaded by Lloyd Morrison at BFL, investigates the basis for *S. invicta*'s dominance over *S. geminata*. We are studying the interactions of these species on the edges of small inholdings of the native ant system in Central Texas. *S. geminata* contends with two species of *Pseudacteon* which are absolutely species-specific. Surprisingly, when competing directly for food with *S. invicta*, *S. geminata* is a more than worthy adversary in the presence or absence of its parasitoid flies--this holds in the laboratory or in the field. However, when *S. geminata* forages alone, the arrival of phorids causes defensive posturing and a reduction of foraging as noted by Feener and Brown (1992). Thus, in the parlance of community ecology, *Pseudacteon* influence exploitative, but not interference, competition between these species (Morrison and Gilbert in preparation). Our studies of *S. geminata*-*S. invicta* interaction zones is also intended to provide baseline data for monitoring the impact of releasing *S. invicta*-specific *Pseudacteon* from South America in Texas. We anticipate being able to detect an expansion of native ant "islands" in a "sea" of imported fire ant as phorids which attack the latter reduce their relative advantage and return parity to the ant community.

Porter et al. (1995a) in tests involving 13 genera of ants have determined that South American *Pseudacteon* are highly specific to the genus *Solenopsis* as collecting records suggest (Disney 1994). Therefore, a third line of our research addresses the issue of whether South American *Pseudacteon* species exist which are as host restricted on the *S. invicta* species group as Texas *Pseudacteon* are to *S. geminata* and its species group. The answer, based on work completed over the last year at BFL (Gilbert et al. in preparation), is that several species are highly restricted to *S. invicta* while others are less discriminating. We used a conservative no-choice test in which individual test flies are first placed in a glass-covered tray with a few hundred *S. invicta* workers. If the fly shows motivation to oviposit on its known host, we then transfer it to a tray of *S. geminata* for a set period and carefully observe any indications that it might show interest in our native species. Finally, we move the fly back to the tray of *S. invicta* to make sure it was indeed interested in ovipositing while confined with the non-host. The "+ - +" pattern of response repeated over an adequate sample of individual females of a species was the criterion for adequate specificity for use in biocontrol. We obtained USDA APHIS permits to release three species in May 1995. At least one other species failed this test by attacking both *S. invicta* and *S. geminata*.

Further lines of research are related to the initiation of introduced populations in Texas. If captive flies are indicative (they may not be!), *Pseudacteon* species have a brief adult life span of several days in nature. At any given instant, most of a population will be at some stage of development inside fire ant hosts. Thus, while harsh weather might kill a cohort of adults above ground, the larval population persists in an environment buffered by the behavior of the ants. Even so, the phorids of tropical Brazil may not be suited to survival in the more extreme temperature zone climates now occupied by IFA in

the United States. Therefore, with the help of Patricia Folgarait in Buenos Aires, Argentina, we have been learning details of the ecology and activity cycles of *Pseudacteon* in a climate much more similar to that of Texas and the southeastern United States than that of Brazil. The goal of the work is to identify species of *Pseudacteon* that may thrive outside of subtropical south Texas and Florida, and to screen more widely for suitable biological control potential within *Pseudacteon*.

Although the BFL group (Morrison et al. in preparation) and Porter et al. (1995b) have reared a few *Pseudacteon* from egg to adult in the laboratory, maintaining a breeding population has not been accomplished. Thus, to attempt introduction, we have collected fire ant workers from outdoor colonies, exposed them to appropriate species of wild caught *Pseudacteon* (usually from 1 to 48 hours after the phorids have arrived from Brazil). Attacked ants are removed by observers, held in the laboratory for a brief period, then returned to source mounds.

Unfortunately, each of the first three attempts coincided with extremely harsh (hot or cold) weather during the brief period when adult flies were expected to emerge, mate, and oviposit. While Brazil also may have episodes of harsh weather which might kill adult populations, any losses will soon be replaced by adults eclosing from pupae. The presence of eggs, larvae and pupae in the natural population acts as a buffer against short-term disaster. The problem we face for biocontrol attempts is how to introduce a *Pseudacteon* population with appropriate age structure so that the success or failure of a particular age cohort is not so critical. One possibility is to control the conditions where introductions are attempted. Thus, we are initiating the construction of a large tropical greenhouse designed to allow *Pseudacteon* to build up populations in a semi-natural state. Even so, it may take repeated collecting trips at weekly intervals to initiate an age-structured population (one with all developmental stages coexisting). A goal for this year is to develop the capacity to grow *Pseudacteon* populations in a greenhouse or laboratory here in Texas. This has proven to be a challenge but should not stall things too long.

Finally, we know more about the larval life (e.g., Porter et al. 1995b) of *Pseudacteon* than the adult life. We are only able to keep adults alive 2 - 5 days at normal room temperature. They do feed on sugar solution, but adult diets in nature are not known. When we disturb mounds, phorids seemingly appear out of nowhere, even in some rather harsh and bleak situations (dry, little lush vegetation). Where are these flies while waiting for the opportunity to attack ants? Can they live longer than we think by resting in special microsites? This is crucial natural history information that we do not possess and that is difficult to obtain.

By their mere presence, phorid flies alter the capacity of host ants to forage efficiently for food or defend nests. Their most significant impact, therefore, is not to reduce populations through direct mortality, but rather to reduce the capacity of target species to compete with other ants for food or (presumably) nest sites. Such indirect effects must translate into lower equilibrium population densities through reduction in the rates that resources can be provided for raising brood. The expected result is that a balanced and diverse phorid community will prevent any ant species from achieving overwhelming dominance. Our goal is to achieve such a balance.

In much of Texas, high-density polygyne fire ant populations are vulnerable to a phorid epidemic simply because flies won't have to search long for hosts. Moreover, if the imported ants have lost some of their anti-phorid vigilance over the last seven decades, phorids may be more effective in rates of oviposition, and this may initially impose a high direct mortality. In this scenario, mortality-caused natural selection by phorids would, through time, restore the avoidance behavior seen in South American *S. invicta*. At that point indirect effects would again become relatively more important to biocontrol. If *S. invicta* anti-fly behavior has not been lost since the ants' introduction, we expect indirect effects to be important from the outset of introducing South American *Pseudacteon* to Texas.

Either way, however, the presence of intact remnants of the native ant community are critical to the success of this approach. Without native ants to take advantage of phorids harassing *S. invicta* during the day, the rate at which phorids reduce the impact of *S. invicta* will be much reduced. In anticipation of using *Pseudacteon* to control *S. invicta*, it will be of critical importance to minimize harm to native ants, including native fire ants (and, indeed, any components of the faunal system which compete for food or space with *S. invicta*). In particular, education of citizens on the distinctions between native and imported fire ants (Fig. 7) is of critical importance if phorid flies are to be given a fair chance as agents of biological control. Our minimal goal with current funding is to learn enough in three years to be able to "fish or cut bait" concerning the use of phorids in the control of imported fire ants. As far as I know, there has never been a successful biocontrol of a pest ant. My colleagues and I would like to change that dismal fact.

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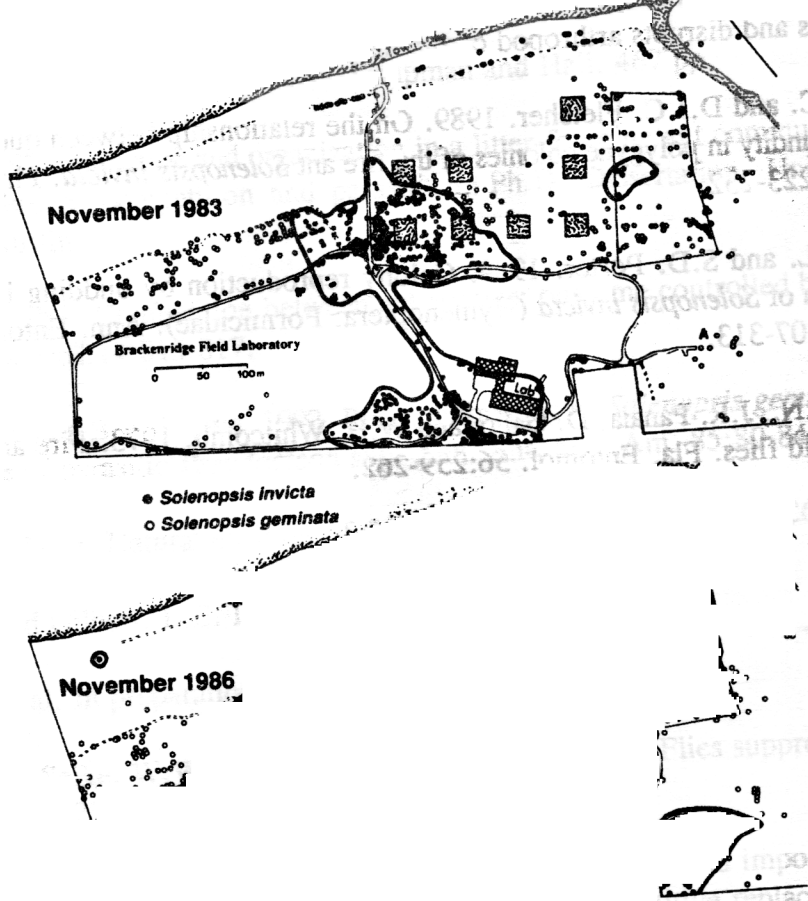


Fig 1. Distribution of native and imported fire ant mounds at Brackenridge Field Laboratory in November 1983 and 1986. A heavy solid line separates the two populations. In 1983 (above), an IFA outbreak occurred in an area which had recently received pesticide treatment. Otherwise, only two (both monogyne) IFA mounds occurred outside the main invasion front (Lower map, top left and right) (Porter et al. 1988).

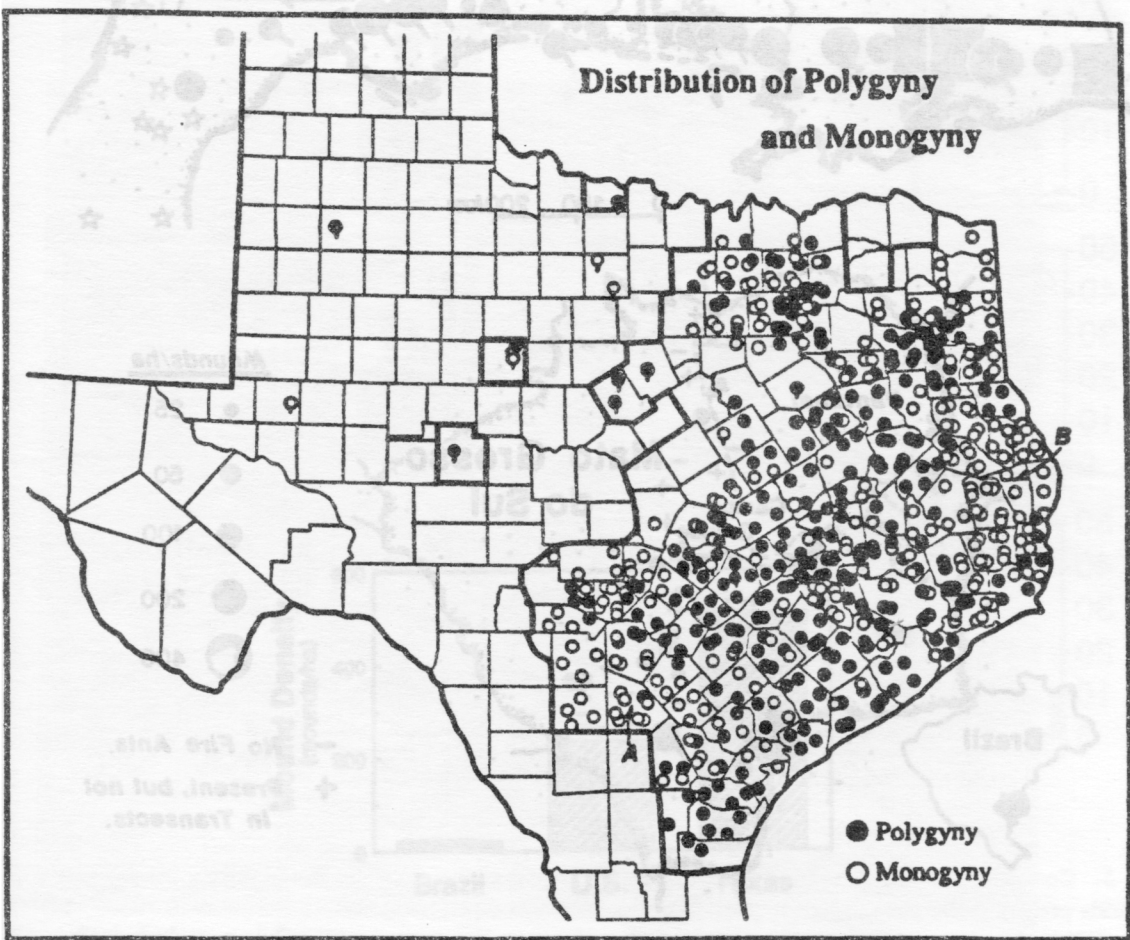


Fig. 2. Distribution of sample locations with polygyne and monogyne colonies in Texas as reflected by samples taken in 1988 - 1989 by Texas Department of Agriculture employees trained at BFL (Porter et al. 1991).

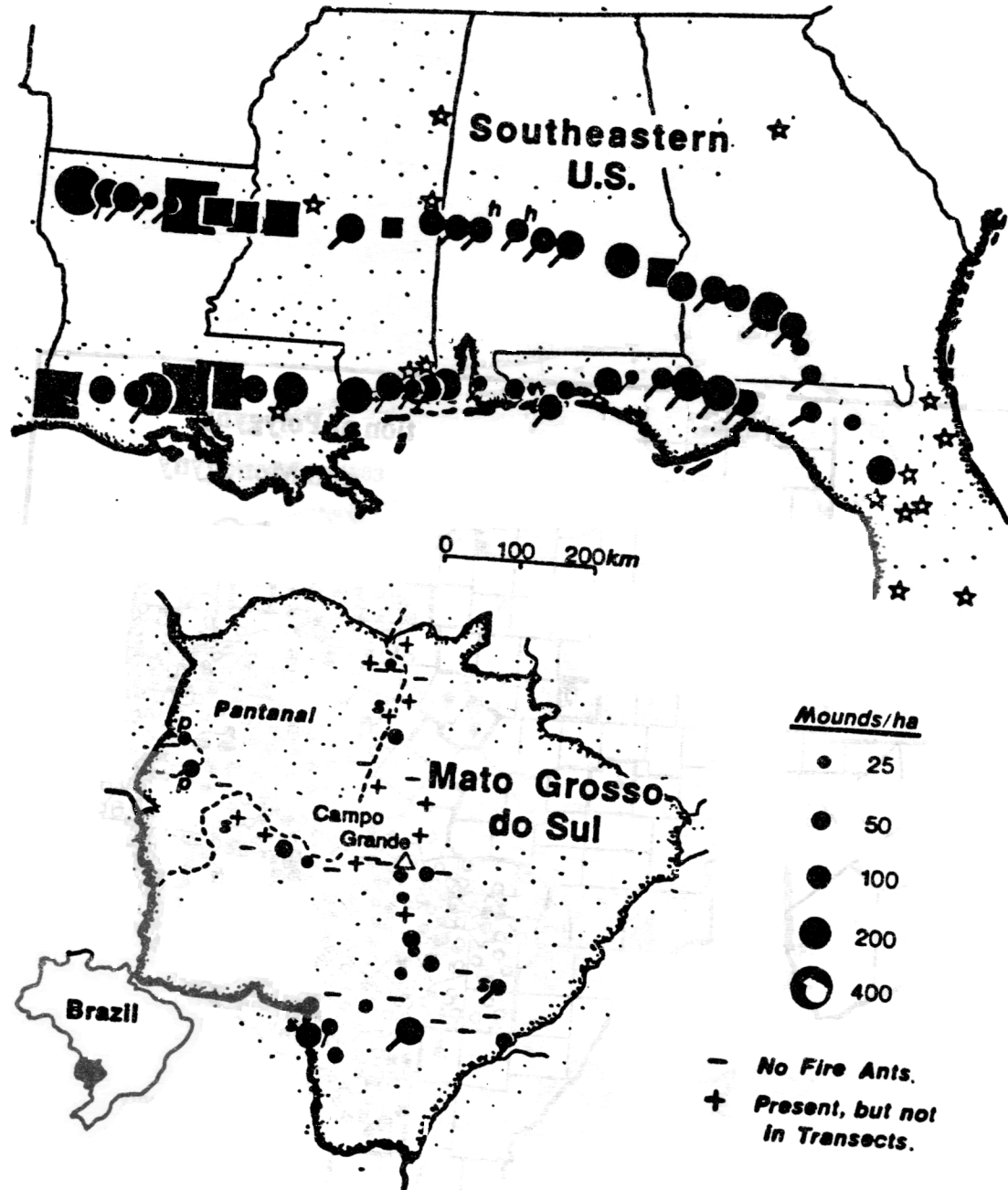


Fig 3. Abundance of fire ant mounds at sample sites in the southeastern United States and Mato Grosso do Sul, Brazil. Areas of circles and squares are proportional to mound density. Circles indicate monogyny; diagonal tails on circles indicate confirmed monogyny. Squares indicate polygyny (Porter et al. 1992).

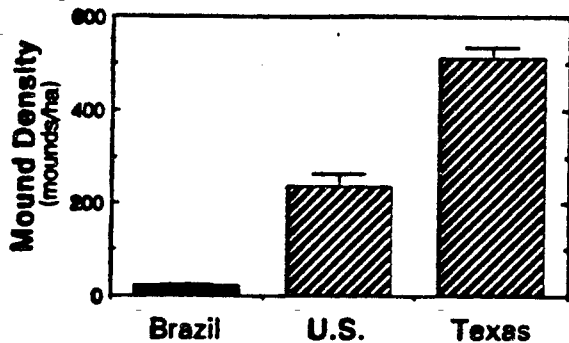


Fig 4. Comparison of fire ant mound densities at roadside sites in Brazil ($n = 50$), the Southeastern United States ($n = 52$) and Texas ($n = 377$). Both polygyne and monogyne sites are included in these figures. Standard errors are plotted above each bar (Porter et al. 1992).

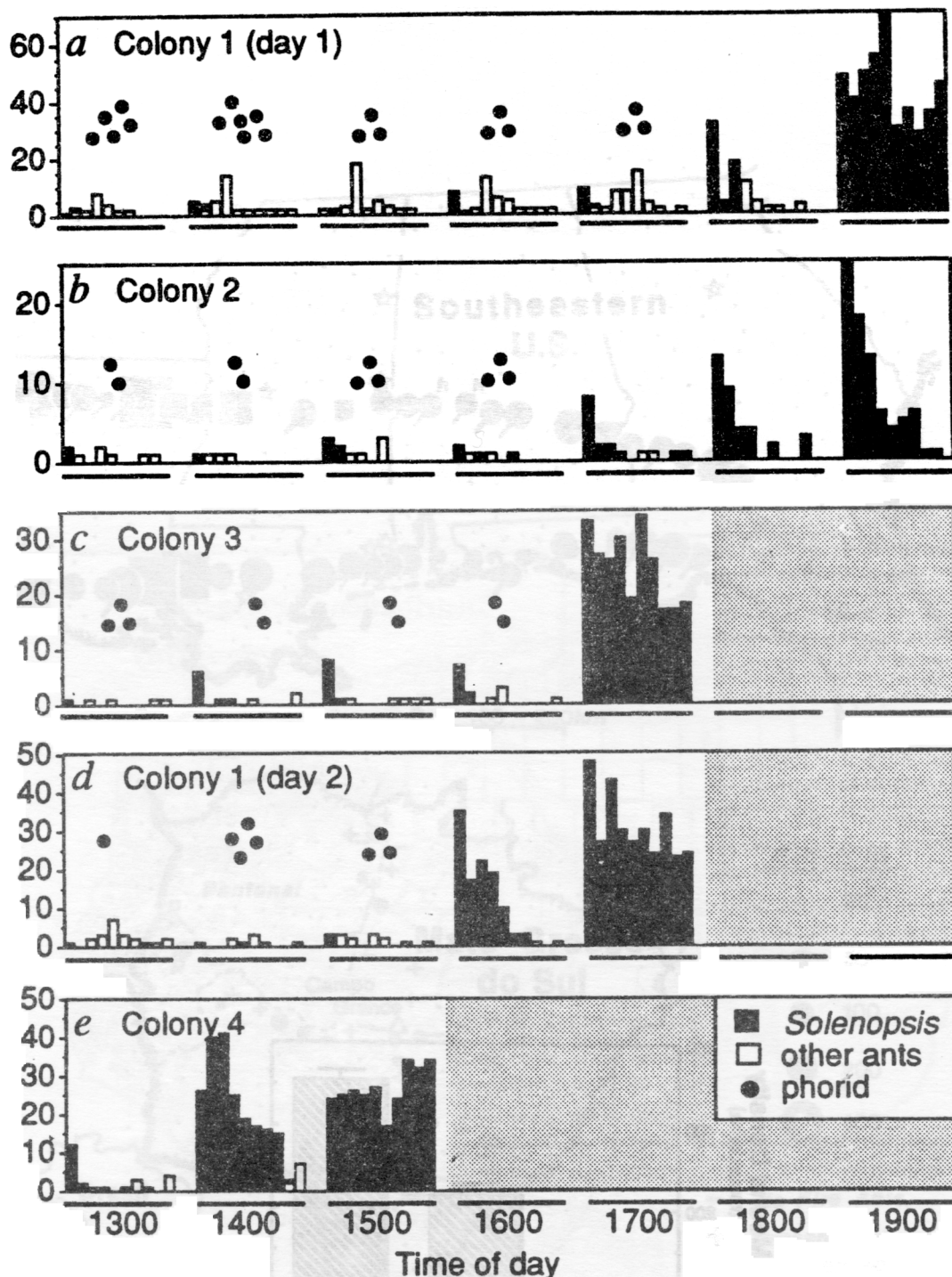


Fig 5. Comparison of foraging by fire ants with and without phorid flies. In Brazil during the day and with phorids present (solid circles), ant species other than fire ants (open bars) control food at each 10-cm interval over a meter-long transect starting near the nest (left) and proceeding away (right). Only near dusk do fire ants (solid bars) surge out to dominate baits. However, when phorids are removed experimentally, fire ants are able to dominate baits progressively earlier in the day according to the time phorids are removed (removal times are progressively earlier from the top to the bottom panel). Note that the body size of other ants tended to be very large--e.g. *Campanotus* and *Ectatomma*, and so small numbers obscure actual impact. (Orr et al. 1995).

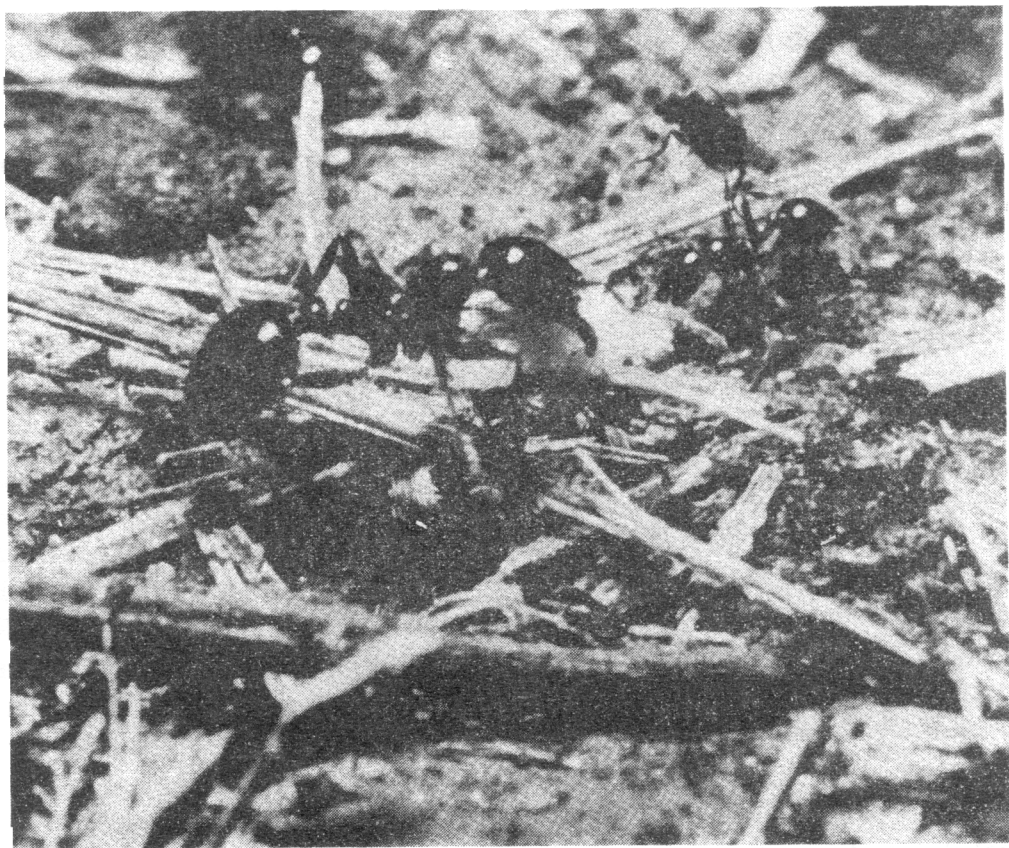


Fig 6. *Pseudacteon solenopsis* approaches a *Solenopsis invicta* worker head on. After 1 - 2 minutes of harassing the ant, the fly darts around to the back or side and darts in to inject an egg into the ant (near Campinas, Brazil).

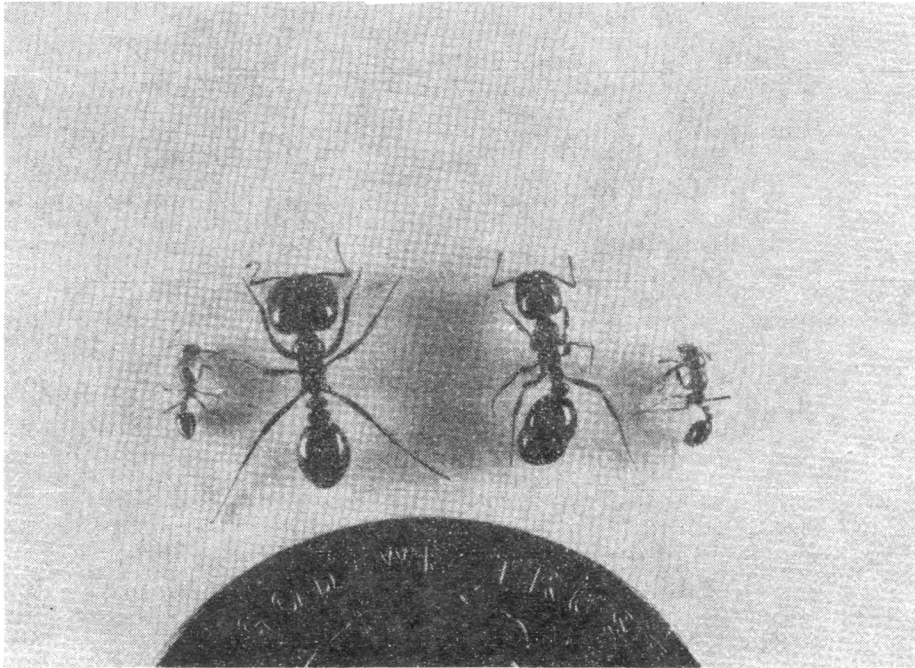


Fig 7. Distinguishing native (*S. geminata*, left) from imported (*S. invicta*, right) fire ants in the field requires only that one observes the full range of workers in a disturbed mound. While smaller cast sizes are difficult to distinguish, the larger cast is diagnostic. The key trait is the *relative* size of the head of the largest workers. In native fire ants, major worker heads are conspicuously wider than the abdomen.