

The red imported fire ant, *Solenopsis invicta*:
An exotic species invades the United States.

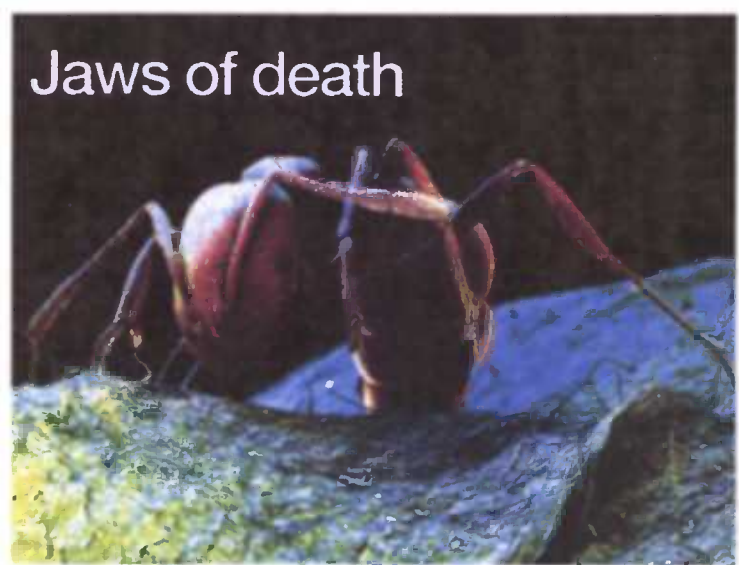


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Jonathan Beard: "Life's no picnic when the ants arrive. But some aren't just irritating, they're killers"
(Opinion, in *New Scientist* Vol. 167 No 2258, september 2000)

Introduction

In the 1930s, the fire ant *Solenopsis invicta* Buren (or red imported fire ant –RIFA) was introduced from South America into the United States, at the port of Mobile, Alabama. In 1918 another fire ant species, *S. richteri* (also native in S.-America) or the black imported fire ant had been introduced at the same place; however, this species were not to be as successful as the red imported fire ant.

RIFA commenced to expand its life area, interbreeding with the black imported fire ant, in the end almost totally replacing *S. richteri*: Today RIFA inhabits more than 275 million acres in the United States of America, yet still continues spreading.

Fire ants are a serious pest in urban environments, because they interfere with gardening and outdoor activities, and occasionally invade human habitations. They commonly infest lawns, schoolyards, athletic fields, golf courses and parks. In these places, they pose a medical threat to people and animals.

Fire ants may attack with little warning. After firmly grasping the skin with its jaws, the fire ant arches its back as it inserts its rear-end stinger into the flesh, injecting venom from the poison sac. It then pivots at the head and typically inflicts an average of seven to eight stings in a circular pattern. Fire ant venom is unique because of the high concentration of toxins, which are responsible for the burning sensation (hence the name *fire ant*).

Several studies confirmed that the social organization of *S. invicta* in its new homeland has altered, compared to the mother population in South America. Does this account for the success of the red imported fire ant, *Solenopsis invicta*?

Following a brief synopsis on social insects and ants Formicidae in particular, attention will be paid to the factors responsible for the successful invasion, and finally some points for future research will be listed.

Range Expansion of RIFA in the U.S. From 1918-1998

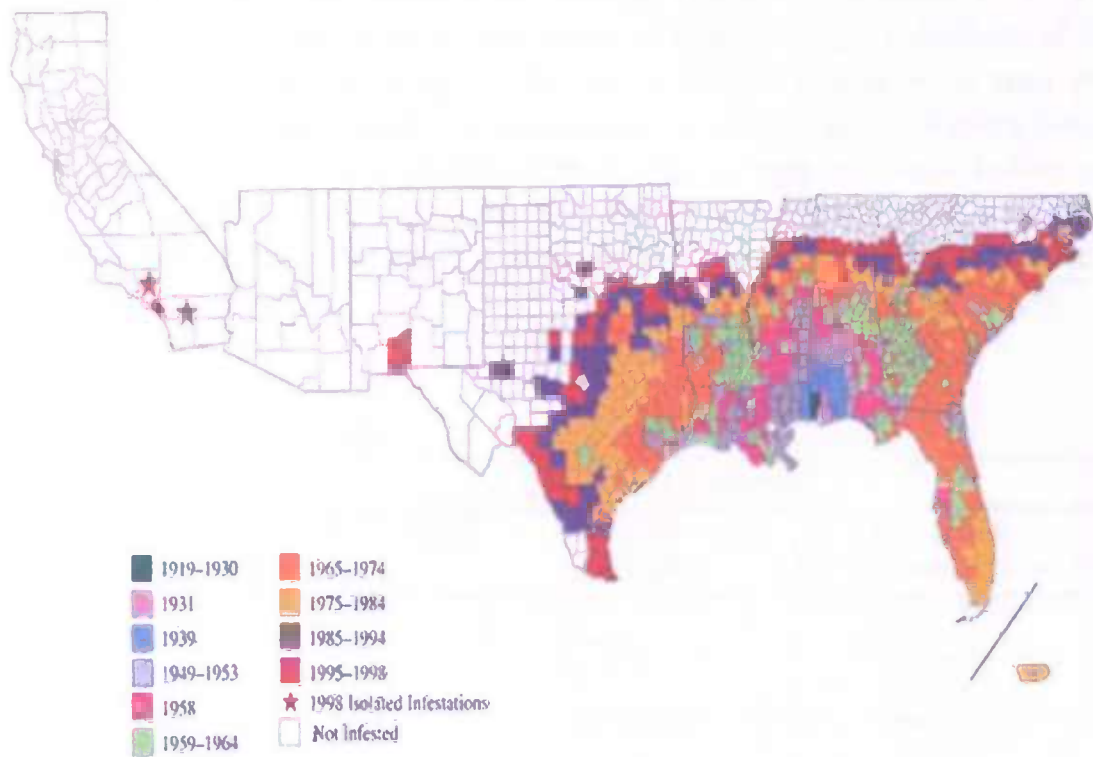


Figure 1: Historical progression of the Red Imported Fire Ant (RIFA), *Solenopsis invicta*. First introduced into the port of Mobile, Alabama, nowadays, RIFA infests more than 275 million acres in the USA, and still continues spreading .

1. Social Insects

A colony of social insects can be seen as a superorganism. Composed of numerous individuals, each performing their specialized functions, the colony acts as a single organism. But, first of all, what is understood with the term social?

Several degrees of sociality are defined in literature; from solitary, subsocial and communal to quasisocial, semisocial and eusocial (Table 1A)(Michener 1969). The degree of sociality is defined by the possession of three traits: (1) Individuals of the same species cooperate in caring for the young; (2) An overlap of at least two generations in life stages, capable of contributing to colony labor (offspring assists parents), and (3) reproductive division of labor, with more or less sterile individuals working on behalf of fecund individuals. The common possession of these three traits defines the 'truly' or eusocial insects, that include ants, all termites and the more highly organized bees and wasps.

TABLE 1A: Degrees of sociality

Degrees of sociality	Qualities of sociality		
	Cooperative brood care	Overlap between generations	Reproductive division of labor
Solitary *			
Subsocial	–	–	–
Communal			
Quasisocial	+	–	–
Semisocial	+	–	+
Eusocial	+	+	+

* Subsocial insects have adults that care for their own nymphs or larvae for some period of time. Communal insects show members of the same generation using the same composite nest without cooperating in brood care

In an insect society an organized structure is present, the individuals fulfill their own function, which they do best: all the individuals' specialized tasks together ensure the proper functioning of a colony. This structure is translated into a system of castes, which has evolved in the social insects: Polyethism or division of labor. In such a social society, reproduction is carried out by a few individuals (queen(s) and male) – the reproductive caste; another group of individuals 'takes care' of the new offspring – the worker caste; in other words that means nourishing the brood, foraging, and defending the colony.

In social insects a distinction can be made between caste polyethism and age polyethism: The former implies morphological different castes serving different functions, and the latter implies individuals passing through different forms of specialization, as they grow older.

The following sections will give a general impression of the truly or eusocial insects: All termites, social bees and wasps, and last but not least, ants.

1.1 Social insects: The Termites

Termites are the only eusocial insects that do not belong to the Order Hymenoptera (ants, termites, and social bees and wasps are Hymenoptera). All of the termites together comprise the Order Isoptera. With the closely related cryptocercid cockroaches, they are the only wood-eating insects that depend on symbiotic intestinal flagellates. Their cellulose diet may provide the clue to their social beginnings: In order to transmit the symbionts, the termites need to engage in a unique form of anal liquid exchange, an arrangement that necessitates at least a low order of social behavior. It is even possible that the symbiosis was the primary cause of social life in termites in the first place.

Castes in termites are constituted of both sexes. Unlike social Hymenoptera, termites are *hemimetabolous*: the immature stages are not really distinct in form and behavior from the mature stages. A colony starts with the primary reproductives: After they meet during the nuptial flight (mating flight of winged males and females), the primary reproductive male stays with the queen, helps her construct the first nest and fertilizes her intermittently as the colony develops. On the other hand, in the eusocial Hymenoptera, the male fertilizes the queen during the nuptial flight, but dies soon afterward. The worker caste is numerically dominant in the colony. The soldier caste is highly specialized in head structure and behavior, for colony defense. Thus, basically a colony consists of the reproductive caste (primary reproductives, but supplementary reproductives may replace these after removal), a soldier caste and a worker caste.

1.2 Social Insects: Social Bees and Wasps

All the bees together comprise the superfamily Apoidea. The honeybee (*Apis mellifera*) has been by far the most intensively studied social insect. It is counted among the highest eusocial insects, by criteria of social complexity such as colony size, altruistic behavior among colony members, complexity of chemical communication and thermoregulation of the nest interior. The waggle dance, a most remarkable form of communication puts this species apart from all other insects.

Queens and workers are morphologically very different from each other; queens are larger than workers, typically producing over 1.000 eggs a day, highly specialized for reproduction. At the beginning of the spring reproductive season, or any other time that the mother queen dies or loses her vitality, new queens are produced. A pheromone called the "queen substance", that is manufactured in the mandibular glands of the mother queen, inhibits this production of new queens. When the queen

loses her vitality, or dies, the workers are no longer inhibited of raising new queens. The caste of individuals is determined by a complex interaction between pheromone-mediated behavior on the part of nurse workers, and specialized diets fed to the larvae.

The caste systems of the social wasps have not evolved as far as the other social insects, only a relatively small number of wasp species is truly social. Eusocial behavior is almost entirely limited to the family Vespidae. Wherever there exist morphological differences, they appear to have a relatively simple nutritional basis. Division of labor among workers and programmed behavioral changes during lives of individual workers are either absent or very weakly developed. Paper wasps of the genus *Polistes* (all of which are truly social) have been studied mostly, because of their nests: they build naked combs in exposed sites and can therefore be observed during the entire colony life cycle without special preparation. Multiple egg laying queens exist in a colony; no external morphological differences are apparent between dominant "queens" and subordinate "workers". The worker caste is kept in a subordinate position by aggressive dominance behavior on the part of the egg laying females.

1.3 Social Insects: Ants

Ants are the most widely distributed of the major eusocial groups, ranging from the arctic tree line south to Tierra del Fuego, to the tip of South Africa, and to Tasmania, and occurring on virtually every oceanic island between Iceland and the Aleutians in the north and Tristan da Cunha and Campbell in the south. Numerically, they are the most abundant of social insects, and contain a greater number of known genera and species than all other eusocial groups combined.

The ants constitute all of the superfamily Formicoidea and, within that, the single family formicidae (table 1B). Two major branches are distinguished in the Formicidae: The 'myrmecoid' complex, and the 'poneroid' complex of subfamilies (Brown 1954). The names of the complexes were derived from the most primitive subfamilies known to belong to them at that time, namely the Myrmeciinae and Ponerinae. Fig. 1 shows the external anatomy of an ant, with the principal features used in taxonomy.

The majority of ant groups exhibit a highly variable degree in prey choice, while a few have come to subsist primarily on seeds. Species of the ponerine genus *Leptogenys* prey only on isopods; species of the ponerine genera *Discothyrea* and *Proceratium* feed only on arthropod eggs (Brown 1957); all the members of the subfamily Cerapachyinae prey exclusively on other ants (Wilson 1958). Others rely entirely on the "honeydew" secretions of homopterous insects reared in their nests or on special mutualistic fungi cultured on insect dung or vegetation (Way 1963; Weber 1966).

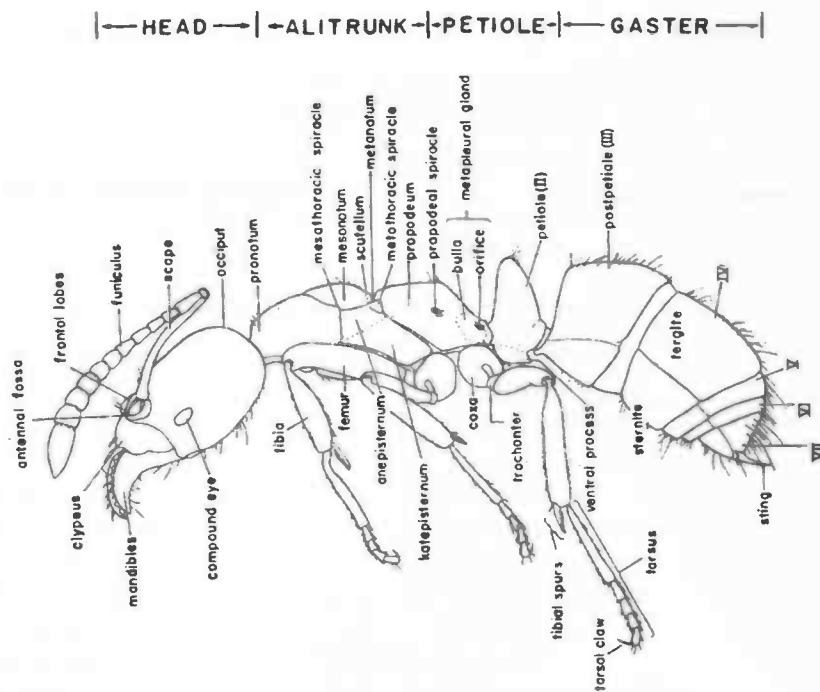


Figure 1. External anatomy of a worker of the New Zealand ponerine ant *Pachycondyla* (= *Mesoponera*) *castanea*; it also shows some of the principal features used in taxonomy (from Hölldobler and Wilson 1990)

TABLE 1B: Ant taxonomy (From Wilson 1971; Hölldobler and Wilson 1990)

The ants: Family Formicidae	
The Myrmecoid Complex	The Poneroid Complex
Subfamilies Tribes	Subfamilies Tribes
SPHECOMYRMENAE † MYRMECINAE NOTHOMYRMECINAE ANEURETINAE Aneuretini PSEUDOMYRMECINAE Pseudomyrmecini DOLICHODERINAE Dolichoderini Leptomyrmecini Tapinomini FORMICIINAE † FORMICINAE Gesomyrmecini Myrmelachistini Prenolepidini Myrmoteratini Myrmecorhynchini Melophorini Plagiolepidini Oecophyllini Formicini Camponotini Lasiini	PONERINAE Acanthostichini Aenictogitini Amblyoponini Ceropachyini Cylindromyrmecini Ectatommini Typhlomyrmecini Platythyreini Ponerini Thaumatomyrmecini Odontomachini CERAPACHYINAE Sphinctomyrmecini Ceropachyini LEPTANILLINAE Leptanillini Anomalomyrmini DORYLINAE Aenictini Dorylini ECITONINAE Cheliomyrmecini Ecitonini MYRMICINAE Myrmicini Pheidolini Melissotarsini Metaponini Leptothoracini Myrmicariini Crematogastrini Solenopsidini Pheidologetini Meranoplini Tetramoriini Ochetomyrmecini Cephalotini Basicerotini Dacetini Agroecomyrmecini Phalacromyrmecini Attini

1.3.1 The fire ant *Solenopsis invicta*

Kingdom	Animalia
Phylum	Arthropoda
Class	Insecta
Order	Hymenoptera
Superfamily	Formicoidea
Family	Formicidae (poneroid complex)
Subfamily	Myrmicinae
Tribe	Solenopsidini
Genus	<i>Solenopsis</i>
Specie	<i>invicta</i>

The scientific name of the red imported fire ant is *Solenopsis invicta* Buren, taxonomically identified by Dr. William Buren in 1972. It is placed in the genus *Solenopsis* by its 10 segmented antennae with a 2-segmented club.

The life cycle of an individual consists of four stages: Egg, larva, pupa and imago. Often eggs are confused with pupae, but the eggs are much smaller than pupae. The eggs, larvae and pupae together comprise the brood of a colony. Once a colony has been established, a single queen can lay up to 2,000 eggs per day. After the egg has been laid, it takes about 7 to 14 days to reach the larval stage; as the larvae grow, they molt 4 times, generally reaching the pupal stage in 12 to 15 days. Approximately 10 days later the imago appears. Depending on temperature it may take 20-45 days for an egg to develop into an adult. Life spans are usually between 1 and 6 months, with a maximum of 9 months, also depending on temperature. Queens grow much older; they can live up to 6 or 7 years.

The castes include winged males, winged females (unmated queens), infertile wingless workers, and one or more mated queens. The workers (only females), numerically predominant in the colony, vary in size and perform different tasks: They nourish the brood, carry out repairs in the nest, forage, and defend the nest. They can forage both during the day and the night, generally when air temperatures are between 70° and 90° F. After they have mated, the queens lose their wings, so unmated queens and reproductively active queens are distinguishable in this way.

Fire ants are omnivorous feeders, feeding on carbohydrates (e.g. honeydew, plant exudates, sugars, syrups), proteins (e.g. insects, meats), and lipids (e.g. grease, lard, oils from seeds). Depending on the nutritional requirements of the colony, the food preferences change. In spring and summer, when the food is abundant, the colony produces new offspring, and the protein needs of the colony increase. Fire ants are only able to ingest liquids; solid proteinaceous food is liquefied by the larvae: It is placed in front of the mouth of the oldest larvae (fourth instar: fire ant larvae usually molt four times), which regurgitate digestive enzymes onto the food. Once liquefied, the fourth instar larvae suck up the protein and regurgitate it to the workers, which pass it on to the rest of the colony.

2. Social evolution of *Solenopsis invicta*

2.1 *Solenopsis invicta* as an exotic species

The red imported fire ant *Solenopsis invicta* possesses many of the characteristics commonly ascribed to successful invaders (Ehrlich 1986): (1) It prefers heavily disturbed habitats associated with human activity (Tschinkel 1988). (2) It tolerates a wide range of climatic conditions and (3) utilizes a wide variety of food resources (Vinson and Greenberg 1986). (4) It is relatively abundant in its homeland (Banks *et al.* 1985). (5) Workers are highly variable in size (Porter and Tschinkel 1985). (6) Mated queens are capable of establishing new colonies after transport (Vinson and Greenberg 1986). (7) Finally, colonies of this species have a high reproductive capacity; they grow rapidly (Porter 1988) and can produce thousands of reproductives per year (Vinson and Greenberg 1986).

An additional factor that helps to explain the success of the red imported fire ant as an invader is its impact on the endemic fauna of its new homeland. In the paper of Porter and Savignano (1990), it was demonstrated that the invasion of polygyne fire ants has a negative impact on the native ant society, and they found that in areas

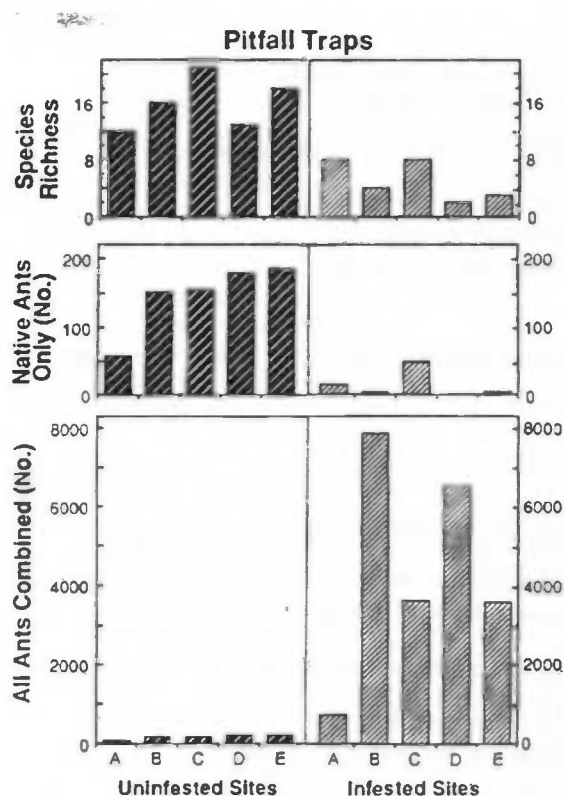


Figure 2: Impact of the imported fire ant on ant species richness and the abundance of worker ants collected in pitfall traps. Infested and uninfested sites with the same letter were paired by habitat (Porter & Savignano, 1990)

infested by the red imported fire ant species richness had decreased.

Figure 2 shows the impact of the imported fire ant on ant species richness, and the abundance of worker ants collected in pitfall traps, in both sites uninfested and infested by *S. invicta*. The average number of ant species trapped in the sites not infested by *Solenopsis invicta* was much higher compared to the sites that were infested by the red imported fire ant. Native ants occurred much less frequently in infested sites: The average number of native ants trapped in sites infested by the red imported fire ant was 14.2 ± 8.7 , compared to 145 ± 23 in the uninfested sites. Furthermore, in the infested sites a much larger amount of ants were trapped in the pitfall traps, compared to the uninfested sites, with a difference in magnitude of almost 30 times: 4469 ± 1254 vs. 165 ± 23 , respectively; this difference was entirely due to the

presence of *S. invicta* in the infested sites.

In short, in the areas invaded by the imported fire ant species diversity and the number of native ants had decreased, compared to the uninfested areas. On the other hand, the total amount of ants collected in pitfall traps in the sites infested by *S. invicta* was much higher compared to the sites not infested by *S. invicta*. These results lead to the following two conclusions: (1) The imported fire ant inhibits the endemic ant species in its new homeland, and (2) *S. invicta* is able to maintain much higher population densities in the United States than native ant species.

Additionally, the influence of imported fire ants on other non-ant species (other surface-active arthropods) was investigated. The relationship between the number of

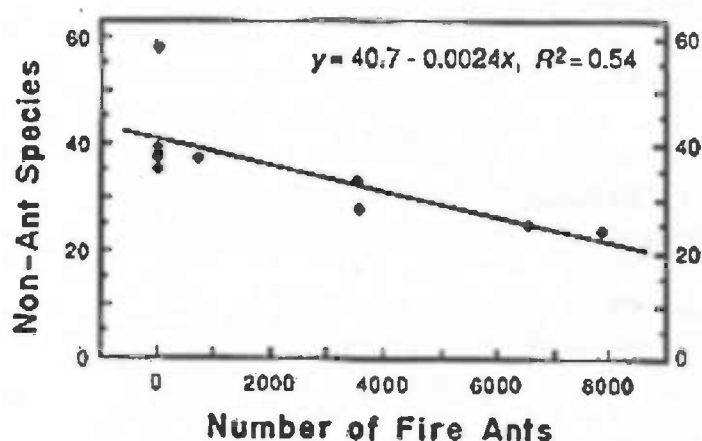


Figure 3: Relationship between the number of fire ants (*Solenopsis invicta*) and the number of non-ant species collected in pitfall traps at 10 sample sites (Porter & Savignano, 1990).

fire ants and the number of non-ant species is plotted in figure 3. Approximately 176 non-ant species were collected in pitfall traps in the infested and uninfested areas. Fifty species were found in both the infested and the uninfested areas; of the remaining 126 species, 45 were found solely in the infested area, whereas 81 non-ant species were found solely in uninfested areas.

These results show that not

only the red imported fire ant inhibits native ant species, it also has a negative impact on non-ant species.

2.2 Bottleneck

For evolutionary (socio-) biologists, the introduction of the fire ant *Solenopsis invicta* into the United States provides a unique opportunity to study recent social evolution, by comparing social organization in the native and newly colonized areas. The introduction of a species into a new environment, which is geographically separated from the native population, results in a loss of genetic variation, or what is referred to as a bottleneck: Only a fragment of the variation of the native population is transferred with the introduced individuals, to the new area, there representing the total amount of variation present. A decrease in genetic variation may promote inbreeding, moreover such a decrease in variation may influence how the introduced species reacts to natural.

Such a loss is likely to have a pronounced effect on sex-determination in social Hymenoptera such as fire ants, because of their unique genetic mode of sex determination. Sex is determined by a system of genetic complementarity (Box 1), whereby diploids heterozygous at the sex-determining locus become females, and

haploids (hemizygotes) or homozygous diploids become males (Cook and Crozier 1995).

Box 1: Complementary Sex Determination (CSD)

In most species of the order hymenoptera sex appears to be determined by genotype at one or a few loci. Diploid individuals heterozygous at the sex-determining locus (or heterozygous at one or more loci in a multilocus system) develop into females, whereas diploid individuals homozygous at the locus (loci) or haploid individuals (with hemizygous genotypes) develop into males. Individual sex alleles do not have particular tendencies, instead female phenotype will develop as a result of the complementary action of two different alleles.

Single-locus CSD

- * $A_i A_j$ → Females
- * $A_i A_i / A_j A_j / A_i / A_j$ → Males

Unmatched matings occur when a female ($A_i A_j$) mates with a haploid male that carries a different sex allele (A_k). Consequently all diploid offspring will be females.

Matched matings occur when a female ($A_i A_j$) mates with a haploid male that carries a sex allele identical with one of her own (A_i or A_j). As a consequence, 50 % of the offspring are homozygous diploid males.

For instance, when a population bottleneck causes loss of genetic variation, it also accounts for a decrease in the number of sex alleles in the population. The decreased number of sex alleles results in an increase of the probability that during reproduction diploid males (homozygous) are produced.

2.2.1 Variation in the genetic sex-determining system

Indeed, a recent study has revealed that genetic variation has been lost in the red imported fire ant. Ross *et al.* (1993) have shown that this is associated with a large increase in the frequency of diploid males in introduced polygyne populations, compared to South American polygyne populations. The population bottleneck has lead to a decrease in genetic variation, which is especially evident at the sex-determining locus.

The allelic diversity of the sex alleles has decreased significantly: Introduced fire ant populations show a smaller number of different sex alleles compared to native populations in South America. The proportion of matched matings (see Box 1) has significantly increased in the introduced populations (Ross *et al.* 1993). The loss of allelic diversity of sex alleles and, consequently, the increased frequency of matched matings, account for the increased production of diploid males (Box 2) in introduced polygyne populations of the fire ant *Solenopsis invicta*.

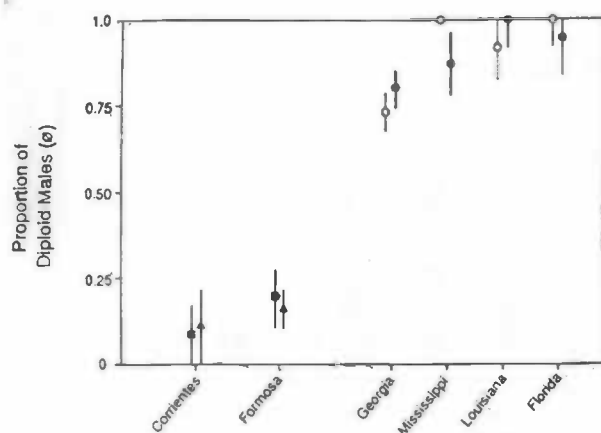


Figure 4: Proportions of males that are diploid in two native and four introduced populations of polygyne *S. invicta*. The number of polymorphic markers used to assess male ploidy was 9 in Corrientes, 10 in Formosa and 2 in each of the USA populations. Filled squares, estimates based on examination of multilocus genotypes; Filled triangles, means of maximum likelihood estimates from single loci; Open circles, maximum likelihood estimates from *G 3pdh-1*; Filled circles, Maximum likelihood estimates from *Est-4* (Ross et al. 1993).

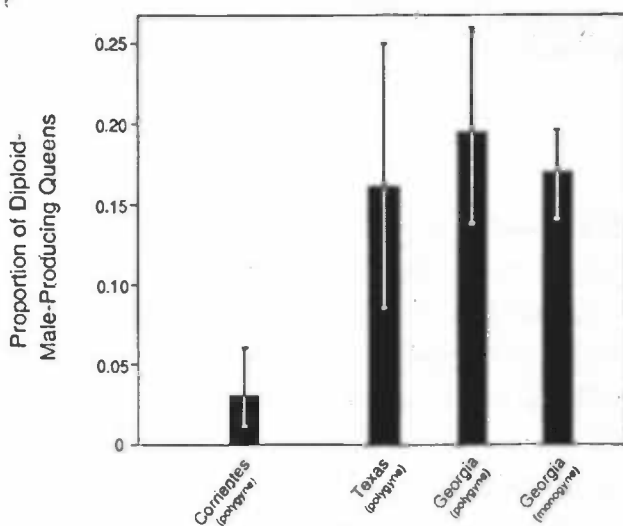


Figure 5: Proportions of DMP queens in 1 native and 3 introduced populations of *S. invicta*. The data are derived from newly mated queens collected immediately after their mating flights in the single monogyne population and from fertile, actively reproducing queens collected within their nests in the polygyne populations (Ross et al. 1993).

In the experiment carried out by Ross et al. (1993) four introduced populations (Georgia, Mississippi, Louisiana, Florida) and two native populations (Corrientes, Formosa) were included. Estimates of adult males indicated that 75-100% of all the males were diploid in the introduced populations, whereas 10-25% of all the males were diploid in the native populations.

Another method was used to measure variation in the genetic sex-determining system, by assessing the proportion of mated queens that produced diploid males. One native population (Corrientes, polygyne) and three introduced populations (Georgia and Texas, polygyne; Georgia, monogyne) were studied during the experiment. The data were derived from actively reproducing queens in the polygyne populations, and in the monogyne population (introduced area) from newly mated queens collected immediately after their mating flights (diploid are rare or absent in monogyne colonies, see also Box 2). Whereas the native population showed some 4% diploid male producing queens, the proportion of diploid male producing queens was much higher in the introduced populations, 15-20%.

Diploid males in social species are produced largely at the expense of workers, whose labor is essential to optimal colony growth, survival and reproduction (Page 1980); because of abnormalities in their reproductive physiology, they are functionally sterile (Hung et al. 1974).

Box 2: Diploid Male Production (DMP)

DMP depletes the worker force in a colony. In the honeybee, workers can recognize diploid male larvae and eat them (Woyke 1986), but fire ant workers don't possess this capability (Ross and Fletcher 1986). Polygyne fire ant colonies can afford it to produce diploid males (multiple queens, dependent colony founding), instead in monogyne fire ant colonies no diploid males are produced. The fact that independent colony founding (queen without worker assistance) is the dominant mode of establishing new colonies in monogyne fire ants explains this phenomenon. Diploid males occur in the polygyne form but not in the monogyne form due to the differential mortality of nests producing such males in the two forms.

Colonies founded independently by M queens (monogyne) that produce diploid males invariably die early in development because resources are diverted from production of workers (the labor of which is crucial to colony growth and survival) to production of males (Ross and Fletcher 1985/86). This source of mortality does not afflict the polygyne form because colonies are generally founded by fissioning, during which a sizeable worker force is already present to ensure sustained colony growth.

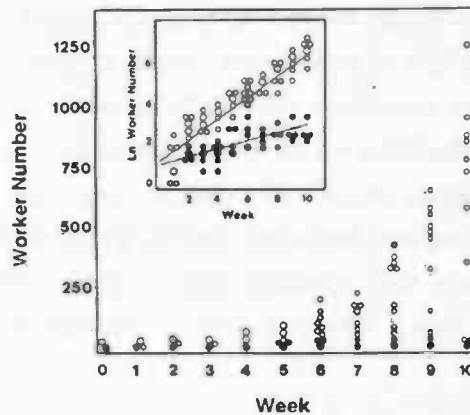


Figure 6: Numbers of workers in newly founded diploid male producing (darkened circles) and worker producing (open circles) monogyne colonies of *S. invicta*. Inset: Semi-log (base e) plot of same data with fitted least squares regression lines (Ross and Fletcher 1986)

In addition to producing no useful labor to the colony, diploid male fire ants consume inordinate amounts of nutriment as brood, that would otherwise be used to rear workers or fertile sexuals (Ross and Fletcher 1986).

These data demonstrate a population bottleneck and an associated change in social organization in the red imported fire ant. However, it presents a paradoxical situation, the invasion of *Solenopsis invicta* into the United States is associated with an increase in frequency of diploid males in polygyne colonies. The production of diploid males imposes a large fitness penalty, with diploid males occurring much more frequently in introduced polygyne populations. Porter *et al.* (1992) have shown that introduced populations of *S. invicta* reach much higher population densities than they do in their homeland. A possible explanation is that the fitness cost of the increased production of diploid males in introduced populations, as a result of the population bottleneck, does not counterbalance the advantages of their new homeland, such as release of native enemies, competitors and parasites.

2.2.2 Sex ratio

The reduction in sex-allele diversity in the newly colonized areas has led to increased homozygosity at the sex-determining locus, and consequently, to elevated frequencies of diploid males in the USA. The production of diploid males appears to occur at the expense of the production of haploid males. Because only haploid males are fertile, this results in a lower number of males available for mating in introduced fire ant colonies. Such an increase in male sterility together with an increased number of queens in polygyne *S. invicta* colonies can explain the large proportion of reproductive queens that remain unmated in polygyne red imported fire ant colonies (25–40%). Although reproductively active, these queens produce few viable eggs (Vargo and Ross 1989). The proportion of unmated queens is much lower in native polygyne *S. invicta* populations (2–12%).

Estimates of the numerical sex ratio of red imported fire ants in the United States reveal a modest male bias in the monogyne form (0.7 female:1 male) and female bias in the polygyne form (1.4:1) (Vargo 1995, *unpubl.*). However, the exclusion of the high proportion of sterile diploid males produced in the polygyne form results in a much stronger female bias (6.2:1) in the numerical ratio of polygyne imported fire ant colonies.

The exclusion of infertile haploid males in the polygyne imported fire ant populations for sex ratio estimates is important, because it affects the operational sex ratio (OSR), the relative abundance of members of each sex available for mating. Both sexes mate only once (Ross 1993) so the OSR is equivalent to the numerical sex ratio for fertile sexuals in *S. invicta*. Thus, the OSR is strongly female biased in the polygyne form of the red imported fire ant, which may account for the fact that a high proportion of the reproductively active queens in introduced polygyne colonies remain unmated compared to native polygyne colonies.

2.2.3 Sex allocation

Colonies of social insects have to face the decision of how to allocate resources between growth (worker production) and reproduction (production of sexuals). Compared to solitary organisms, the eusocial Hymenoptera are unique, because the decision involves two parties, workers and queens, that have conflicting interests over the allocation of colony resources between maintenance and reproduction and in the relative investment in male and female reproductives. This conflict stems from the relatedness asymmetry that arises from the haplodiploid system of sex determination, which causes females to be more closely related to sisters ($r = 0.75$) than to daughters ($r = 0.5$), sons ($r = 0.5$) or brothers ($r = 0.25$). Trivers and Hare (1976) were the first to point out that workers should thus prefer a female biased sex ratio, whereas queens should prefer to invest equally in males and females. Variation in colony queen number can affect this relatedness asymmetry; different dispersal strategies associated with variation in queen number also affect the preferred ratio.

The monogyne (M) and polygyne (P) forms of *S. invicta* differ in the amount of resources allocated to production of workers and sexuals, with M colonies producing a higher proportion of sexuals among their offspring than do P colonies (Table 2A, Vargo 1996). This difference in caste resource allocation reflects the difference in mode of colony founding of the two forms. Colonies of the M form usually establish new colonies by independent colony founding, without worker assistance, producing a lot of sexuals for swarming. Instead, P colonies usually establish new colonies by dependent founding, which requires a substantial amount of workers.

TABLE 2A: Sex investment ratios in a monogyne and a polygyne population of the fire ant *S. invicta*. The dry weight investment ratio was determined by weighting the numbers of sexuals of each sex by the respective average dry weights of mature sexuals of each social form. To correct for sex-specific differences in metabolic rate, Vargo used the energetic cost conversion of Boomsma (1989). The totals given for each form are weighted averages, reflecting the contribution of each season to the yearly total production of sexuals (From Vargo 1996).

Social form	Season	No. males	No. females	Proportional investment in females (Mean \pm S.D.)	
				Dry weight	Energetic cost
Monogyne	Spring	41.076	15.642	0.492 ^{0.267}	0.452 ^{0.280}
	Summer	4.722	10.411	0.869 ^{0.160}	0.842 ^{0.179}
	Fall	35.361	32.460	0.670 ^{0.213}	0.645 ^{0.229}
	Total	81.159	58.513	0.653 ^{0.207}	0.607 ^{0.241}
Polygyne	Spring	6.657	14.922	0.755 ^{0.035}	0.732 ^{0.037}
	Summer	1.696	915	0.379 ^{0.131}	0.355 ^{0.127}
	Fall	5.153	2.719	0.349 ^{0.302}	0.336 ^{0.301}
	Total	13.506	18.556	0.642 ^{0.106}	0.616 ^{0.108}
* Total excluding diploid males				0.879 ^{0.070}	0.858 ^{0.079}
* Total counting diploid males as females				0.938 ^{0.018}	0.931 ^{0.018}

However, the weighted averages of the proportional investment in females, based on both dry weight and energetic cost conversion, is very similar in the two social forms, with no significant difference between them. Although resource allocation numerically differs between the two social forms, the energetic resource allocation appears to be more or less equal.

2.3 Population density

Ecological studies have revealed that introduced fire ants attain colony sizes and densities far in excess of those that occur in the native range (Porter *et al.* 1992); it has been suggested that this is due to ecological release from the effects of natural enemies that normally limit the survival and growth of established nests (Jouvenaz 1983; Wojcik 1986; Porter and Savignano 1990).

Ants can establish new colonies in two ways: (1) By independent colony founding: Queens establish new colonies after the nuptial flight, without assistance of workers. (2) By dependent founding, where queens establish new colonies (not necessarily after the nuptial flight; mating may occur within the nest) assisted by workers. This form of colony founding is also called budding or fissioning: Part of a colony (workers with a queen) leaves the nest to establish a new colony. Another difference between these two modes of colony founding is that independent founding is usually associated with very large dispersal. On the other hand, colonies founded by budding are usually in close proximity of the 'mother' nest.

2.3.1 Mono- and Polygyny

Some species of ants have colonies that always contain a single queen (monogyny), whereas others have colonies that contain multiple queens (polygyny). Colonies in monogynous populations are simple families headed by a single reproductive queen, and colonies in polygynous populations are multi-family groups that contain up to several hundred reproductive queens (Ross and Fletcher 1985; Ross 1993). These two distinct forms of social organization exist both in the red imported fire ant, *Solenopsis invicta* (Table 2A/2B); current genetic, biochemical and taxonomic evidence has indicated that both forms are the same species (Ross *et al.* 1987).

TABLE 2B: Major differences between monogyne and polygyne social forms of the fire ant *S. invicta* in the United States (From Ross and Keller 1995).

	Monogyne form	Polygyne form
Number of wingless (reproductive) queens per nest	1	2-200
Relative fecundity of wingless (reprod.) queens	High	Low
Unmated wingless (reprod.) queens in nests	Absent (or rare)	Frequent
Mode of colony founding	Independent	Dependent
Relative weight of winged (non-reprod.) queens	High	Low
Relative worker size	Large	Small
Relative nest density	Low	High
Connections between nests	No	Yes
Genetic relatedness of nestmate workers	Close to 0.75	Variable, often close to 0
Diploid males	Absent	Frequent
Relative number of new sexuals produced	Many	Few

Variation in queen number is often associated with parallel variation in other reproductive traits. The presence of a single queen per colony (monogyny) typically is associated with colony reproduction by the emission of sexuals, mating away from the nest during the nuptial flight, extensive queen dispersal, and independent colony

founding by queens (no worker assistance). By contrast, the presence of several queens –in *Solenopsis invicta* up to 200– often coincides with loss of mating flight (with mating occurring within the nest), limited dispersal, and dependent colony founding (workers assist queens). These different reproductive strategies are associated with particular queen phenotypes. Monogyne queens tend to have larger body sizes (Keller and Passera 1990), higher nutrient reserves (Keller and Passera 1989), longer life spans (Keller and Passera 1990) and higher fecundity (Vargo and Fletcher 1989) than do their polygyne counterparts.

The increased population densities in the new homeland may play an important role in the alteration of the social organization. The differences in reproductive patterns, dispersal habits and reproductive phenotypes associated with variation in queen number support the hypothesis that ecological constraints on independent colony founding are a major factor selecting for polygyny. When suitable nest sites are located relatively close to each other and independent founding is risky and/or nest sites are limited, reproduction through budding is an effective means of dispersal, since queens are accompanied by workers that can protect them efficiently. Queens accompanied by workers are also likely to outcompete single queens for available sites. The high population densities in the United States are likely to reduce the availability of new nesting sites as the open, disturbed habitats required by this species for nesting (Tschinkel 1988) become increasingly saturated. It is hypothesized that increased habitat saturation influences colony queen number by favoring the adoption of new queens into existing nests and inhibiting solitary nest foundation by dispersing queens (Keller 1995). Increased queen number is generally associated with a decrease in individual reproductive output of queens (Keller and Vargo 1993). However, dispersal and independent colony founding are extremely risky, so the best reproductive option for young queens generally is to enter an established colony.

2.3.2 Worker altruism

Introduced populations of polygyne *S. invicta* differ dramatically from native populations of this form in the number of egg-laying queens per nest, and the relatedness of these queens. Introduced fire ant populations contain over twice as many mated queens per nest (estimated indirectly from genetic data) compared to native populations. The increase in queen number in polygynous populations in the United States is accompanied by a pronounced drop in the average relatedness of nestmate queens (Ross *et al.* 1996). In the experiment of Ross *et al.*, two introduced fire ant populations (Georgia, Texas), and two native populations (Corrientes, Formosa) were studied. The relatedness of mated egg-laying queens of introduced fire ant populations was on average 0.03 and 0.02 (Georgia and Texas, respectively), whereas nestmate egg-laying queens of the two native populations had an average relatedness of 0.45 and 0.46 (Corrientes and Formosa, respectively).

Not only are the queens little related to each other: Also the relatedness between workers and young winged (non-egg-laying) queens (which they rear) is much lower in introduced fire ants; Ross *et al.* found $r=0.24$ and $r=0.15$ for two argentine polygyne fire ant populations (Corrientes and Formosa, respectively), but $r=0$ for an introduced polygyne population (Georgia).

Box 3: Kin selection

Kin selection can be defined as the alteration of the frequencies of genes shared by relatives through actions that favor or disfavor their relatives' survival and reproduction. For instance, if an allele appears in a population that causes its bearer to act so as to increase the reproduction of one or more of the bearer's brothers and sisters, the allele will spread rapidly through the population.

As a matter of fact, kin selection is one of the three hypotheses (kin selection, mutualism and parental manipulation) to explain the origin and evolution of eusociality:

- *Kin selection*: By reducing personal survival and reproduction, workers nevertheless increase the survival and reproduction of genes they share with other members of the colony by common descent.
- *Mutualism*: Individuals do better in personal survival and reproduction (although this does not account for sterile workers) when they live in groups than when they live alone, even though they defer to other colony members and sacrifice on their behalf to some extent.
- *Parental manipulation*: One or both parents (actually, the mother in ants and other social hymenopterans) are able to neuter and control some of their offspring so as to produce a larger total number of offspring. The parents' personal fitness is raised even though that of some of the offspring is lowered.

The concept of kin selection was originated by Charles Darwin in his *The origin of species*: How, he asked, could the worker castes of insect societies have evolved if they were sterile and produced no offspring? Lamarck's theory of evolution by the inheritance of acquired characters did not account for this phenomenon. The modern genetic theory of kin selection and sterile castes was inaugurated by Hamilton, who recognized two ways for alleles to be past to future generations, namely by personal reproduction, and by promoting the welfare of brothers, sisters and other relatives besides offspring who possess the same alleles by reason of common descent.

Low within nest relatedness raises the question of what selective forces maintain worker altruism. Keller (1995) suggested that because the workers have no reproductive capabilities, they are 'trapped' in their helper role; the worker sterility, which is a relatively rare phenomenon in other ant species (Passera 1994), may be essential for colonies with low within-nest relatedness to be stable.

Subsequently, low within-nest relatedness raises the question of what selective forces maintain the worker caste. There is little indirect benefit for a larva to develop into a worker, which makes it unlikely that maintenance of the worker caste can be explained

by kin selection (Box 3) only. Worker control over caste determination seems to be an important factor: They benefit by directing larvae into the worker developmental pathway when this increases colony productivity, because the inclusive fitness of workers increases with colony productivity when their relatedness to the brood is higher than zero (even if very low) (Keller 1995).

The high population densities in the USA suggest that appropriate nesting habitats for the red imported fire ant are more often saturated, and thus opportunities for independent founding by dispersing queens are correspondingly more limited than in the native range (Nonacs 1993). Queens attempting either to remain in their natal nest or to enter another nest to become egg layers may have higher average reproductive success than queens attempting to found nests independently, even though queens using the former strategy have reduced fecundity compared to independently founding queens (Vargo and Fletcher 1989). Moreover, habitat saturation may promote incidental mixing of nonnestmates, potentially eroding the discrimination abilities of workers involved in the recruitment of new queens and the regulation of colony queen number (Hölldobler and Michener 1980).

2.4 Introduced vs. Native *Solenopsis invicta*

The social organization of the red imported fire ant *Solenopsis invicta* in its new homeland, the United States of America, clearly differs from its native counterpart in South America (Table 2C).

TABLE 2C: Differences between native and introduced fire ants *Solenopsis invicta*

Characteristic	Introduced fire ants (United States)	Native fire ants (South America)
Proportion of diploid males in <i>polygyne</i> colonies	High → operational sex ratio highly female biased	Low
Number of permanently unmated queens in <i>polygyne</i> colonies	High	Low
Number of mated egg-laying queens in <i>polygyne</i> nests	High	Low
Relatedness of mated egg-laying queens in <i>polygyne</i> nests	Low	High
Relatedness between workers and young winged (non-egg-laying) queens	Low	High

The operational sex ratio is highly female biased in the polygyne introduced fire ants, as a result of the high proportion of diploid males produced in these colonies. This increase however is not 'voluntary', but instead forced by the population bottleneck that they went through, upon introduction into the United States. Production of diploid

males accounts for a fitness penalty, so strong selection may be expected to increase variation at the sex-determining locus, so as to decrease the amount of diploid males produced. It is unlikely that such a load could persist in ecologically balanced communities, and indeed, male diploidy is uncommon in native populations (Ross *et al.* 1993). Many queens per nest that are little related to each other may even help to increase sex allele variability.

Many queens remain permanently unmated in introduced polygyne fire ant colonies and not in South America, which supports the proposal that male sterility caused by a loss of genetic variation at the sex determining locus has led to elevated abundance of such queens in the introduced range. Laboratory and field studies using *Pgm-3* as a marker to estimate the magnitude of interform matings suggested that 80-100% of mated polygyne queens are inseminated by males originating from monogyne colonies (Ross and Shoemaker 1993), because fertile (haploid) males are rare in polygyne nests; virtually all monogyne queens become mated (Ross and Fletcher 1986).

The reproductively active queens (mated egg-laying queens) in polygyne nests of the introduced fire ant are much less related to each other than in polygyne nests of native *S. invicta* (Ross *et al.* 1996). This is influenced by the fact that introduced polygyne nests contain many more queens (reproductively active) than native polygyne nests. Additionally, workers are less related to the brood they nourish in introduced polygyne fire ant populations.

3. Discussion & Conclusions

3.1 Discussion

The inadvertent introduction of *Solenopsis invicta* in the United States from South America is an example of an exotic species that has managed to attain colony sizes and densities far in excess of those that occur in the native range; it has provided the opportunity to study recent social evolution. Several studies have confirmed that the social organization has changed in the introduced populations of *Solenopsis invicta*, compared to the native populations (Ross *et al.* 1993, 1996). In addition to the fact that two forms of social organization can occur within this species, with the introduction of *S. invicta* in the United States it has become clear that such a social organization is not necessarily rigid, but is capable of undergoing changes.

Queen number, which has attracted much attention because it is an important trait in insect social organization, was shown to differ between (polygyne) populations in the two ranges. In the introduced polygynous populations of *S. invicta*, queen number can be up to 200. Multiple-queen colonies are common in social insects, but the presence of multiple queens in a nest poses an evolutionary paradox. In monogynous colonies, social insect workers are highly related to the brood they rear, where altruism may have evolved through kin selection, the donor and recipient of altruistic acts related to each other (as generally is the case in social birds and mammals). However, with the presence of several queens in the nest the relatedness among colony members decreases. Ross, Vargo and Keller (1996) demonstrated that relatedness among mated egg-laying queens in introduced polygynous populations was close to 0, and also the relatedness between workers and young queens they reared was virtually 0. At first sight this seems in contradiction with kin selection theory (Box 3), because what benefit would insect workers have from rearing unrelated brood? In his review about multiple-queen colonies (1995), Keller gives an answer to this question. With low within-nest relatedness there is strong selection for workers to lay male eggs. However, fire ant workers are obligately sterile; the workers have no reproductive capabilities. Worker sterility may thus be a precondition for colonies with low within-nest relatedness to be stable.

As a result of the population bottleneck, the variation in sex alleles has decreased, and the proportion of diploid males in (polygyne) introduced colonies is very high (73-100%, Ross *et al.* 1993). This means that virtually all the males in such a colony are sterile; therefore, it is not a surprise that 80-100% of mated *polygyne* queens (in the introduced area) are inseminated by males originating from *monogyne* colonies (Ross and Shoemaker 1993) –a fact that inhibits differential speciation of the two social forms. Diploid male production imposes a large fitness penalty; therefore strong selection of variation in sex alleles may be expected. Indeed, diploid male production is very low in native (polygyne) populations (Ross *et al.* 1993), but *S. invicta* has not been introduced long ago (~ 60 years). It may be expected that, with time, diploid male

production will decrease, through selection of variation of sex alleles (This would even be facilitated by following repeated introductions of new *S. invicta* individuals from South America –which is not unlikely to occur). So with time, the species naturally will evolve to produce more efficient (polygynous) colonies (Diploid male production in monogynous colonies is practically absent, due to the fact that newly founding diploid male producing queens have a very low probability of surviving: The diploid male production seriously depletes the worker production). But during this period, native ant species may counteradapt to the introduced fire ant, towards a more balanced ecosystem –such a process appears to have occurred in the Caribbean after invasions of *S. geminata* ~200–500 years ago (Wilson 1971).

The occurrence of the two social forms is likely to make the species very successful. When at first conquering a new range, the monogyne form is the most efficient social form: The dominant mode of colony founding is by independent founding, where queens mate during the nuptial flight and dispersal is very large. In this way, large areas can be infested, and spreading of the species is fast. When environments are suitable, colonies will flourish, and population density will increase. However, monogynous colonies have more aggressive territorial behavior than do polygynous colonies, so a threshold of population density is reached. Moreover, because of the increased population density, independent founding success will have decreased. The way to even increase the population density more, when food is not limiting, is switching to polygynous colonies. Their dominant mode of establishing new colonies is by dependent founding; queens accompanied by the assistance of workers are now more likely to successfully establish a new colony, compared to independently founding queens. Moreover, queens that have mated during the nuptial flight might try to enter an already established nest, instead of founding a new nest independently.

Porter & Savignano (1990) reported that the USA's native fire ant *Solenopsis geminata* was totally replaced by the exotic fire ant *Solenopsis invicta*, that reaches much higher population densities. In the paper, it was shown that not only the overall ant community was affected, but also other surface-active arthropods, especially members of the Isopoda.

Invasions can affect host communities via competition, predation, parasitism and/or disease (Diamond and Case 1986). The most probable mechanism accounting for the replacement of N.-America's native fire ant is competitive replacement. The fast invasion into North America strongly suggests that physical factors are not limiting. Disturbed habitats (associated with human activity) are preferred by red imported fire ants (Tschinkel 1988); they appear to colonize new, disturbed areas in a more effective way, outcompeting native ants and other native arthropods. As a consequence, natural habitats occupied by native fire ants more likely will be invaded by the red imported fire ant, when human activity is involved: Chances are high that red imported fire ants show up in areas populated by the human species.

Predation is another possibility, but fire ants rarely kill and eat other ants except occasionally when attacking nests or founding queens, situations that are considered

aggressive interference. Pathogens and parasites are unlikely mediators because of their host specificity and paucity in North American fire ant populations. The diet of the two fire ant species are similar (Tennant and Porter *unpubl.*), yet imported fire ant workers discovered and recruited artificially provided baits much more quickly than other species, both on the ground and in the vegetation (Porter & Savignano 1990). Nesting requirements are similar for native and introduced fire ants (Tschinkel 1988); consequently, huge numbers of *S. invicta* almost certainly usurp vital resources.

Additionally, *S. invicta* workers are 30% smaller than native ants, which may allow more individuals to be supported on the same energy base. However, this difference in size would only account for a small percentage of the difference in abundance, especially considering that smaller ants have slightly higher metabolic requirements.

Ecological release is another possibility for explaining the high population densities of *S. invicta* in North America. In the United States *S. invicta* have very few pathogens (Jouvenaz *et al.* 1977) and parasites (Wojcik 1983). The absence of these natural control factors in the United States may have allowed *S. invicta* to outcompete the native ant fauna.

Other invasive ant species

Other species of polygyne ants also have severe impacts on their host communities (Hölldobler and Wilson 1977). The polygyne Argentine ant *Iridomyrmex humilis* has invaded California. When they occupied riparian habitats in north-central California, species richness decreased more than half (Ward 1987). In southern California Argentine ants totally replaced three native ants (Erickson 1971). Clark *et al.* reported that in the Galápagos Islands, polygyne colonies of the little red fire ant *Wasmannia auropunctata* seriously inhibited other ant species. In Australia, the occurrence of *Pheidole megacephala* at rehabilitated mine sites was correlated with a 50-80% drop in ant species richness (Majer 1985). The polygyne ant *Paratrechina fulva* can reach densities of >16000 nests/ha in Colombia (Zenner-Polanía 1990). In such amounts, *P. fulva* eliminates almost all other ants and apparently causes substantial problems with livestock and wildlife.

3.2 Conclusions

1. The success of the fire ant *Solenopsis invicta* may be due to the capability of modifying its social organization. (i) In the United States, colony queen numbers are much higher than in S.-America, (ii) Population densities are much higher, despite the increase in diploid male production and (iii) Polygyne colonies remain stable, despite the low relatedness among colony members, compared to native polygyne colonies.
2. Additionally, ecological release may have facilitated the fast invasion of this ant species. (i) In the United States, *S. invicta* have very few pathogens and (ii) parasites do not seriously affect *S. invicta*.
3. *Solenopsis invicta* prefers disturbed habitats –associated with human activity; the disturbed habitats may be easier to invade. This is associated with some consequences: (i) Red imported fire ants will appear in areas associated with human activity. (ii) With the invasion of *S. invicta*, native ant populations will be inhibited (or even replaced). (iii) Additionally, also other surface-active arthropods are likely to be inhibited.
4. The ecosystem with the introduced fire ant *Solenopsis invicta* should not be considered evolutionary stable yet. (i) Expected strong selection on variation of the sex alleles could lead to even more successful *S. invicta* (by decreasing diploid male production). (ii) On the other hand, other ant species may counteradapt to this ant species. (iii) Parasites may change their host specificity to the new introduced ant species.

3.3 Further research

For science, the introduction of *Solenopsis invicta* in the USA is of particular interest. Social evolution can be followed very closely. Because of the relatively short time of introduction, the ecosystem with the introduced fire ant *Solenopsis invicta* should not be considered stable yet; other ant species may evolve mechanisms to 'strike back'. Parasites may change host specificity, and start predating the introduced ant species. Further research may be directed towards the identification of differences between *Solenopsis geminata* and *Solenopsis invicta*. Also, why the black imported fire ant, *Solenopsis richteri*, did not invade the USA so dramatically, even though it arrived before the red imported fire ant *Solenopsis invicta* (*S. richteri* 1918; *S. invicta* 1930s).

Of economic importance, possible introduction of natural competitors/enemies of *S. invicta* could be investigated. The research towards (biological) predation of RIFA by phorid flies deserves support. Also, research for trapping devices using natural pheromones must be supported. It is my strong opinion that insecticides against such ants must be avoided.

Recommended sites on the WWW

- | | |
|---|---|
| – http://www.myrmecology.org/ | (Ants in general) |
| – http://www.uaex.edu/natural/fireant/firehome.htm | (Arkansas University
RIFA websites) |
| – http://ipmworld.umn.edu/chapters/lockley.htm | (Minnesota University
RIFA websites) |
| – http://fireant.tamu.edu/index.html | (Texas University
RIFA websites) |

Recently published:

- Gotelli N.J. and Arnett A.E. (2000) Biogeographic effects of red fire ant invasion. *Ecology Letters* 3: 257–261.
- *Fire Ants* by Stephen W. Taber, Texas A&M University Press; ISBN 0890969450.

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4. Glossary

Alate: Winged.

Altruism: Behavior performed for the benefit of others.

Bottleneck: Event where a few individuals become (geographically) separated from the mother population, establishing a new population. Only part of the complete genetic variation of the mother population is transferred to the new population.

Brood: The immature members of a colony collectively, including eggs, larvae, and pupae.

Budding: Colony multiplication by the departure of workers from the nest, accompanied by one or more queens (*budding=fissioning*).

Caste: Group of individuals that is specialized to perform a set of closely linked behavioral acts, performing specialized labor in a colony.

Colony: Group of individuals, other than a single mated pair, which constructs nests or rears offspring in a cooperative manner.

Dependent founding: Queens establish a new nest without worker assistance.

Eusocial: Degree of sociality defined by the common possession of the following three traits: Cooperation in caring for the young; reproductive division of labor, with more or less sterile individuals working on behalf of individuals engaged in reproduction; and overlap of at least two generations of life stage capable of contributing to colony labor. (More informal expressions used are "truly social" or "higher social").

Fissioning: see *budding*.

Haplometrism: Founding of a new colony by a single queen (see also *pleometrism*).

Hemimetabolous: Undergoing development that is gradual and lacks a sharp separation into larval, pupal and adult stages. Termites, for example, are hemimetabolous (see also *holometabolous*)

Holometabolous: Undergoing a complete metamorphosis during development, with distinct larval, pupal and adult stages. The Hymenoptera, for example, are holometabolous (see also *hemimetabolous*)

Inclusive fitness: The sum of an individual's own fitness plus all the individual's influence on the fitness of relatives other than direct descendents, hence the total effect of individual selection and kin selection.

Independent founding: Queens establish a new nest with the help of workers.

Instar: Any period between molts (shedding) during the course of development.

Kin selection: The selection of genes of one or more individuals' favoring or disfavoring the survival and reproduction of relatives who possess the same genes by common descent.

Monogyny: Colony headed by a single queen (see also *polygyny*).

Myrmecology: The study of ants.

Nuptial flight: The mating flight of the winged queens and males.

Pgm-3: Electrophoretic marker; this gene plays a key role in the maturation of polygyne queens.

Pleometrism: Founding of a new colony by multiple queens (see also *haplometrism*).

Polyethism: Division of labor among members of a colony. A distinction can be made between caste polyethism, in which morphological castes are specialized to serve different functions, and age polyethism, in which the same individual passes through different forms of specialization, as it grows older.

Polygyny: Colony headed by multiple queens (see also *monogyny*).

Polymorphism: The coexistence of two or more functionally different castes within the same sex.

RIFA: Red imported fire ant.

Society: A group of individuals belonging to the same species and organized in a cooperative manner.

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**6. Queen Invicta
(Fire Ant Invincible)**

Lyrics by Bill Oliver

She stepped off of the boat in Mobile,
Alabama
Sometime back in the thirties from her home
in deep Brazil
She had six legs and a stinger, fire in her eyes
And the ability to recreate herself a billion
times

She didn't plan to come here, to become
chaotic
Imported and exotic, she came against her will
She stalked the Southern states, from Florida
to Texas
Gained a reputation as the Queen Ant of the
Hill

And they call her Queen Invicta
Fire Ant Invincible
Nothing here could stop her
Predator or chemical

The horror stories then grew, like nutria and
kudzu
Nobody knew what to do, to stop the fiery tide
And they sprayed the land with chlordane
They sprayed the land with Heptachlor
They sprayed the land with Mirex, but the ant
refused to die

Puzzled entomologists, chemists and biologists
Bureaucrat apologists still wondered what to
do

For climbing up the food chain, came
Heptachlor and chlordane
The fire ants would remain, the chemicals
would, too

Refrain

Pesticides persistent, created ants resistant
Eliminated natural foes, going about their
business
The cure employed to hit them became worse
than the symptom
The efforts to eradicate threatened the whole
system

So they banned the searing spray, and they
banned the deadly dust
Before they bring the Silent Spring springing up
on us
This much we can say, the ant is here to stay
The final bill of over-kill is much too high to
pay

Refrain

You who live in cities, cultivated neighborhoods
Fire ants, it's understood, may come and take
their stand
The males that die in nuptials, the queens that
come in multiples,
The fire ant, combustible, is hard to understand

In backyards it's no picnic,
but think before you panic
This isn't the Titanic: don't give up the land

The poison preparations, blind exterminations
Research the implications, analyze your goal
Reactions based on bedlam may only serve to
spread them
To some extent accept them, search for safe
control

They call her Queen Invicta
Fire Ant Invincible
In our quest to stop her
Let us first be sensible

Audiotape available from

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