

L. MOREL

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FIRE ANT LIBRARY

BIOLOGY AND CONTROL OF IMPORTED FIRE ANTS¹

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C. S. Lofgren, W. A. Banks, and B. M. Glancey

Insects Affecting Man Research Laboratory, Agricultural Research Service, U.S. Department of Agriculture, Gainesville, Florida 32604 and Imported Fire Ant Research Laboratory, Agricultural Research Service, U.S. Department of Agriculture, Gulfport, Mississippi 39501

Two species of imported fire ants, *Solenopsis invicta* and *Solenopsis richteri*, were introduced into the United States at Mobile, Alabama, about 35 and 56 years ago, respectively. *S. richteri* is now found in a relatively small area in northeastern Mississippi and northwestern Alabama, while *S. invicta* has spread and occupied a much greater area, since it is found in nine states from the Carolinas to Texas. The warm, wet weather of the South is ideal for the imported fire ants, and their colonies have flourished in the prime grazing and crop land, along roadsides, and in parks and lawns. The most extensive and rapid spread of the imported fire ants occurred during the 1940s and 1950s. Eventually, the mound-building and stinging habits of the ants caused farmers in the infested areas (mounds sometimes numbered 125 to 150/ha) to demand relief. Thus, in late 1957, the U.S. Congress authorized a cooperative federal-state eradication or control program. Since that time, a continuing, but at times limited, program of research has investigated the biology, zoogeography, and taxonomy of the fire ants in the United States and in their homeland in South America. Also, considerable work has been devoted to development and improvement of methods of chemical control. More recently, studies have begun on biological control. Taxonomy of the ants has become more critical with the initiation of this work since many biological control agents are species specific. Our purpose here is to review this research, although because of space limitations we cannot fully review much of the recent work concerning the chemical toxicology and persistence of mirex, the chemical currently used for control of imported fire ants.

¹Mention of a pesticide or commercial or proprietary product in this paper does not constitute a recommendation or an endorsement of this product by the USDA.

TAXONOMY OF FIRE ANTS

The taxonomy of the many species of fire ants on the South American continent remains largely unresolved. Wilson (117) recognized quite early that there might be two forms of the imported fire ant in the United States, but the characterizations were made on color only and no taxonomic separations were proposed. Since he recognized that the red form (or light phase) ants were more vigorous and were spreading more rapidly than the original black phase, he postulated that the red form was an offshoot that had arisen from the original population after its invasion. A year later, Wilson (118) changed his opinion and postulated that the light phase ants arose as the result of hybridization between forms that he treated as *Solenopsis saevissima richteri* and *Solenopsis saevissima saevissima* in a postulated blend zone in South America, and that there had been a second importation of one of these hybrid forms. The double invasion hypothesis was largely ignored by subsequent authors until Buren (25) in his taxonomic revision separated six species of the *S. saevissima* complex, including the two species that have invaded the United States. The first of these two species, the species that was detected in Alabama by Creighton (33), was restricted and separated as *S. richteri* Forel; it is now known as the black imported fire ant. The second and more important of the two importations was named and described as *S. invicta* Buren and given the common name, red imported fire ant. In this taxonomic revision, Buren demonstrated that (a) there are two species of imported fire ants in the United States, and that they may be distinguished by the morphology of the head, thorax, and postpetiole, as well as by color; (b) that the two species have remained phenotypically constant since the time of importation and moreover are unchanged from parental populations in South America; (c) that hybridization appears rare; and (d) that the two homeland ranges in South America are geographically distinct.

Cupp et al (36) have suggested that species discreteness in *Solenopsis* is not complete. They worked with purported field-collected hybrids of *S. richteri* and *S. invicta*. However, their distinctions were based only on color and no morphological characters were given. Nevertheless, these investigators were able to force-mate the two species in the laboratory and obtain known hybrids. Their studies need to be continued and broadened to include very careful morphological examination and comparison of the laboratory-produced hybrids with specimens from field populations to determine the extent of natural hybridization. However, determinations of hybridization by color appear questionable. Buren, in published (25) and unpublished work, has found that the color of *S. invicta* is variable, and ranges from light reddish brown to strongly dark brown; also the light-colored spot on the gaster may be present or absent, even in nestmates. In the absence of correlative morphological characters, the color differences appear to be normal intraspecific variation or, at most, localized color strains. If extensive hybridization were occurring, species discreteness would eventually break down, and there is no evidence that this happened to *S. richteri* or *S. invicta* in North America. Indeed, specimens of *S. richteri* (ca 150 nest collections examined by Buren) taken in northeastern Mississippi and northwestern Alabama from 1968 to 1972 appear morphologi-

cally identical to specimens of *S. richteri* taken at Mobile in 1927-1928 by W. S. Creighton.

The present authors feel that hybridization is not occurring to any noteworthy extent in *Solenopsis* and that the limited amount that may be occurring is having no measurable effect on the phenotypes of the species. Bigelow (14) and Wing (125) give possible reasons why a limited amount of hybridization may not measurably affect a population gene pool even when the hybrids are fully fertile.

ZOOGEOGRAPHY

Distribution in South America

The postulated distribution of *S. invicta* and *S. richteri* in South America (26) is shown in Figure 1. Further surveys will be necessary to fully delimit the actual distribution of the two species. The work to date indicates that the distribution of *S. richteri* is much more restricted than Wilson (118) believed. The homeland range of *S. richteri* was shown to be in southernmost Brazil (Rio Grande do Sul), Uruguay, and Argentina. The state of Mato Grosso in Brazil, and specifically the Pantanal (the large flood plain of the head waters of the Paraguay River and its fringes), was shown to be the homeland of *S. invicta* (5, 26). Buren et al (26) also showed that the species extended northward along the Guapore River to Porto Velho, Rondonia, and to the south along the Paraguay River at least as far as the province of Chaco, Argentina. The regions near the Paraguay River in Paraguay and those in easternmost Bolivia into which the Pantanal extends have not yet been sampled, but they are probably a part of the range of *S. invicta*. The species has not been taken, however, in the Campo Cerrado areas to the east of the Pantanal or in any part of the state of Sao Paulo, or in any of the upland areas of Bolivia, though other species of *Solenopsis* are indigenous. Buren et al (26) speculate as to why the range of *S. invicta* in South America is as circumscribed as it appears to be.

Importation and Spread in the United States

Since there are two species of imported fire ants rather than one, it follows that there were two importations rather than one. There are many references to the supposed 1918 date of introduction, giving a period of 56 years for "the imported fire ant" to have reached its present distribution. Now the thinking on this subject must obviously be changed. Only *S. richteri* was imported as early as 1918, and this species has been only moderately successful in its spread. *S. invicta*, however, may have been in the United States only 30 to 35 years. It has achieved its phenomenal spread because of dispersal in mating flights and because of transport by man (34, 75), particularly on nursery stock in the 1940s and early 1950s. The matter has been further confounded by the fact that importation of both *S. richteri* and *S. invicta* apparently occurred in the Mobile, Alabama area. The reason why will probably never be fully resolved. Buren et al (26) suggest that *S. invicta* was successful because *S. richteri* had preconditioned the Mobile area. Perhaps *S. richteri* exerted considerable competitive pressure against the Argentine ant, *Iridomyrmex humilis*, and against native ants that were present without fully occupying the available

ecological niche. Massive populations of *I. humilis* existed at New Orleans and in other parts of the Southeast between 1933 and 1945 and may have prevented *S. invicta* from gaining an initial foothold at New Orleans.

Lennartz (57) established, by personal communication with W. S. Creighton and from other data, that *S. invicta* was probably imported into the Mobile area between 1933 and 1945. She was not able to definitely associate the importation with any specific cargo. The Brazilian coffee that was imported in the 1930s and 1940s came principally from the states of Sao Paulo and Paraná where *S. invicta* has never been found. The few recorded shipments of mahogany to Mobile during the 1933–1945 period were entirely from Central America. No records show that potted plants from Brazil entered during the critical period, and other imports, rubber, Brazil nuts, manganese ore, Quebracho wood, and skins and hides, were not likely transport media for various reasons. Shipping records show that while much grain was shipped from Argentina during the drought years in the United States (the late 1930s), the amounts shipped to Galveston and New Orleans greatly exceeded the amount shipped to Mobile. It seems likely that the exact mode of entry of the ants into the United States will never be determined.

The ants have been spectacularly successful in establishing themselves in the southeastern United States (*S. invicta* more so than *S. richteri*) since they now occupy more than 52 million ha of land (Figure 2). With the exception of some resistance which the native fire ant, *Solenopsis geminata*, appears to be exerting in parts of Florida, the ultimate distribution of the imported fire ants in North America may be dependent on abiotic factors (26). Winter severity may limit the northward progression since *S. invicta* lacks the ability to hibernate and winter kill probably is roughly proportional to the depth at which the soil becomes frozen. The deserts of western Texas should halt the natural spread of the species to the west. If inadvertently transported by man's agency, we feel that the species could establish in California and be successful in watered lawns or irrigated areas of the Southwest. *Solenopsis xyloni* and *I. humilis* are successful in these areas and could be displaced by *S. invicta*.

BIOLOGY

Colony Founding, Growth, and Seasonal Life Cycle

COLONY FOUNDING The founding of colonies by imported fire ants is typical of most nonparasitic myrmecine ants and begins when new queens alight on the ground after their nuptial flight. Typically, a colony is started by a single queen; however, in heavily infested areas more than a dozen dealated queens often group together under debris such as paper, cans, and pieces of wood. Markin et al (72) reported that more than half of the new nests of *S. invicta* in a field near Gulfport, Mississippi, were each started by one queen, but the remaining nests contained 2–5 queens. The queen usually breaks off her wings and begins excavation of her burrow within 4 hr after the mating flight. The burrow may be made in open areas or under solid objects. Within 6–7 hr, 90% of the queens may have completed their burrows and

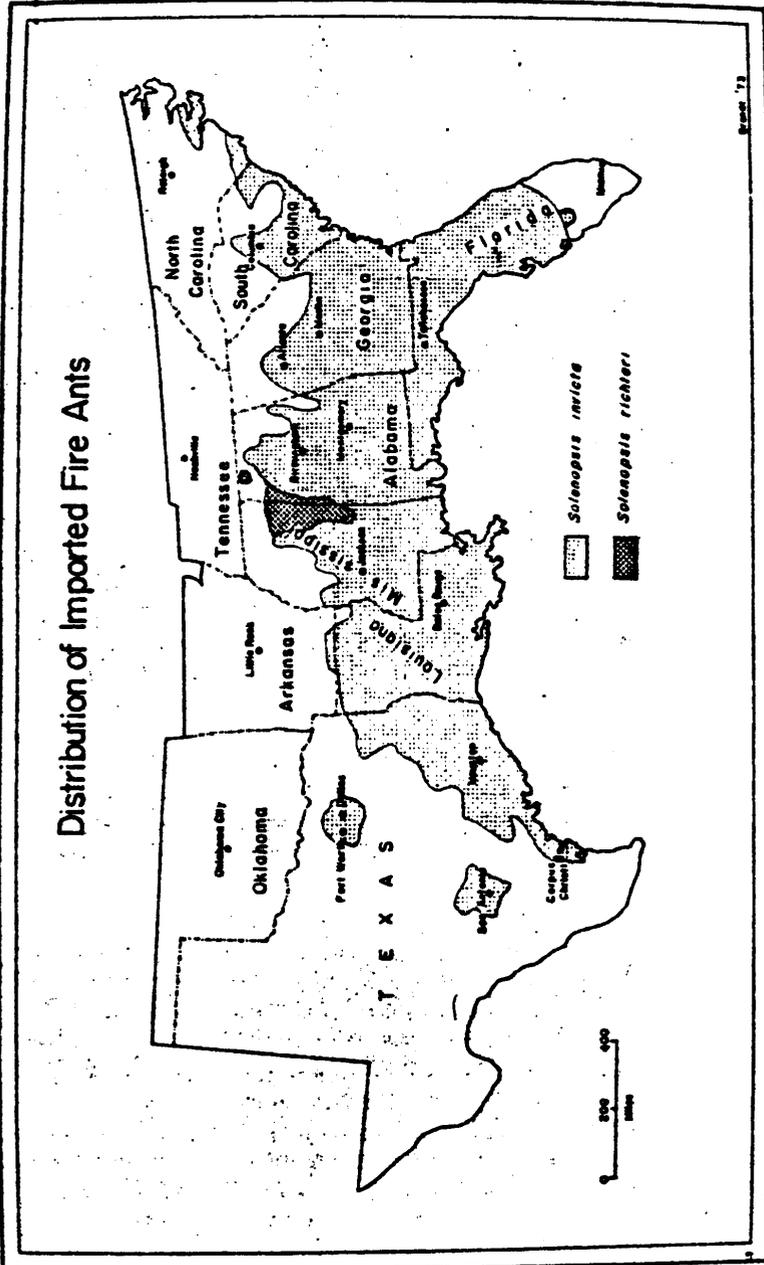


Figure 2 Distribution of *Solenopsis invicta* and *S. richteri* in the United States [used by permission from Buren et al 1974 (26)].

plugged the entrances. The burrow of *S. invicta* consists of a vertical tunnel 3–12 cm deep with a small cell located about 1 cm from the upper end and one, or rarely several, small cells at the bottom (72). The cells are ca 7–10 mm wide and 3–12 mm deep. Green (48) describes the burrow of *S. richteri* as running vertically for about 12 mm and then turning parallel to the soil surface for about 5 cm; a cell is located at the end. Both species of fire ants normally lay their first eggs within 24–48 hr after completing the burrow.

In laboratory studies, *S. invicta* queens laid 15 to 20 eggs within 2–3 days and had produced a total of 20–125 eggs by the time the first larvae emerged (72, 103). The queen constantly attends the eggs and thus probably prevents their decimation by fungi or bacteria (86). Glancey et al (42) reported that 26–58% of the first eggs are trophic eggs which serve as food for the first- and second-stage larvae. When the fertile eggs hatch (within 4 to 7 days), the larvae rotate their heads until they locate a trophic egg which they begin to eat. However, O'Neal & Markin (86) claim that both trophic and viable eggs are eaten indiscriminately by the larvae and that queens were observed feeding both types of eggs to second-instar larvae. Such a habit by the queen would seem to be self-defeating since it would decrease the number of minim workers that could care for her. Further observations are needed to clarify this point. Late second-, third-, and fourth-instar larvae receive only regurgitated food which is derived from the dissolution of the wing muscles of the queen (86). Total development time for the 4 larval instars ranged from 6 to 10 days at optimum temperatures in the laboratory (29.5 to 32°C); pupal development required 7–8 days. The entire developmental time from egg deposition to emergence of the minim worker at these temperatures was 20–21 days. Field tests conducted from May through July showed that 22–33 days were required for minim workers to develop when the queens were held in vials or cages buried in the soil. Observations on the naturally occurring nests indicated that 24–30 days were needed to complete development (72).

The success of the colony founding process is contingent on many factors which are ill-defined but they must include the physical properties of the soil, the climate, the vegetation, the availability of food, inter- and intraspecific competition for food and living space, and the presence of pathogens, parasites, and predators. Green (47) indicated that soil moisture (from frequent rain showers) is an extremely important factor in colony founding by *S. richteri*. His subsequent discovery (48) that the burrow of *S. richteri* is in the top 2.5 cm of the soil would make soil moisture a more critical factor for this species than for *S. invicta* which builds a deeper burrow. Queens from nuptial flights that occur between April and August have the best chance for successful colony establishment because climatic conditions are most favorable and soil temperatures are optimum (25–30°C) during this period. In addition, there is usually sufficient time for the queen to produce several thousand workers that can excavate a nest of sufficient depth to provide protection from winter temperatures (66, 74).

Hundreds of small colonies (in some cases over 2500/ha) are commonly found in newly infested land (without mature colonies) in the fall (48, 74), but the majority do not survive the winter. Therefore, eventually, the number stabilizes at some level

that is probably governed by the availability of food and the presence of suitable nest sites. In many instances workers from one small colony may abandon their queen and amalgamate with another colony (74, 90). This probably accounts for some of the decline in the number of colonies. Amalgamation might also result in very rapid development of the colony due to the increased complement of workers. In the laboratory we have noted substantial differences in the rate of development of colonies established by different queens despite similar food availability and identical environmental conditions. If the same differences occur in the field, then slowly developing colonies obviously could not compete for food and territory, and they would be absorbed by other colonies or die.

The effect of predators on colony founding is discussed in the section on biological control of imported fire ants.

COLONY GROWTH AND SEASONAL LIFE CYCLE The growth of the colonies and the seasonal life cycle of the red imported fire ant were discussed in detail by Markin & Dillier (73) and Markin et al (74). They reported that the first workers (10–20 minims) appeared about 30 days after the queen laid her first eggs. By 60 days, the number of workers (minims and a few minor workers) increased to about 85 and in 90 days to 225. At 5 months, colonies averaged over 1,000 minor workers and a few major workers (minims had disappeared); after 7 months, there were 6,500 to 14,000 workers with about 3% major workers; after 1 year colonies averaged 11,000 workers, after 1½ years 30,000, and after 2½ to 3 years contained from 52 to 69,000 workers. The colonies were generally considered mature after 3 years when some contained as many as 230,000 workers. (The number of workers generally declined during the winter since brood production essentially ceased.)

The estimates of populations in these cited studies (73, 74) were made by driving a large cylinder into the soil around the mound and slowly flooding the mound to force the ants out onto the surface of the water. The ants were then taken to the laboratory where the numbers were determined. The investigators (74) estimated, but did not offer supporting evidence, that they collected 90% of the ants within a colony. Observations in the laboratory suggest that much more than 10% of the ants are away from the nest foraging at any given time, particularly when the weather is favorable. Thus, we believe they have grossly underestimated worker numbers, especially in the older colonies.

Although mature colonies have a seasonal pattern of brood production, considerable variation occurs between colonies in the southern and northern areas of the range of *S. invicta*. For example, brood production essentially ceases in the winter in areas north of 30° latitude, but in central and southern Florida, brood has been noted in some mounds throughout the year. In general, the seasonal reproductive cycle begins in March. The first eggs that are laid give rise to both worker and sexual castes even though the sexuals may appear to predominate because of their size. Even at the time of maximum abundance of sexual larvae and pupae in May, they comprise only about 8.7% of the total colony biomass as compared with about 2.5% of the biomass in September. The highest percentage of adult sexuals (9.6% of the

biomass) is found in June and there is a steady decline subsequently, except that Green (46) reported *S. richteri* to have a second period of high sexual brood production in the fall.

The data of Markin & Dillier (73) show that the biomass of females is greatest in August and September rather than in June when the biomass of males is the greatest. They estimated that over an entire year 76.3% of the colony is comprised of worker forms. In the spring the numbers of worker larvae and pupae peak in May (31% of biomass) and the percentage then declines during the summer to about 20%. In September, it increases again to 30% and finally reaches a maximum peak for the year (34% of the biomass) in October. Thereafter the worker brood drops sharply: the lowest numbers occur during January, February, and March.

Markin et al (74) found that the first reproductive forms (males) appeared in the mounds at Gulfport, Mississippi at 7 months. Rhoades & Davis (90) found reproductives in 5-6-month-old colonies in north Florida (no indication was given as to the sex). We have found that field colonies in Florida contain reproductives of both sexes when the colony is 5 months old, though this is not the norm. Markin et al (74) have further indicated that 1 to 1½-yr-old colonies produced very few sexual forms; however, our studies in both Mississippi and Florida show that colonies of this age have definitely produced sexuals that participated in mating flights. (In one field near Tampa, Florida, 46% of the colonies contained sexuals when they were 1 yr old.) Also, in the laboratory our studies and those of Wilson (120) showed that 1-yr-old colonies produced numerous sexuals.

Markin et al (74) reported that when the nest is opened by the first minor workers, it consists of nothing more than the original burrow dug by the queen. The workers immediately begin deepening the tunnel: By 60 days, several distinct chambers are apparent. By 90 days, a soil surface mound (3-7 cm diam and 5-7 cm high) containing numerous chambers is evident, and horizontal tunnels radiate out from the mound. From 5 to 15 additional vertical tunnels branch at various depths from the main vertical tunnel. By 5 months the surface mound is still larger and has taken on the spongelike appearance of older mounds. After 2½ to 3 years, the mound has taken on a typical dome-like shape and the galleries and tumulus occupy a volume of up to 40 liters. The vertical tunnels extend a meter or more into the ground to the water table.

The size of the aboveground mounds may vary greatly with different soil types, soil moisture, and vegetation. Mounds in sandy areas tend to be flat and rather broad, while mounds in clay soils may be ½ to 1 m high and 1 m wide at the base. Also, recent evidence indicates that large colonies may utilize several mounds. Some colonies maintain the same mound for many years, and others may move their nest frequently for distances of from a meter to over 30 m. The mounds allow the colonies to maintain brood at the optimum humidity and temperature since it may be moved up or down as the need arises. In hot summer weather, brood is usually found deep within the underground tunnels while in the spring or fall, brood is kept on the warm sunny side of the mound near the surface.

Reproduction

NUMBER OF QUEENS PER COLONY Until recently, it was generally accepted that mature fire ant colonies contained only one queen; however, recent information has shown that there may be more than one fertilized queen in many colonies. Glancey et al (41) collected 20 inseminated queens from one colony and two from another near Jackson, Mississippi. In a study near Gulfport, Mississippi, they found that 2 of the 35 colonies they examined had two fertile queens each. (Fertility was determined by holding the queens in the laboratory with workers to determine whether they had laid fertilized eggs, that is, whether worker brood developed.) Similarly, Markin et al (74) found that at least 5% of the colonies in southern Mississippi that were over 2 yr old contained more than one fertile queen.

Still more recently, Glancey et al (submitted for publication) found an even more extreme instance of polygyny in *S. invicta* colonies. About 30 mounds of *S. invicta* were found on a relatively narrow ditch bank at a garbage dump near the Mississippi-Alabama boundary. A portion of the tumulus of a mound (with the ants) was scattered on the asphalt highway; then the queens could be easily collected by observing the clustering of many workers about them. Ten mounds contained from as few as 7 to as many as 677 dealated queens. The presence of sperm in the spermathecae of 521 queens indicated that they had mated. Other queens that were placed individually in containers with workers oviposited and produced workers. Eventually, over 3000 fertile queens were collected from these mounds. Further studies are needed to determine the prevalency of this type of polygyny and to determine its significance in the survival, spread, and economic importance of imported fire ants.

MATING BEHAVIOR Although nuptial flights of imported fire ants have been noted in every month, peak activity occurs from late May through August subsequent to the periods of highest production of sexual brood (75). Glancey (unpublished data) has found that about 7-10 days are required for the males and queens to reach sexual maturity after they eclose from their pupal stage.

Little is known of the factors that trigger mating flight activity in a colony. Flights may be localized with only a few colonies participating or they may be very generalized and may include many colonies in several states (75). However, the flights will generally occur within 1 to 2 days after a rain, especially if the rain has been preceded by a period of dry weather. Also, Rhoades & Davis (90) found that the relative humidity during flights was always over 80%; observed no flights of *S. invicta* on days when soil temperature at a depth of 4 inches was below 18°C; and found that all flights occurred when the ambient air temperatures were between 24 and 32°C. In contrast, Green (48), in Mississippi, noted flights of *S. richteri* when the air temperature was 21°C, and Markin et al (75) reported flights of *S. invicta* in the winter in Louisiana when the temperature ranged from 20 to 26°C. No correlation of flight activity with cloudiness or barometric pressure has been found. In most cases the wind velocity at the time of flight was less than 5 mph; however, a few flights were observed when some wind gusts exceeded 15 mph (75).

The activity of the workers gives an indication of impending mating flights from mounds. About 30 min to 1 hr before a flight, large numbers mill excitedly over the surface of the mound and the surrounding vegetation and soil surface. During this time they open exit holes, 6 to 12 mm in diameter, in the surface of the mound. The males take flight about 30 min to 1 hr before the females. Flights usually occur from about mid-morning to late afternoon.

Markin et al (75) studied the aerial distribution of alates by collecting them in nets fixed to an aircraft. They found that males concentrated at an altitude of 90 to 150 m and remained airborne for several hours. Female and male alates were collected at a maximum altitude of 150 and 300 m, respectively. Since 98% of the alates captured were males, the females must ascend into the male swarm, become mated quickly, and then descend rapidly to the ground. It is apparent that the imported fire ants do not produce the prominent mating swarms typical of some other species of ants; however, their layering type of swarm is evidently efficient in assuring mating. Markin et al (75) reported that 95% of the queens picked up from the soil after a flight were inseminated though they calculated that there is probably no more than 1 male per 90 m³ of air during a normal flight. Logically then, one or more pheromones must be utilized during the mating flight, to initiate activity and to assure that contact is made between the males and females in the air.

Markin et al (75) felt that the queens selected the sites in which they landed after a mating flight since they found more queens and new mounds on recently cultivated fields or dirt roads than they did on heavily vegetated areas. They also interpreted their finding that more male alates were captured over pasture than over adjacent swamp as further evidence of habitat selection. The queens may indeed select the sites on which they land; however, the findings by Markin et al (75) do not necessarily lead to this conclusion. The ease with which queens can secret themselves would make it much more difficult to find them on vegetated areas than on cleared areas, even though about the same number might be present. It would appear logical that more mounds would be found on cultivated fields or dirt roads since the soil is usually soft and the queens can quickly excavate a burrow and escape predation and dehydration to a greater extent than on some other sites. The heavier concentrations of males over the pasture rather than over the swamp probably can be attributed to the fact that the mounds producing the flights were numerous in the pasture and very sparse or absent in the swamp. The alates simply congregated over the area from which they arose. Further study is needed on habitat selection by the queens.

Considerable data have been accumulated in recent years on the numbers of alates produced by individual colonies though much of it is not yet published. The most extensive research has been done in north Florida. There, Morrill (80) found that in June the number of alates that left a mound for a flight averaged 690 and that the average number of alates produced per hectare per year from mounds located in four habitats (pasture, road ditch, pine woods, pipeline) was about 462,000. During vigorous flights up to 100 alates per minute were observed leaving mounds. Although 90% of the flights observed from any particular mound were composed predominately (> 74%) of one sex, enough mounds containing each sex produced

flights so that total numbers of each sex were about equal, and the sex ratio for the entire area was about 1:1. Colonies were found that produced predominately one sex at one time of the year and the other sex at a different time, but no colonies produced only one sex throughout the year. Total alate production per acre did not necessarily correlate with mound density, e.g. a pasture with 50 mounds/ha produced more alates than did a ditch with 125 mounds/ha.

Studies in Arkansas (93) gave results similar to those obtained in Florida. The largest flight from one mound produced 3168 alates within a 24-hr period, and the largest number collected during the study period (152 days) from one mound was 7600. Flights of *S. invicta* occurred from 1 to 3 PM; flights of the southern fire ant, *S. xyloni*, occurred primarily from 3:30 to 5:30 PM.

Food, Food Gathering, and Exchange

FOOD Fire ants have been described as voracious feeders on crops and domestic and wild animals. These descriptions have been based, to a great extent, on hearsay instead of scientific evidence. The ants are highly omnivorous and opportunistic so they may feed upon whatever plant or animal material they encounter. Several scientific reports (48, 51, 122, 124) have established that the primary diet of fire ants is insects, spiders, myriapods, earthworms, and other small invertebrates. Although some feeding on plants does occur, it seems to be the exception rather than the rule, and it usually involves eating the germ plasm of newly germinated seeds or girdling the stems of small seedlings. The damage occurs most often when a previously uncultivated area is brought under cultivation and the ants are thereby deprived of their normal food sources. Vinson (108) observed the red imported fire ant feeding on *Paspalum* seeds but found on close examination that only seeds infested with ergot were collected. He concluded that the fungus was reacting with the seed to produce certain carbohydrates desired by the ants.

Efforts to develop effective toxic baits for control of imported fire ants led to food acceptance studies to find materials attractive enough to the ants to elicit collection of a bait applied area wide in the field. Hays & Arant (50) and Lofgren et al (62, 64) evaluated a wide variety of food materials and found that fats and oils were consistently the most acceptable foods. An evaluation of the food preferences and nutritional needs of the ants conducted at Mississippi State University (91, 92, 106, 107, 110) showed that practically any insect was acceptable as food for the ants, but that some were more acceptable than others. Soybean oil was distributed to all castes in the colony to a greater extent than were protein or carbohydrate, and two natural components of the soybean oil (linoleic and linolenic acid) proved to be phagostimulants for imported fire ants. Two amino acids, leucine and valine, were well accepted by the ants; however, aqueous solutions of various electrolytes did not induce any strong feeding response. Lipase was the most widely distributed digestive enzyme present in the workers.

FOOD GATHERING Food for the fire ant colony is collected by the foraging workers who leave the mound through foraging tunnels that radiate from the mound at a depth of 6 to 12 mm under the soil surface. Green (48) reports that a mound

usually will have 5 or 6 such tunnels extending from the mound in somewhat fixed positions though the extremities are temporary and change according to need. These tunnels branch repeatedly over the foraging area, and extend as far as 15–25 m from the mound and have openings to the soil surface at irregular intervals. The worker ant exits to the soil surface through one of these openings and forages at random until a source of food is located. Once food is located, the forager returns to the tunnel laying a trail with the trail pheromone. The additional workers recruited by the original forager then establish a continuous stream of ants between the food source and the nest.

The size of the area foraged by a colony depends upon the food requirements of the colony and the availability of food in the area. Wilson et al (123) reported that the area foraged by a given mound is discrete, and little or no interrelationship or food exchange exists between adjacent mounds. However, more recent evidence indicates that though a given mound may be an entity, there is often communication between many adjacent mounds in an area. In tests in central Florida (W. A. Banks et al, unpublished data) a dyed food that had been buried within a selected mound appeared in the ants in 22 other mounds within 23 m of the baited mound. Moreover at only two of the ten test sites did the dye fail to appear in at least one other mound. The exact mechanism of food transfer is unknown. The same test repeated in Texas (J. W. Summerlin, personal communication) had similar results. Also, when ants were sprayed with fluorescent or aluminum paint at one mound some were collected later from a different mound—an indication of a possible exchange of workers between adjacent mounds (B. M. Glancey, unpublished data). Likewise, Morrill (80) reported that after alate ants taking flight from a mound were captured, marked with paint, and returned to the mound, he later captured these same alates taking flight from a different mound. Mounds of the imported fire ants, therefore, are not necessarily distinct entities, and there may be food exchange and exchange of workers and alates between mounds.

The foraging of the ants is regulated to a great extent by the prevailing soil temperatures. Markin (personal communication) found that no significant foraging occurred when soil temperature at the 5 cm depth was below 15°C or above 37°C. Maximum foraging occurred between 21 and 35°C. Our studies (unpublished) confirm these observations, though we found that limited foraging occurred between 10 and 15°C if the day was sunny (not if the sky was overcast).

FOOD EXCHANGE The return of the foraging worker to the nest with food begins a fairly complex system of distribution of the food through the colony biomass. Wilson (121) indicates that this exchange not only provides nourishment but plays an important role in the social organization. Food exchange occurs between all castes in a colony. Dye incorporated into food offered to worker ants shows up quickly in the larvae, and more than 90% of the individuals in the colony have received the dye within 48–72 hr. G. P. Markin (personal communication) found that an insecticide administered in peanut butter to the workers appeared in highest concentration first in the minor workers and then in the small larvae. During the seven days of the test, the highest concentrations were found in the large larvae with

lesser amounts being found in the small larvae, minor workers, major workers, and alate females in that order. Vinson (106) found that oil, carbohydrate, and protein were distributed throughout a colony after being taken in by the foraging workers; the larvae received a greater proportion of all three foods than any other caste. Our own unpublished studies have shown that a ^{32}P -labeled diet high in lipid and protein fed to 12 colonies reached 99% of the minor workers, 95% of the medium workers, 93% of the major workers, 80% of the larvae, and 10 of 12 mother queens within 9 hr. However, levels of radioactivity were highest in the larvae so individual larvae received more of the labeled food though the percentage of larvae fed was lower than for the other castes.

O'Neal & Markin (86) showed that both oral and proctodeal food exchange occurs from larvae to workers. Our own unpublished studies confirm the transfer of material from larvae to worker; however, we did not establish the mode of exchange.

Glancey et al (45) found evidence that the larger major workers in the colony retain oil in their crops for many months. Thus these workers may be a replete caste such as occurs in the genera *Myrmecocystus* and *Prenolepis*. Such repletes could provide food for the colony in times of stress or food shortage.

Chemical Secretions of Fire Ants

VENOM

Chemistry The chemistry of the venoms of several species of *Solenopsis* was carefully studied under the direction of M. S. Blum at the University of Georgia (19, 20, 69, 70). These investigators isolated, identified, and synthesized the following five major alkaloidal compounds of the venom of *S. invicta*: solenopsin A (*trans*-2-methyl-6-*n*-undecylpiperidine); solenopsin B (*trans*-2-methyl-6-*n*-tridecylpiperidine); solenopsin C (*trans*-2-methyl-6-*n*-pentadecylpiperidine); dehydrosolenopsin B [*trans*-2-methyl-6(*cis*-4-trideceny) piperidine]; and dehydrosolenopsin C [*trans*-2-methyl-6(*cis*-6-pentadeceny) piperidine]. However, they found no *trans* C₁₅ or *trans* C_{15:1} alkaloids in *S. richteri*.² Thus this species lacks two of the major constituents of the venom of *S. invicta*. The venom of workers of *S. xyloni* contains *cis*-2-methyl-6-*n*-undecylpiperidine (*cis* C₁₁) as the main alkaloidal constituent, and *trans*-2-methyl-6-*n*-undecylpiperidine (*trans* C₁₁) is present in about one fourth the amount of the *cis* C₁₁ isomer. Significantly, neither the *trans* C₁₃ nor the *trans* C₁₅ alkaloids are present in the venom of *S. xyloni*. Also, the venom of workers of *S. geminata* lacks the C₁₃ and C₁₅ alkaloids, and only the C₁₁ dialkylpiperidines are present. However, there is about 1½ times more *cis* C₁₁ than *trans* C₁₁ so the venom of *S. geminata* differs from the venom of *S. xyloni* which contains 4 times more *cis* C₁₁ than *trans* C₁₁.

The same investigators compared the ratio of *cis* C₁₁ to *trans* C₁₁ in queens and workers. The workers of *S. xyloni* and *S. geminata* contain much more *cis* C₁₁ than

²The abbreviated terms C₁₁, C₁₃, C₁₅, and C_{15:1} are used to designate the venom components. They indicate the carbon length and the presence or absence of unsaturation in the 6-alkyl substituent on the piperidine ring but do not signify the total number of C-atoms in the molecule.

trans C₁₁. The workers of *S. richteri* and *S. invicta* contain much less *cis* C₁₁ than *trans* C₁₁. However, the queens of all four species always contain more *cis* C₁₁ than *trans* C₁₁. The venom of workers of *S. invicta* contains primarily *trans* C₁₃ and C₁₅ dialkylpiperidines; the venom of the queens lacks these compounds. Similarly, the venom of *S. richteri* workers is dominated by C₁₃ alkaloids; the venom of the queen lacks these compounds.

Since the difference in the type of alkaloids in the workers and their ratios to each other proved to be consistent for the species studied, they can serve as fingerprints that may be and have been used to substantiate the validity of the taxonomic classification of the species.

The venom of another, probably undescribed, species of *Solenopsis* from Brazil was found (71) to contain only the *cis* and *trans* isomers of a compound that was previously undiscovered in fire ants, *trans*-2-methyl-6-*n*-nonylpiperidine.

Evolutionary implications Brand et al (21) constructed, and MacConnell et al (71) expanded upon, a hypothetical model for the evolution of the fire ants based upon the venoms of the different species. It would seem unwise to speculate further on this hypothesis until the taxonomy of the fire ants is much further advanced and the venom chemistry of more species is known.

Toxicology The venom of the fire ants is used to immobilize or kill prey for food and has been shown to possess insecticidal, bactericidal, and fungicidal activity (16, 55). It is also an extremely effective defensive weapon for preventing large animals from disturbing their mounds. In the typical stinging of man, the worker ant bites or attaches to the skin with the mandibles and then lowers the tip of the abdomen to insert the sting. Several separate stings may be produced by a single ant if it is not removed. The morphology and histology of the sting apparatus, venom gland, and poison sac was described by Callahan et al (27). The immediate reaction to the injected venom is an intensive burning sensation that explains the common name of the ants. When the sensation subsides after a few minutes, a wheal appears at the site of venom injection. A few hours later, a superficial vesicle containing clear fluid appears. By 24 hr, the fluid becomes purulent as a result of the necrotizing properties of the venom. The pustule is sterile and may persist as long as a week if it is not broken. During this time the pus is absorbed leaving a crust and, in many instances, scar tissue. Occasionally an individual may have systemic reactions including nausea, vomiting, dizziness, perspiration, cyanosis, asthma, and other symptoms typical of severe allergic reactions. In severe cases, if medical assistance is not received, the individual may die (102).

PHEROMONES Pheromones play a highly important role in the organization and coordination of activity in ant colonies. In fact, Blum (15) stated that the social cohesiveness of an insect colony appears to be maintained primarily through chemical communication. Wilson (120) recognized at least five distinct areas of chemical communication among workers of the imported fire ants: nest odor, body surface attractants, food exchange, trail following, and alarm. Various investigators have demonstrated communication among the ants by a trail-following pheromone and

by surface contact pheromones produced by the queen and the brood to elicit care by the workers.

Trail-following pheromone More study has been devoted to the trail-following pheromone than to any other pheromone produced by fire ants. Wilson (119) reported that the trail pheromone is produced in the Dufours gland of the worker ant and is extruded through the stinger. Subsequently (120, 121) he discussed in detail the function of the trail pheromone in recruiting and orientating the workers during mass foraging and reported (120) that it was highly species specific. More recent work (M. R. Barlin and M. S. Blum, personal communication; 56) has shown that each species is generally more responsive to the pheromone of its own species, but specificity is not as strong as Wilson (120) indicated (see Table 1). Indeed, some of the differences that are noted probably result from differences in bioassay techniques and in the criteria for determining a positive response. For instance, Wilson (120) used only extracts of Dufours gland; Barlin and Blum (personal communication) used extracts of Dufours glands and natural trails; and Jouvenaz et al (56) used partially purified whole ant extracts and naturally laid trails. Moreover, the locations from which Wilson (120) obtained his specimens of *S. geminata* (Costa Rica) and *S. xyloni* (California) present the possibility that these tests were not made with the same species used by Barlin, Blum, and Jouvenaz since there is still some question as to the taxonomy of these species.

Studies are currently underway to identify the chemical nature of the trail pheromones of both the red and the black imported fire ants. Walsh et al (111) reported

Table 1 Response of fire ant workers to trail pheromone of their own and other species as reported by three authors^a

Source species	Author ^b	Response of indicated test species ^c			
		<i>Solenopsis geminata</i>	<i>Solenopsis xyloni</i>	<i>Solenopsis invicta</i>	<i>Solenopsis richteri</i>
<i>Solenopsis geminata</i>	W	4	1	0	NT ^d
	B	4	3	0	1
	J	4	3	1	1
<i>Solenopsis xyloni</i>	W	3	4	4	NT
	B	3	4	0	3
	J	3	4	1	1
<i>Solenopsis invicta</i>	W	0	2	4	NT
	B	0	2	4	3
	J	4	1	4	4
<i>Solenopsis richteri</i>	W	NT	NT	NT	NT
	B	0	1	2	4
	J	2	1	4	4

^aThe numbers shown are relative values based on data of these authors.

^bW = Wilson, B = Barlin & Blum, J = Jouvenaz.

^cIntensity of response 4 = highest to 1 = lowest. 0 = no response.

^dNT = not tested.

that they had purified, but not identified, a trail pheromone (apparently of *S. invicta*). Elucidation of the nature of the trail pheromone is proving to be somewhat difficult. Present evidence suggests (M. S. Blum, personal communication) that the pheromone is a sesquiterpene type $C_{16}H_{26}$ hydrocarbon. Bioassays of known sesquiterpenes, however, have not elicited any response from the ants at the concentrations tested. Bioassays with purified fractions from GLC chromatographic separation of whole ant extracts show excellent activity over at least 10^6 -fold range of dilutions.

Queen-tending pheromone A fertile queen confined to a spot on a square of blotter paper releases an attractive substance that makes the spot more attractive to worker ants than other parts of the paper (54). The attractive substance is soluble in organic solvents and remains attractive for 72 hr when impregnated onto absorbent paper. B. M. Glancey (unpublished data) applied hexane extracts of *S. invicta* queens to queens of other ant species (*S. richteri*, *S. geminata*, *Camponotus pennsylvanicus*). The foreign queens were then temporarily treated as *S. invicta* queens when they were placed with *S. invicta* workers; untreated queens of the other species were immediately killed by the *S. invicta* workers. Neither the chemical nature nor the site of production of the queen pheromone is yet known.

Brood pheromone Glancey et al (44) suggested the presence of a brood pheromone in fire ants when they found that inanimate objects coated with a hexane slurry of fire ant larvae caused the objects to be treated as larvae. An in-depth behavioral study (112) with the brood pheromone revealed that it occurs uniformly over the body surface of the larvae and is apparently nonvolatile, requiring contact by the workers to be effective.

ARTHROPODS ASSOCIATED WITH IMPORTED FIRE ANT COLONIES

Many arthropods have been collected from nests of imported fire ants in the United States and South America (30, 97), however, only three of the species commonly found in nests in the United States can be classified as inquilines: a scarabaeid beetle, *Myrmecaphodius excavaticollis*; a staphylinid beetle, *Myrmecosaurus* sp.; and an undescribed thysanuran. The scarabaeid beetle was originally described from Argentina (127); the staphylinid belongs to a genus (not previously reported from the United States) associated with ants in South America. Thus, the two beetle species may have been introduced into the United States with the original introduction of the imported fire ant. Also *Gymnolaelaps shealsi* (53), a genus of mites normally associated with ants, has been collected from imported fire ants in Mississippi.

ECONOMIC IMPORTANCE OF IMPORTED FIRE ANTS

The literature fails to give much valid data concerning the economic importance of the imported fire ants. Assessments have too often been based on hearsay and personal emotions rather than scientific fact. Thus, the ants are variously viewed by both scientists and laymen as serious economic and public health pests, as minor

nuisance pests, as totally innocuous, or even as beneficial. Obviously, their real importance lies somewhere between the extremes.

The greatest difficulty in evaluating the importance of fire ants probably derives from the fact that they affect a broad spectrum of "things" but are not major pests on any one thing. However, when all areas in which fire ants are pestiferous are summed, the ants must be considered an important economic pest in the southern United States. The majority of entomologists who are conversant with imported fire ants, agree that they are primarily nuisance pests. The fact, however, does not justify claims that they are not important pests to man and his possessions. For example, the state of Florida and the various mosquito control districts within the state spend more than \$10 million annually to control mosquitoes whose primary importance is that they bite and annoy man (J. A. Mulrennan, personal communication).

Some of the more important problems created by imported fire ants include feeding on plants (particularly seedlings or germinating seeds and okra flowers), stinging of livestock, damage to farm machinery that strike mounds, loss of hay and grazing area, refusal of workers to enter heavily infested fields to cultivate or harvest crops, and hazards to human health from stings that may cause systemic reactions or complications from secondary infections (1, 32, 48, 83, 103). Also, reports have been received and documented of telephone cable and lighting cable for airport runways being gnawed by the ants to the extent that water entered and created short circuits; the ants have been observed tending aphids and mealy bugs on plants (a habit that could result in increased plant disease transmission on some crops), and girdling young citrus trees. In addition there are documented cases of destruction of the nest and young of ground nesting birds and other animals, killing of small pigs, and predation of beneficial arthropods.

On the other hand, predation by imported fire ants has in some cases played an important role in reducing damage by pest insects, e.g. that done to sugarcane by sugarcane borers *Diatraea saccharalis* (89). They are, however, nondiscriminatory in their predation and attack beneficial as well as harmful arthropods. Thus, elimination of fire ants in some areas has resulted in an upsurge of harmful pests, largely because the ant had previously eliminated other insects that would have preyed upon these pests. Biological control authorities agree that the more diverse the predator population, the more likely that effective pest management can be attained. It is therefore regrettable that in areas where imported fire ants abound, they have become the dominant and in some areas the sole predator. For example, Roe (93) showed that *S. invicta* competitively displaced *S. xyloni* and severely reduced populations of some other ant species in Arkansas. Whitcomb et al (115) found that *S. invicta* sharply reduced the diversity of ant species of Florida soybean fields.

Reductions of populations of lone star ticks, *Amblyomma americanum*, and Gulf Coast ticks, *Amblyomma maculatum*, in Louisiana were attributed to imported fire ants. Supporting evidence is rather meager, however. Harris & Burns (49) released ticks in fields infested with fire ants and in fields that had been cleared of ants by using mirex bait. About 75% of the ticks released in the mirex-treated plot were recovered after 5-6 months while none were recovered from the ant-infested plots. It is likely that any arthropod released into an ant-infested field would be preyed

upon by the ants, although possibly not being preyed upon in a natural situation. Further work is needed to determine if the ants are indeed reducing natural populations of the ticks.

An estimate of the problems and losses caused by imported fire ants was made in 1973 when a private research agency (Chilton Research Services, Radner, Pennsylvania) was commissioned by the Allied Chemical Corporation to conduct a survey of farmers and county agricultural agents in the infested states (F. L. Bailey, personal communication). The individuals surveyed were selected randomly and requested by telephone or personally to respond to a questionnaire designed to provide their estimate of problems and losses caused by imported fire ants and to determine the attitude of the respondent toward control of the ants. From 7 to 23% of 400 farmers indicated that fire ants had caused them to lose hay, had damaged equipment, or had caused them to spend money for veterinary or medical services. Calves were cited as the farm animal most often harmed. Also, 50% had spent money for pesticides to control the ants. In the 261 generally infested counties surveyed (400 counties are known to be infested), economic losses in 1972 were estimated to be \$48 million. Net decrease in land value was estimated at \$500 million. While the validity of such a survey might be questioned, since documentation of actual losses was not required, the fact that 50% of the farmers spent money on pesticides indicates that they consider imported fire ants to be important economic pests. Further documentation of actual losses due to the ants is needed before we can fully assess the impact of the ants on the economy of the affected states.

Recent medical studies indicate that the imported fire ant is assuming greater importance as a public health hazard. Triplett (102) and Brown (23) found that allergic symptoms exhibited by 20 patients stung by imported fire ants ranged from urticaria and angioedema through respiratory problems, nausea, and vomiting to anaphylatic shock and collapse. In addition, in 1971, Triplett, who is at the Mississippi Allergy Clinic, Jackson, Mississippi, surveyed physicians in selected areas of Mississippi, Alabama, and Georgia to determine the extent of medical problems associated with the fire ant. Of the 2,485 physicians contacted in this survey (as yet unpublished), 1,336 responded, and 901 reported treating patients for fire ant stings or complications arising from stings. These physicians had treated totals of 9,224 and 11,937 patients for fire ant stings in 1969 and 1970, respectively, and had seen 12,438 patients for stings in the first 7-9 months of 1971. Average medical costs for each patient treated in 1971 was \$28.32. The physicians indicated that the incidence of complications from stings appeared to be increasing. We know of at least two deaths in southern Mississippi since 1971 that were caused by complications arising from fire ant stings. The available evidence suggests that the medical importance of the imported fire ants may be far greater than heretofore suspected.

CONTROL

Efforts to control imported fire ants in the southeastern United States have stirred a controversy that has raged for more than a decade (24, 28, 31, 38, 100, 105). In

a previous section of this paper we discussed the conflicting views regarding the status of the ant as a pest. Irrespective of these views, most landowners in generally infested areas want to be rid of the ants, and almost every conceivable method of control has been utilized by some property owners. These include the use of every available insecticide, burning the nest with a flammable such as gasoline, and physical destruction of the nests by digging or plowing.

Excellent reviews exist of organized control programs against imported fire ants with residual insecticides (heptachlor and dieldrin) and with mirex bait (6, 13). We will therefore restrict our discussion on control to the development and use of mirex bait for this purpose.

Development of Toxic Baits

Studies conducted by Auburn University in the late 1950s (50) determined that a bait consisting of 0.125% Allied Chemical GC-1189 (dodecachlorooctahydro-1,3,4-metheno-2*H*-cyclobuta[*cd*]pentalene-2-one) (Kepone®) in peanut butter gave excellent control of imported fire ants. Concurrent studies by scientists at a US Department of Agriculture Methods Development Laboratory, established at Gulfport, Mississippi, in 1957, revealed that mirex, an analog of Kepone, was as effective as Kepone as a bait toxicant and had a more favorable mammalian toxicity (65). The scientists subsequently (60, 61, 64, 99) developed a toxic bait formulated with once-refined soybean oil as the food, corncob grits as the carrier, and mirex as the toxicant, that gave excellent control of the ants. In 1962 it replaced heptachlor as the standard control agent. Initially, the bait was applied at a rate of 11.2 kg/ha of a 0.075% formulation; however, further studies (12, 60) showed that an increase in the content of mirex in the bait would permit reductions in the bulk rate of application. Thus, in rapid sequence, application rates were reduced to 5.6 kg/ha of 0.15% bait, then to 2.8 kg/ha of 0.3% bait and finally to the current rate of 1.4 kg/ha of 0.3% bait. The amount of toxicant applied remained constant at 8.4 g/ha until the last rate change when a 50% reduction, to 4.2 g/ha, was achieved.

Field studies showed that wherever the bait was properly applied, excellent control of the ants was obtained. The average control obtained on 63 plots of ca 0.4 ha was 98% (12, 60, 61, 99); the average control obtained on large areas (259–405,000 ha treated by aircraft) was 96% (8, 10, 11, 60).

Research, however, has continued in an attempt to improve the performance and extend the field life of the bait. Markin & Hill (78) demonstrated that the technique of encapsulating insect pathogens and insecticides (39, 88) could be used successfully with the soybean oil-mirex fire ant bait. The microcapsules (200–800 μ diameter) were composed of ca 85% soybean oil, 2% mirex, and 13% capsular wall material and were as effective at a rate of 247 g/ha as 1.4 kg/ha of the 0.3% standard corncob grit bait. Also, the effective field life of the capsular bait was greater than 30 days vs 3–4 days for the corncob grit bait. The encapsulated bait, although superior to the standard, has not gained wide usage because of high production costs and lack of available equipment for application. (The fragility of the capsules prohibits the use of standard equipment.)

Studies revealed that coating the bait with acrylic latex allowed more oil to be added to the bait and increased the availability of oil and mirex to the ants (9, 11). In subsequent studies the method of formulation was changed (10) so that one coat of neat soybean oil was applied to the corncob grits and a second coat of oil containing the mirex was applied 24 hr later. The latex coating was then applied. This procedure concentrates the mirex on or near the surface of the corncob grit where it can be more easily removed by the ants. Field tests in Georgia in 1971 (10) showed that 1.12 kg/ha of this formulation containing 0.1% mirex (1.12 g/ha active ingredient) was as effective as the 0.3% standard bait at 1.4 kg/ha (4.2 g/ha AI). Some more recent tests (W. A. Banks et al, unpublished data) indicate that the latex coating may be omitted from the formulation without serious decline in effectiveness. However, difficulties in formulation, application, and storage life have slowed the acceptance of the coated baits as control agents.

In 1967, a special committee established by the National Academy of Sciences (79) concluded from information available at that time that eradication of the fire ant was biologically and technically impossible, and inadvisable were it possible. However, a series of eradication trials conducted subsequent to that report indicated that eradication is technically feasible (8). Lofgren & Weidhaas (66) in a theoretical appraisal of eradication calculated that from 3 to 9 applications of mirex bait could be required, dependent upon the effectiveness of a given application and the effective rate of increase of the species. We used only 3 applications in the eradication trials (8) and the results obtained indicated that eradication could be accomplished with 3 or 4 sequential applications that were properly timed if contiguous areas were progressively treated.

About this time, however, several laboratory studies showed that mirex had undesirable effects on nontarget animals (17, 40, 67, 68, 81, 104, 113), so questions arose concerning the environmental safety of the bait. Subsequently, data became available that showed that residues of mirex were appearing in nontarget organisms after large area applications for fire ant control (7, 18, 29, 76, 82). As a result, the Environmental Protection Agency in 1971 issued notice of cancellation of the registration of products containing mirex. The registration was ultimately reinstated but with severe restrictions on the application of the bait in estuarine and prime wildlife habitats (94). Therefore, since 1971, the federal-state program has been aimed at providing relief in areas infested with large populations of the ants.

TECHNIQUES AND EQUIPMENT FOR APPLICATION OF CHEMICALS Chemical control of fire ants before 1957 was achieved by individual mound treatment or by broadcast treatments on limited areas with ground equipment. Eden & Arant (37) demonstrated that individual mound treatment or limited area treatment gave good control with residual insecticides if the materials were properly applied. However, mound treatments with mirex bait at rates as high as 14 g/mound, gave poor control in two series of tests (C. S. Lofgren et al, unpublished data).

In any case the large acreages involved in the cooperative federal-state program made treatment of individual mounds impractical and ground equipment was also impractical except for limited areas. Therefore, aircraft have been used almost

exclusively in this program. Initially, single engine planes were used. However, by 1959–1960, some multiengine aircraft were in use. By the late 1960s, numerous multiengine planes, mostly converted World War II bombers, had been equipped for application of mirex bait (2). Dispersal equipment has been continually improved so most large applicator planes now have auger or chain-fed systems mounted within the wings of the aircraft. However, the development of the microencapsulated bait has now created a need for a new dispersal system, and the Aircraft Operations Section of the Animal and Plant Health Inspection Service, US Department of Agriculture at Beltsville, Md., has developed the prototype for a system to handle this bait (77).

The application aircraft were guided by helium-filled balloons (Kytoons®) until about 1966 when electronic guidance was introduced. The guidance systems, which consist of a master radio transmitter and two slave stations arranged in a triangular pattern within the area to be treated, produce electronic signals in a hyperbolic grid over the area. Numbers are assigned to the lines of the grid, and computerized receiving equipment in each aircraft is preset to home on a given numbered coordinate. Deviation of the aircraft from the prescribed flight path is indicated by an indicator needle in the cockpit and on a chart recorder. The operation and the use of the guidance systems in the fire ant program have been discussed in a number of articles (3, 43, 52, 87).

Standard operational procedures until 1970 required that the aircraft disperse the bait at an altitude of ca 23–46 m. However, a series of studies (Glancey et al unpublished data) showed that dispersal of the bait from an aircraft flying at an altitude of 213.5 m produced a wider swath and more uniform distribution on the ground. When wind speed and direction at dispersal altitude were determined with pilot balloons and a theodolite, the increased altitude coupled with crosswinds, increased the swath width 2 to 3 times the normal effective swath width of the aircraft. Since the increased swath width greatly increased the coverage of an aircraft per unit of flying time, costs of application were substantially reduced because the bid price for single spacing was reduced 25% and 50% for acreage flown at double or triple spacing, respectively.

Future Prospects for Control

CHEMICAL The outlook for alternative chemicals for control of imported fire ants is not promising. Screening programs to evaluate chemicals as residual soil surface treatments or as bait toxicants have been conducted since 1958 by the USDA and its cooperators. More than 150 chemicals were evaluated as residual soil surface treatments (59; W. A. Banks et al, unpublished data), but the only chemicals that were very effective in the field were cyclodiene type compounds. Since the use of these compounds has been very restricted since the early 1960s, only a limited amount of work has been done with residual compounds since 1963.

The bait screening tests have evaluated more than 2050 chemicals (58, 63, 126; R. Levy et al, unpublished data) from all the different classes of insecticides available. Stringer et al (99) determined that an effective bait toxicant must (a) exhibit delayed toxicity (less than 15% mortality after 24 hr and more than 90% mortality

after 14 days) over at least a tentfold and preferably above a hundredfold range of doses; (b) be readily transferred from one ant to another and result in mortality of the recipient; and (c) not be repellent to ants. Only 23 chemicals of the more than 2050 tested have met these requirements; 3 of the 23 were not available for field testing, and field tests with 11 showed that mirex and closely related compounds are the only ones that consistently give control effective enough to suppress populations (i.e. 90% or higher kill). The other 9 compounds were only recently tested, and sufficient quantities are not yet available for field tests; however, they are all organophosphorus chemicals, and all previous field tests with such materials have resulted in very poor control. The laboratory evaluation of additional chemicals is continuing.

Recent laboratory tests with several juvenile hormone analogs (35, 101, 109) indicate that these compounds may have some potential as control agents for fire ants. Methoprene and hydroprene caused anomalous prepupae, pupae, and adults and prevented larval metamorphosis. Some other compounds were found to produce similar effects (109). In addition, temporary sterility was induced by methoprene and hydroprene (85, 101). Field tests with these compounds have caused some deformities and some worker ant mortality, but have not effectively reduced infestations of the fire ants.

BIOLOGICAL

Pathogens Surveys of fire ant populations in the areas infested with *S. invicta* and *S. richteri* in the United States revealed few indigenous pathogens (B. A. Federici, personal communication; 22). A species of *Pseudomonas* bacteria was found in dead ants taken from mounds in southwestern Mississippi. Subsequent investigations in the laboratory showed the bacterium to be highly toxic to fire ants, since it killed within 5 days 100% of the larvae fed on a glucose solution containing vegetative cells. Also, a glucose-bacteria suspension placed on corncob grits killed 50% of the worker ants allowed to feed on the grits. Three fungi were found to be pathogenic to both species of fire ants in the laboratory. *Beauveria bassiana*, *Metarrhizium anisopliae*, and *Aspergillus flavus* caused 80%, 40%, and only occasional mortality, respectively, to fire ants within 5 to 10 days after exposure (22, 95). *B. bassiana* and *A. flavus* have been recorded previously from *Atta texana* in Louisiana, and *M. anisopliae* has been recorded from *Solenopsis richteri* in Uruguay (98). Allen (4) indicates that *B. bassiana* and *M. anisopliae* appear to be important pathogens of ants in South America. There is no evidence, however, that any of these pathogens are exerting any appreciable control of any field population of imported fire ants in the United States.

The most promising development from the standpoint of possible biological control of fire ants is the finding by Allen & Buren (4) that microsporidian pathogens occur in *S. invicta*, *S. saevissima*, and other species of the *S. saevissima* complex in Brazil. These are the first protozoan pathogens to be reported in Formicidae. In some colonies 50 to 95% of the adults appear to be infected. Workers with a heavy infection may have the gaster packed with spores and the abdominal organs greatly reduced. How the disease is transmitted, whether each microsporidian is host spe-

cific, the length and course of the infection process, and whether these pathogens could be effectively utilized as biological control agents are all subjects of recently initiated research.

Predators and parasites The role that predators and parasites play in regulating populations of imported fire ants in the United States has not been studied in depth. Whitcomb et al (114) reported that the queens of *S. invicta* are attacked and killed by a variety of predators from the time they take flight until successful colony establishment is achieved. O'Neal (84) recorded predation on larvae of *S. richteri* by *Neivamyrmex opacithorax*. Also, the thief ant, *Solenopsis molesta*, was found living in the nests of both *S. invicta* and *S. richteri* and preying on the eggs and young larvae. Another ant, *Paratrechina melanderia arenivaga*, was found preying on the eggs of *S. invicta* in nests in southern Mississippi.

A nematode, as yet unidentified, has been found in *S. richteri* in Oktibbeha County, Mississippi, and has been established as being pathogenic to the ants (B. R. Norment, personal communication).

No evidence exists that any of the foraging parasites or predators are exerting sufficient restraints to reduce populations of fire ants in any area to even tolerable levels, nor does it appear likely that they will be able to do so in the future.

Studies have shown that the endoparasite, *Neoaplectana dutkyi*, (DD-136) is effective against the fire ants in the laboratory; however, field tests have not been extremely encouraging to date (Norment, personal communication).

In the homeland of the fire ants in Brazil, the states of Mato Grosso and Sao Paulo, *Solenopsis* species are beset by a large number of parasites. R. N. Williams and W. H. Whitcomb (submitted for publication) list or discuss 14 species of *Pseudacteon* and one species of *Apodictania* (Phoridae), two species of *Oraesema* (Eucharitidae), and three species of parasitic *Solenopsis*. *Pseudacteon* has been observed attacking fire ants (116) but as yet no one has observed the immature forms of these flies in the ants or determined their potential effect on the colonies. Nematodes have been observed in the gasters of *S. invicta* from Rondonopolis, Mata Grosso (G. E. Allen, personal communication). The possible suppression of *Solenopsis* by competitive species of ants has not been studied but has been speculated upon by Buren et al (26). The range of *S. invicta* in South America well may be restricted by many strong biotic and abiotic factors.

Silveira-Guido et al (96, 97) made an extensive study of the social parasite, *Solenopsis daguerri* (formerly *Labauchena daguerri*), and its effects on fire ant colonies. The parasite is confined to *S. richteri*, the imported fire ant of lesser importance in the United States, and it infests only a small percentage of the colonies. Present evidence suggests that it is not exerting any effective control on fire ants in South America, nor does it appear likely that it would do so on *S. richteri* in the United States.

Pheromones In a previous section of this paper we discussed the role of pheromones in the colony organization of fire ants. Research aimed at the elucidation of the chemical nature of the trail pheromone of both United States species of imported

fire ants is well advanced. The use of this pheromone as a confusion lure, as suggested by Brown (24), may have application in future control of the fire ants. Elucidation of the chemical natures of the brood-tending (44) and queen pheromones (54) may provide effective lures and means of making baits more species specific.

Sterilization or genetic manipulation Neither sterilization nor genetic manipulation appear practical for the control of imported fire ants.

Chemosterilants cannot be used in the field because there are no compounds that are species specific and the effects of a nonspecific chemosterilant on nontarget species could be undesirable. In addition, the sterile male technique that has been used so successfully with some insects is totally impractical. For example, no methods are available for rearing large numbers of males in the laboratory and field studies (80) have shown that nuptial flights can occur on at least 138 days in north Florida producing an average of 239,590 females/ha (an average of ca 1736 females per ha/flight) (114). Then, to overflood with a 9:1 ratio of sterile males to females, we would have to release 15,624 males per ha/flight. If we assume that the releases would have to cover a 259 km² area, a total of 404.9 million males would be required per release. Nuptial flights can occur on any day in the year in any part of the infested area (75), however, those flights that occur during the cooler months may not result in successful colony founding. If we assume that colonies can become established only from flights that occur between April 1 and August 15, then colonies could result from flights on 137 days. Releases would have to be made every day during this period over the entire 259 km² since there are no reliable criteria for predicting time or location of a nuptial flight. Releases over this period on the 259 km² would require more than 55 billion males. These calculations are based upon the average number of females per hectare per flight. Roe (93) has reported a maximum of 3118 females flying from a single nest of *S. invicta*. Actual releases would have to be made on the basis of maximum numbers expected so the calculations are low by a factor of four times or more. It quickly becomes evident that the logistics of rearing sufficient males is overwhelming. In addition, sterile males would have no effect upon the parent colonies, which would continue to produce more potential queens unless an insecticide or some other control was used to eliminate the colony.

At present, our knowledge of the genetics of fire ants is insufficient to allow us to evaluate fully the prospects of genetic manipulation. Techniques for mass forced mating and rearing large numbers of genetically aberrant sexual forms are not available and the chances of developing such techniques appear remote. As with the sterile male approach, even if genetic aberrants could be introduced, the existing population would continue to flourish essentially unaffected by the aberrants.

CONCLUDING REMARKS

Probably no insects have created so much controversy as the imported fire ants. Despite the many hours of research and the many millions of dollars spent during

the past two decades, the ants continue to annoy man and animals and to perplex those who seek new and better methods of controlling them. Eradication of these ants from the United States would be most desirable; however, the prospects of this being achieved appear remote, even though studies have shown that it could probably be accomplished with mirex bait. We must, therefore, find new methods for alleviating the many problems caused by the fire ants in the southeastern United States.

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Entomology, St. Petersburg State University, RUSSIA

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