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The Reproductive Biology of Fire Ant Societies

Fire ant females have many and varied reproductive options

Walter R. Tschinkel

The fire ants are a group of about twenty New World species belonging to the genus and subgenus *Solenopsis* (Trager 1991). Two species, *Solenopsis richteri* and *Solenopsis invicta*, were accidentally introduced into the United States through Mobile, Alabama. *S. richteri* arrived around 1918, and *S. invicta* arrived around 1935–1940 (Lennartz 1973). *S. invicta*, aided largely by transport in nursery products, has spread throughout the southeastern United States, where it has stirred up a great deal of political controversy. Subjected to two failed eradication programs, it receives, on a daily basis, the hatred and ill wishes of millions of southerners, who spend millions of dollars annually on pesticides for fire ant control. Its actual impact ranges from harmful to beneficial (Lofgren 1986, Porter and Savignano 1990). The story of the fire ant invasion has been told in the popular press many times, with varying degrees of sensationalism, and it has even inspired a potboiler novel (*The Fire Ants*; Wernick 1967).

Could an animal so widely hated have repaid us with anything positive? For myrmecology, the answer is an unequivocal yes! Since the late 1960s, the combination of the high political profile of fire ants, their great abundance, and a need for

The fire ant is richly compensating us for the aggravation it continues to cause

knowledge about them has intersected with a flowering interest in ant biology in general to produce a large body of fire ant research that addresses important evolutionary, ecological, behavioral, and physiological questions. As an experimental social insect, the fire ant is a dream. It is easy to collect in the southeastern United States and to maintain in the laboratory, and its colonies can be fragmented, orphaned, re-queened, and manipulated, allowing powerful, generously replicated experiments. It is fairly unspecialized in its biology, so that research findings have broad applicability to other ant species. Among the discoveries of this research is the unexpected complexity of the fire ant's reproductive biology, and it is this subject that I will review in this article.

A thumbnail sketch of *S. invicta*

Several species of *Solenopsis* occur in two greatly different social forms, one with a single functional queen in each colony (monogynous), the other with multiple queens (polygynous; Ross et al. 1988, 1996a, 1996b). Polygyny

arises when, for reasons unknown, workers change from not tolerating to accepting more than one fecund queen. Among the best studied examples of dual social forms is the exotic *S. invicta*, which has polygynous and monogynous populations in both the United States and its native Argentina (Ross et al. 1996b). Both social forms have also been reported for native populations of *S. geminata*, *S. xyloni*, *S. quinquecuspis*, and *S. richteri*, and for the hybrid between the introduced *S. richteri* and *S. invicta* (see MacKay et al. 1990 for references). Polygynous populations always occur as enclaves within monogynous populations. In *S. invicta*, the two forms are genetically indistinguishable (with a small but important exception discussed below; Ross and Fletcher 1985), and it seems likely that the polygynous form has arisen repeatedly from the monogynous form after the ant's arrival in the United States, leading to the observed mosaic of stable enclaves.

Monogynous colonies of all studied species of *Solenopsis* are simple families that consist of the daughters of a single mother (the queen) mated with a single father. Relatedness among these daughters, the workers, is 0.75 (Ross and Fletcher 1985, Ross et al. 1988), as expected for haplodiploid sex determination and a single mating. (Among ants, wasps, and bees, unfertilized eggs develop into haploid males, and fertilized eggs become diploid females. As a result, sisters are more closely related to one another than they are in animals in which both sexes are diploid.)

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Perhaps as a result of this high relatedness, the workers of all *Solenopsis* species are completely sterile, lacking ovaries entirely, and are thus unable to reproduce directly (Hölldobler and Wilson 1990). Their reproductive success comes entirely through helping close relatives, especially their sisters, reproduce by altruistically providing the labor for rearing their own younger sisters and brothers (the indirect component of inclusive fitness; Hamilton 1964, Hölldobler and Wilson 1990).

Some of these sisters and all of the brothers will become winged ants capable of sexual reproduction (called alates), whose function is to initiate new colonies. As in all ants, males play no social role other than colony reproduction. Mature colonies of *S. invicta* contain about 220,000 workers in the nest (other species differ in colony size; Markin et al. 1973, Tschinkel 1988, 1993a); these workers build a conspicuous chambered mound on top of a cone-shaped zone of subterranean chambers (Figure 1a and 1b). At certain times of the year, nests also contain alates destined to participate in colony reproduction through mating and dispersal flights (Figure 1c–1e). Workers of monogyne colonies defend a foraging territory that they scour for food to distribute among their nestmates (Tschinkel et al. 1995). They readily recognize non-nestmate intruders and attack and kill them (Vander Meer et al. 1990). Exchange of workers among nests is thus probably rare.

S. invicta is a “weedy” species whose success (at least during most of its evolutionary history) depended on finding suitable ecological disturbances that are rare and unpredictable in time and space. As with most weeds, this requirement has selected for high investment in reproduction, along with effective dispersal of the “propagules” (the alates), like dandelion seeds.

The multiple queens in polygyne colonies in the United States are unrelated to one another, and these colonies are more like groups of cooperating but unrelated families residing in a common nest. Within-family relatedness is still 0.75 because each queen is singly mated (Ross 1993), but neither interfamily con-

flict nor recognition of family members seems to occur. As a result, workers rear alate reproductives to whom they are not related, suggesting that the benefits of polygyny must derive from mutualism or perhaps group selection, but not from reproduction by close relatives (Ross and Fletcher 1985). This lack of relatedness in polygyne colonies in the United States could, however, be a consequence of the loss of genetic variation associated with the ant’s introduction because in *S. invicta*’s native Argentina, polygyne colonies consist of related queens (Ross et al. 1996b), so that workers are related to the reproductive alates they rear.

For all *Solenopsis* species, comparison of polygyne and monogyne societies shows that the presence of multiple queens causes a cascade of differences in social organization, morphology, reproductive biology, and ecology. In polygyne societies, mating probably occurs near the natal nest, and some alates do not disperse far before seeking readoption into a nest (Christopher J. DeHeer, University of Georgia, 1997, personal communication). Unlike workers in monogyne colonies, polygyne *S. invicta* workers show little aggression toward non-nestmate workers (Vander Meer et al. 1990) and do not defend territories. Exchange of workers and brood among polygyne nests is common (Bhatkar and Vinson 1987). Without the density-limiting effect of territorial defense and perhaps other limits, the density of both nest mounds and workers can be two- to sixfold higher in polygyne than monogyne populations, and the effects of these exotic ants on the native biota are correspondingly greater (Porter et al. 1988, Porter and Savignano 1990).

In the discussion that follows, I illustrate the many and complex reproductive options open to a diploid fertilized egg destined to become a female (Figure 2). These options are shaped decisively by whether that egg hatches in a monogyne or a polygyne colony and by the conditions under which it is reared (as in all social hymenoptera, the differences between sterile workers and sexual alates result from differences in how much and what they are fed during larval development, not from

genetic differences, but this subject is beyond the scope of this article).

Reproduction in the monogyne form

In the monogyne form, colony reproduction proceeds in the familiar ant manner—mating flights followed by colony founding and subsequent colony growth. Research on fire ants has brought to light many interesting complexities of this process.

Mating. Like the majority of ant species, monogyne *S. invicta* colonies reproduce by emitting winged male and female alates during nuptial flights (Figure 1d and 1e; Markin et al. 1971, Morrill 1974). Alate production and flight occur primarily during the spring and early summer. After molting into adults, female alates triple their weight, but male alates gain little (Tschinkel 1993a). Mating flights take place midday in warm, sweaty weather after a heavy rainfall on the previous day (Morrill 1974). Workers open large holes in the nest mound and swarm in large numbers on the mound’s surface, probably alarmed by a pheromone produced by the alates in their mandibular glands (Alonso and Vander Meer in press). Alates take flight and mate on the wing 100–300 m above ground level, where males form large sheet swarms over open areas (Markin et al. 1971). Females fly into this swarm, are mated, and return to the ground approximately 20–30 minutes later (Milio et al. 1988). How males and females find each other up in the heavens is entirely unknown.

Remarkably, more than 95% of the female alates from monogyne colonies mate successfully (Markin et al. 1971), storing the sperm from this single mating in the female’s spermatheca. This stored sperm constitutes the lifetime sperm supply on which the queen draws. In *S. invicta*, this supply averages approximately 7 million sperm (Glancey and Lofgren 1985, Tschinkel 1987), whereas in *S. geminata*, it averages approximately 5 million sperm. Genetic analysis of mature monogyne colonies of *S. invicta*, *S. geminata*, *S. richteri*, and the *S. richteri* × *S. invicta* hybrid indicate unequivocally that



Figure 1. Aspects of the fire ant life cycle. (a) A fire ant mound in a pasture reflects the size of the colony that built it. The chambers in the mound collect solar heat and are used as living space. (b) A plaster cast of the subterranean chambers underneath the mound. The nest is composed of vertical tunnels and horizontal chambers, packed closely side by side. Nests may be up to 1.5–2 m deep. (c) Worker fire ants tending brood. Workers provide all the labor required to rear an egg to an adult ant. (d) A male alate about to take off on a nuptial flight. Both males and females mate singly, and males die after mating. (e) A female alate from a monogyne colony about to take off on a nuptial flight. Having mated, she will found a new colony. (f) A colony-founding queen at the end of the founding period. She produced all the minim workers and brood from metabolic reserves in her body without feeding, expending 65% of her energy content in the process.

each successfully mated queen mates with only one male (Ross et al. 1988).

Colony founding by solo queens. Well-replicated studies have produced a more complete account of colony founding in fire ants than in any other ant species. In the majority of ants, newly mated queens found new colonies independently, without the help of workers, by drawing on body reserves (Keller and Passera 1989) to produce the first workers. Queens probably choose their approximate founding site while still airborne. Little is known about the criteria they apply in making their choices, but they usually choose partially vegetated, recently disturbed areas.

After landing, the queen breaks

off her wings, explores on foot, and usually digs her simple founding nest no more than 2 m from the landing site (Walter Tschinkel, unpublished data). She seals herself into this nest and lays 50–90 eggs over a week or so (Markin et al. 1972, Tschinkel 1993b). Approximately half of these eggs are unembryonated eggs (Voss and Blum 1987, Tschinkel 1993b) that are fed, along with glandular secretions, to the larvae that hatch from the embryonated eggs (Toom et al. 1976). The queen loses over half of her weight and 65% of her energy content in this process (Tschinkel 1993b). The first group of workers is the fastest developing and most diminutive in the life cycle of the colony; these workers are called

minims or nanitics (Figure 1f). Within days, these workers open the nest to the exterior and end the founding period by beginning to forage for food.

Cooperative colony founding. After the mating flight, if the density of newly mated queens (from monogyne colonies) is high, queens are likely to band together in small social groups that cooperate in rearing the first brood (Tschinkel and Howard 1983, Markin et al. 1972). How such a system could have evolved is an evolutionary puzzle because if the group succeeds, all but one of the queens will be killed by fighting among themselves or will be executed by workers. Why should a queen choose to

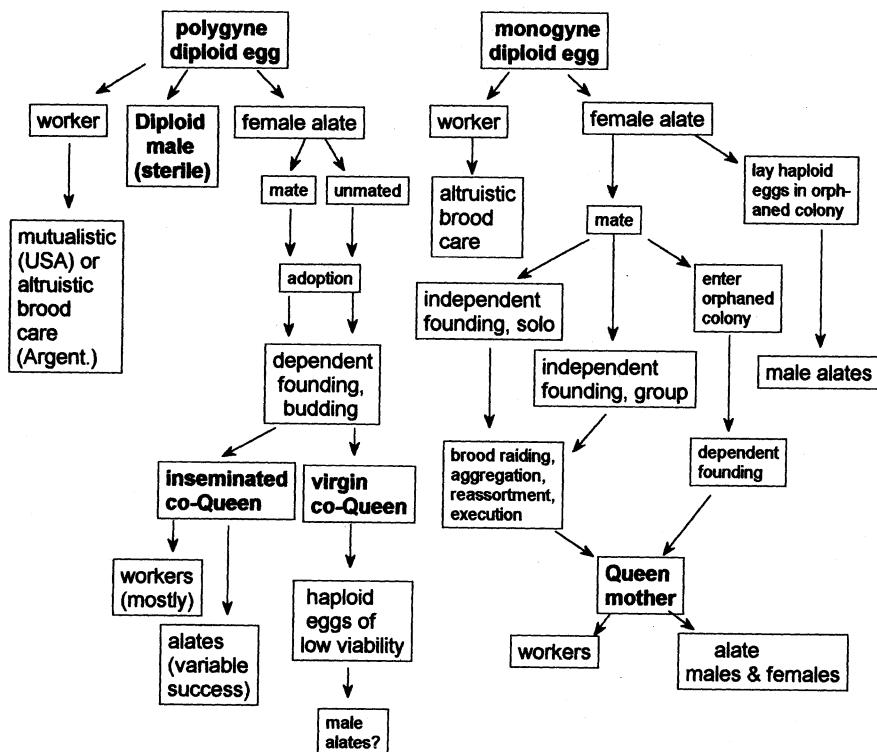


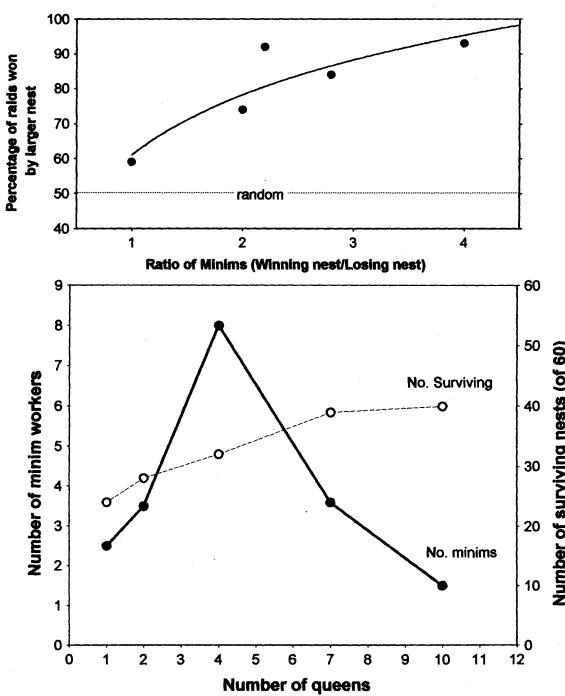
Figure 2. Overview of the routes of reproduction in fire ant colonies, starting with a diploid egg in a polygynous colony and a monogynous colony. See text for details.

join other queens when her chances of dying increase with the number of queens in the group?

Compared to solo founding, a number of benefits of cooperative founding have been identified, although no single benefit has been shown to counterbalance the added risk of joining (i.e., execution). The bal-

ance sheet is still incomplete, but it will probably show that a combination of factors led to the evolution of cooperative founding. Colony founding in the monogynous form is a remarkably dynamic and complex process that involves not only cooperation, but also intense competition.

Figure 3. Queens who join others to found a colony cooperatively gain certain advantages over those who attempt to found colonies alone. The advantage in winning brood raids is with the nest having the greatest number of minims (top). Groups of four queens produce the most minim workers (bottom, solid line). As the number of queens increases, the nest is more likely to survive the founding period (bottom, dashed line). Data for top panel from Tschinkel (1992); for bottom panel, from field experiment in Tschinkel (1993b).



tion. There are several benefits of joining a group (Figure 3; Tschinkel and Howard 1983, Tschinkel 1993b). First, founding groups enjoy higher survival of the founding period than do queens founding alone, and groups of queens are also more likely to survive attack by workers in the field (Jerome et al. 1997, Christopher Jerome and Eldridge Adams, University of Rochester, personal communication). Second, these groups produce more minim workers, with maximum production in groups of four to seven queens, a fact that is important to what follows as colony founding proceeds. Third, post-incipient colony growth is exponential, so that cooperatively founded colonies maintain their relative size advantage over solo ones for at least 100 days (Tschinkel and Howard 1983). In the laboratory, such colonies reach maturity earlier, a clear fitness benefit (Vargo 1988).

The next phase of colony founding demonstrates why maximizing worker production is important and why queens found cooperatively. Soon after they appear, the new minim workers enter the nests of neighboring incipient colonies, where they encounter little aggression and initiate a reciprocal brood-stealing contest ("brood raiding"; Figure 4). Brood is carried back and forth between the contending colonies until one colony wins (Stamps and Vinson 1991). How victory is decided is unknown. The winner of a brood raid is usually the nest with the most workers; thus, cooperatively founded nests are favored. In laboratory and field experiments, multiple-queen colonies have a competitive advantage over single-queen colonies, and workers from the losing nest usually join the winning nest (Figure 3; Tschinkel 1992, Adams and Tschinkel 1995). The victorious nest in turn becomes larger and thus more successful in raiding, and through a sort of self-catalysis, raids may occasionally last weeks and include several dozen nests (Tschinkel 1992).

Losing workers appear to abandon their own mothers when they move to the victorious nest. However, many of these abandoned queens leave their empty nests, follow the raiding trails, and attempt to enter surviving nests (Tschinkel

1992, Adams and Tschinkel 1995). If their own workers (these are not necessarily relatives) are present in the nest, these queens are more likely to be admitted and to displace competing queens (Adams and Tschinkel 1995, Balas and Adams 1996, 1997). Consequently, even after a nest loses a brood raid, the number of workers in the initial brood is probably still important to the eventual success of its queen(s).

Surviving incipient nests regularly have more than one queen, either from the original founding association or from losing queens who entered after a raid. There now ensues a struggle for survival, whose rules have only recently begun to yield to experimentation (Balas and Adams 1996, Bernasconi and Keller 1997). All but one queen is killed, either by fighting with other queens or through execution by the workers, but neither kinship nor worker production determines who survives. In experimental colonies in which all workers were the daughters of one of the two queens, the mother of these workers was no more likely to survive than the nonmother. Queens appear to struggle among themselves for possession of the colony's brood pile, with the heaviest queen most likely to predominate and survive. The queens that are unable to stay on the brood pile are often injured and are then executed by the workers, probably on the basis of their physiological attributes (Balas and Adams 1996).

In the field, mortality of founding nests during the founding period is approximately 80%, and this mortality is further increased by the complex competition among incipient nests. In one case, for example, these processes winnowed the 10,000–20,000 newly mated queens who attempted to found a colony on a 1200 m² plot of unoccupied habitat down to fewer than a dozen mature colonies at the end of four years (Tschinkel 1992).

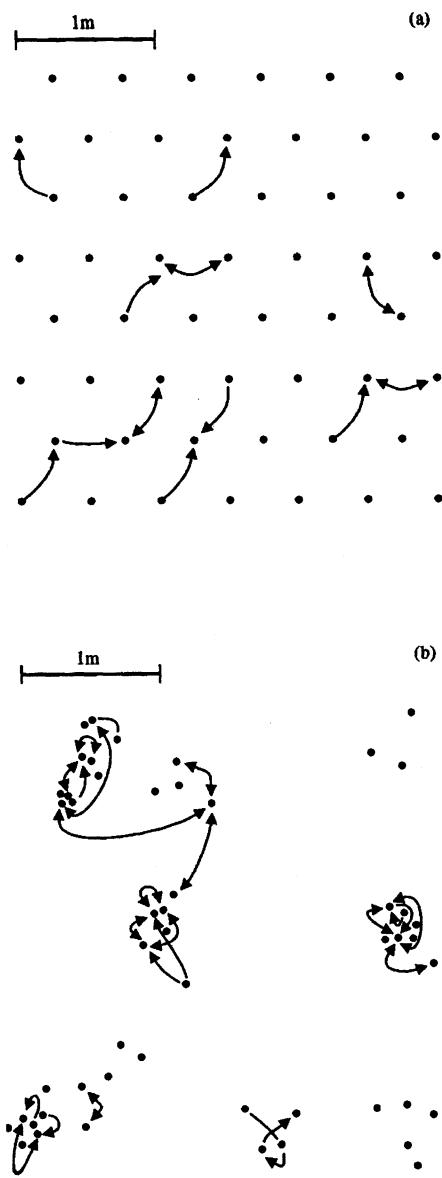
Growth of monogyne colonies. After the incipient phase, colony growth is similar whether the colony was founded by single or multiple queens, except that the colonies resulting from brood raids may begin growth with thousands of minim workers

Figure 4. Brood raiding patterns among experimentally planted incipient nests in the field. Location of nests within the site was either uniform (a) or clumped (b). The closer nests were to each other, the more likely they were to raid one another's brood (Adams and Tschinkel 1995).

and thus reach reproductive size earlier (Vargo 1988); that is, they enjoy a decrease in generation time. As colony growth begins, colonies become territorial and worker brood is produced at a high rate. In young populations, growth is, on average, logistic, with midwinter size leveling off at approximately 220,000 nest workers after four to five years (Tschinkel 1988a, 1993a, Williams et al. 1990). When the colony reaches approximately 10% of its maximum size, it changes from producing workers only to producing both workers and alate reproductives (Vargo 1988, Tschinkel 1993a). The proportion of its energy invested in alates remains constant at approximately 30% for the remaining 90% of colony growth (Tschinkel 1993a). Therefore, colonies produce more alates by becoming larger.

Social regulation of queen fecundity. Colonies grow by rearing new workers, which develop from diploid (i.e., fertilized) eggs. In monogyne fire ants, all eggs are laid by a single queen, whose egg-laying rate must be adjusted to the size of the labor force available for rearing the eggs (i.e., young nurse workers). But the queen is in contact with only a few workers at a time, and she never "sees" the colony in its entirety. How can a colony estimate the size of a subpopulation that is spread throughout up to 70 liters of nest structure and regulate the queen's egg-laying rate to the appropriate level?

The answer is both surprising and, in hindsight, logical. The queen's egg-laying rate can be manipulated experimentally by varying the number of fourth-instar (last molt stage) larvae, whereas varying the number of adult workers has no effect (Tschinkel 1988b). When fourth-instar larvae are removed from large colonies, the queen's egg-laying rate plummets, her weight drops 50–70%, and her ovarian function decreases by up to 90%. When the larvae are added back, the egg-laying rate



climbs once again. Each tenfold increase in the number of larvae results in a doubling of the rate of egg production. Obviously, the more larvae that are already present, the less each additional larva will affect the queen's egg-laying rate, so that eventually, perceptible increases in the egg-laying rate require impossibly large numbers of larvae.

The effect of fourth-instar larvae is exerted primarily by those larvae who have begun metamorphosis (Tschinkel 1995). Workers who tend these metabolizing larvae (but not those tending other larvae) collect some substance from them, probably a liquid from the anal end, and shuttle this material to the queen

Figure 5. An egg-laying queen from a monogyne colony, surrounded by the retinue of workers who feed and groom her. Such a queen lays approximately 50–200 eggs per hour. Her ovaries make up approximately 75% of her weight. "Shuttle workers" collect ovary-stimulating material from metamorphosing larvae, join the retinue, and offer this material to the queen.

(Figure 5), whose ovarian function it stimulates (Figure 6). Because shuttle workers may also share this material with other workers, the effectiveness per larva declines with colony size, as observed.

How does this system determine labor availability and adjust the queen's egg-laying rate accordingly? The time elapsing between the beginning of metamorphosis and the emergence of a young worker (approximately six days) is about the same as that between the laying of an egg and its hatching. By tying the queen's fertility to a "census" of the metamorphosing larvae, the colony has, in effect, predicted the labor force that is soon to become available for brood care (Tschinkel 1988b).

The extent to which this control mechanism also applies to polygyne



colonies is unknown. Vargo and Ross (1989) reported that brood also stimulates oviposition in polygyne queens, as it does in monogyne ones, but the quantitative relationship is not known. It seems possible that the variation in fecundity among polygyne queens (see below) is partly the outcome of competition for the fecundity-stimulating material produced by metamorphosing larvae and distributed by workers. Because the ratio of larvae to workers is so much higher in polygyne colonies than in monogyne colonies, one might expect that there is more fecundity-stimulating "stuff" to go around, and the total fecundity of polygyne

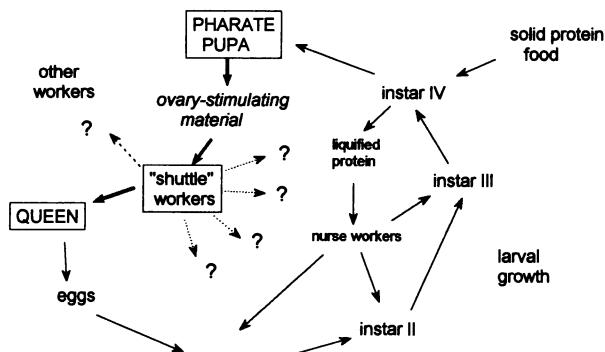
colonies would be higher than that of monogyne colonies, as observed.

Dependent founding in monogyne colonies. Newly mated queens who land in territories of mature colonies are killed on discovery, so that the chances of successful founding in occupied habitat are very low (Tschinkel 1996). This situation (habitat saturation) increases the success rate of an alternate reproductive strategy, dependent colony founding, in which unrelated workers protect and aid newly mated queens during founding. The alates who participate in dependent founding overwinter in the nest and fly on mating flights on the very first warm days of spring (Fletcher and Blum 1983). These alates lack both the behaviors and the metabolic reserves to found their own colonies independently. Instead, they randomly seek out mature fire ant nest mounds and attempt to gain entry. Most are killed by the workers, but if the colony happens to be orphaned, the chance of gaining entry is substantial (Tschinkel 1996). Once accepted, the queen exploits the host colony's labor to rear her own offspring so that the colony gradually comes to consist of her own daughters.

Orphaned colonies are not entirely defenseless against this social parasitism. If the orphaned colony contains female alates, these break off their wings, begin to lay unfertilized eggs, and become queenlike (Fletcher and Blum 1983), causing workers to execute any unrelated alates that attempt entry. Such colonies rear large, all-male broods, giving the colony a last shot at reproductive success through their participation in mating flights. These males could be the progeny of the unmated queens, or they could be reared from eggs present in the nest at the time of orphaning, or both. In all cases, the males would be related to the workers. The entry of an unrelated queen who exploits the host workers to rear her own offspring robs the colony of this last chance, and it is this loss of fitness that identifies this alternate strategy as social parasitism (Tschinkel 1996).

The relative success of independent and dependent colony founding depends on the relative amount of

Figure 6. The social regulation of egg-laying rate in queens in monogyne fire ant colonies. Metamorphosing larvae produce an ovary-stimulating substance that is collected by a special group of workers ("shuttle workers") who offer it to the queen, stimulating oviposition. The eggs are cared for by the young nurse workers that developed from the metamorphosing larvae, growing into metamorphosing larvae in turn and creating a positive feedback loop with the queen's egg laying.



occupied and unoccupied habitat (Tschinkel 1996). When the population is expanding, independent founding (either solo or cooperative) is more successful than dependent founding, but as the proportion of occupied habitat increases the success rate of this mode declines. Conversely, the dependent, parasitic mode requires populations of mature colonies because it depends on the death of colony queens. As the habitat becomes saturated, investment in the parasitic mode of founding should increase and investment in independent founding (either solo or cooperative) should decrease.

Selection in more saturated populations may have produced the condition seen in the congener *S. geminata*, a much less "weedy" ant than *S. invicta*. Populations of *S. geminata* persist in later succession habitat, are more stable, and are not as strongly associated with ecological disturbance as *S. invicta*. Selection for the dependent mode of founding has proceeded so far in this species that not only does it invest 30% of its reproductive output in low-reserve, dependently founding queens (compared to less than 10% in *S. invicta*), but also these queens have smaller bodies, allowing colonies to produce more of them without increasing the cost (Figure 7; McInnes and Tschinkel 1995). Roughly one-third of mature *S. geminata* colonies are headed by a small (dependently founding) queen. In contrast, only approximately 3.5% of *S. invicta* colonies are headed by a dependently founding queen (DeHeer and Tschinkel 1997).

Pheromonal regulation of dealation. In light of the capacity of alates to dealate and begin laying eggs in the absence of the queen, what prevents them from doing so in a nest with a queen? Fletcher and Blum (1983, Vargo 1997) first described a primer pheromone produced by egg-laying queens that prevents virgin female alates from becoming reproductively active within the nest. (Primer pheromones are chemical messengers that

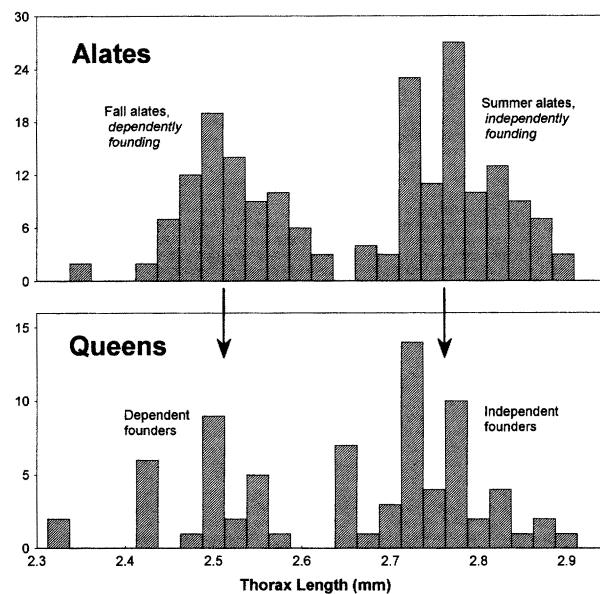


Figure 7. Colonies of *Solenopsis geminata* are headed either by a large (measured as thorax length), independently founding queen or by a small, dependently founding queen who entered the mature colony. The balance of investment in these alternate modes of colony founding probably represents an evolutionarily stable strategy. The Y-axis indicates number of colonies. Modified from McInnes and Tschinkel 1995.

have a delayed physiological effect). Loss of the queen causes some of the alates to undergo ovarian development, shed their wings, and begin to lay eggs. As they begin to reproduce, they take on queenlike characteristics, producing pheromone of their own and causing workers gradually to reduce the number of such dealates. Such dealation and reproduction in the home nest by virgin alates is rare in ants. In fire ants, dealation probably evolved in response to social parasitization of orphaned colonies by dependently founding queens.

The inhibitory pheromone that represses dealation is remarkably potent. The more fecund a queen, the more pheromone she produces (Vargo 1997). Thus, both fecundity (Tschinkel 1988b) and inhibitory capacity increase with colony size, allowing queens to maintain inhibitory control over virgin alate females, no matter how large the colony. Within her nest, a single queen weighing 25–30 mg is able to prevent reproduction by up to several thousand virgin alates among up to 250,000 workers spread through several hundred nest chambers located

from the mound to 2 m below ground level.

The pheromone that prevents dealation is part of a complex of primer pheromones (or is the same pheromone) that affects reproduction of both virgin and mated queens and the production of sexual brood (reviewed in Vargo 1997). These pheromones are nonvolatile, require contact with the queen for effectiveness, and are probably spread through the colony by workers. Dead queens and queen extracts have the same effect as live queens. These pheromones act in both monogyne and polygyne colonies and tie together a number of aspects of reproductive biology. Whether these primer pheromones are identical to the attractants found in the poison sac of the queen's sting apparatus (Vander Meer et al. 1980) is unknown.

Investment in reproduction in monogyne colonies. Generally speaking, organisms (or colonies) may reproduce from current income (i.e., by foraging). Alternatively, they may draw on saved capital (metabolic stores) during reproduction, in which case the organism's condition and success during the savings period may affect reproductive success. In *S. invicta*, a strong seasonal variation in colony size is caused by drawing on stored capital (both fat and workers) during production of alates. This variation is superimposed on colony growth (Tschinkel 1988a). Mature colonies lose half of their size between January and July because they reduce worker brood production in order to produce alate males and females (Figure 8). Worker production thus falls below the rate needed to replace those who die, and colony size declines. After midsummer, colonies switch back to producing mostly workers, causing them to gain back the lost size. The production of alates is also accompanied by a loss of worker fat reserves. This annual fluctuation begins when colonies are large enough to produce their first alates (approximately 10%

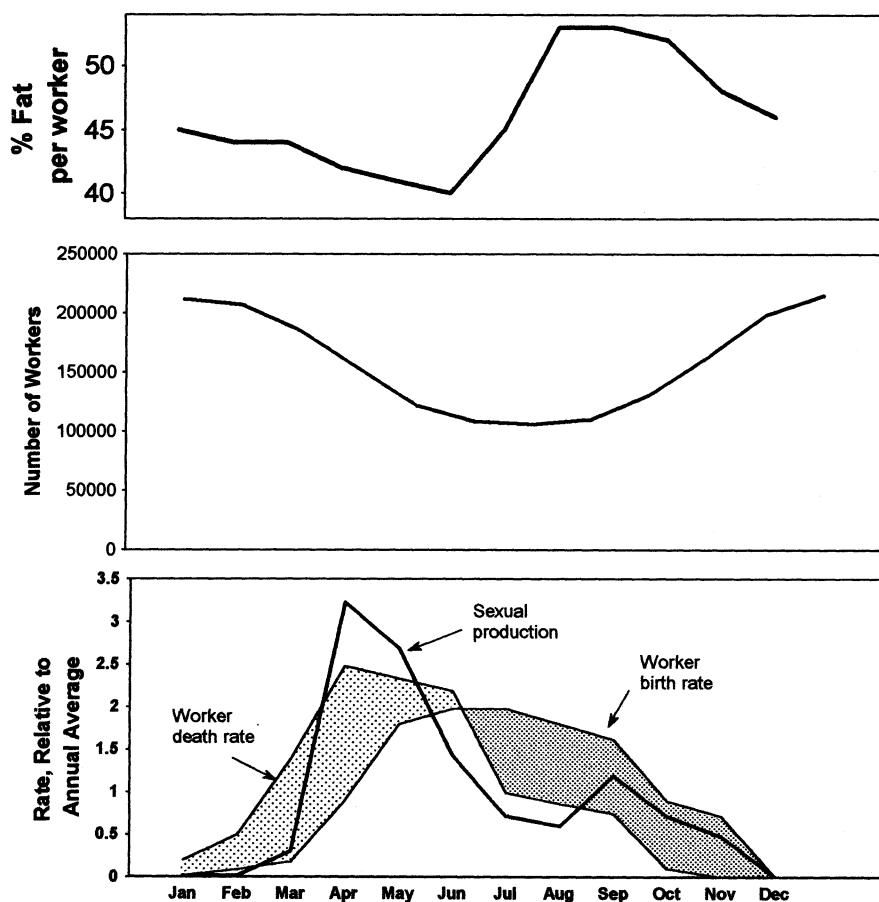


Figure 8. In the spring, mature fire ant colonies produce a large brood of alates, partly from stored "capital" in the form of worker fat (top) and worker bodies (middle and bottom). During alate production, worker production drops below replacement rate (coarse-shaded area in lower panel), and colony size falls (middle). After midsummer, alate production ceases, worker production exceeds the death rate (fine-shaded area in lower panel), and the colony regains its midwinter size and stored fat (redrawn from Tschinkel 1993a).

of their maximal size), and it continues as colonies grow and reach their maximum size (Tschinkel 1988a).

Thus, colonies with more metabolic reserves should produce more alates during the next reproductive period. Indeed, larger colonies produce more alates and decline more in size during their production (Tschinkel 1993a). In this sense, the capital is simply worker number, and the shrinking of colony size reflects the expenditure of this capital.

Little is known about the aging and death of fire ant colonies. Functional queen lifespan is limited by sperm supply because a queen that has run out of sperm cannot produce workers to replace those who have died. Each worker or female alate a queen produces reduces her initial supply of 7 million sperm by a mi-

serly 3 sperm, an astounding efficiency when compared to other animals (Tschinkel and Porter 1988). The sperm decline rate in field colonies of known ages indicates that queens live approximately seven years (Tschinkel 1987). In a repeatedly surveyed population of fire ant colonies, annual colony turnover was roughly 13%, indicating a 7.7-year lifespan (Eldridge Adams and Walter Tschinkel, unpublished data). At least some of the queens who die are replaced by an unrelated, independently founding queen (see above).

The reproductive biology of polygynous colonies

The reproductive biology of polygynous colonies is remarkably complex. Within these societies, queens com-

pete for reproductive success in many and subtle ways.

Suppression of sexual reproduction. Polygynous colonies produce new colonies by colony fission and are unlikely to succeed often at independent colony founding, either alone or in groups, for three reasons.

First, multiple queens suppress alate production in proportion to their numbers, so that many polygynous colonies produce only a few percent as many alates as do monogynous colonies (Figure 9), proportionally reducing the likelihood of successful independent colony founding. In the laboratory, removal of all but one queen causes a dramatic increase in alate production. This inhibitory effect is caused by high levels of a queen pheromone (possibly the same pheromone that prevents dealation in monogynous colonies) that prevents the sexualization of larvae or induces workers to execute male and female alate larvae alike, at least before a critical point in larval development (Vargo and Fletcher 1986, 1987, Vargo 1993).

Second, the mature female alates that polygynous colonies do produce weigh only 10–11 mg and usually have insufficient body reserves for successful independent colony founding (Porter et al. 1988, Keller and Passera 1989, Keller and Ross 1993). Such alates usually cannot rear enough minims to allow colony survival (Porter et al. 1988), although in theory, groups of such alates may occasionally rear enough minims to survive. By contrast, newly mated monogynous queens usually weigh approximately 14–16 mg at the time of flight and rear 10–30 minims workers in their first brood. Polygynous alates weigh less than monogynous alates, mostly because they have only half the fat reserves of monogynous alates (Keller and Ross 1993). This weight difference is not seen in pupae or newly emerged adult alates but arises during the maturation process, a time when female alates in monogynous colonies triple their dry weight but those in polygynous colonies only double in weight (Tschinkel 1993a, Keller and Ross 1993).

Reciprocal transfer experiments have shown that this weight difference is due almost entirely to the

social environment in which alates mature, and not to the type of colony they are from. Whether they came from monogyne or polygyne colonies, alates maturing in monogyne colonies weigh over 13 mg, whereas those maturing in polygyne ones weigh 11–12 mg. Thus, the polygyne and monogyne "syndromes" as expressed in alates are "culturally transmitted" and constrain the reproductive options of the alates in such a way as to perpetuate the social environment in which they were reared. It has been suggested that high levels of queen pheromone not only suppress the production of alate brood but also affect worker behavior to reduce feeding of maturing adult alates. However,

there are some genetic differences between the two social forms (see below), so "cultural transmission" alone cannot account for all the differences.

A third reason that polygyne colonies are unlikely to be produced by independent colony founding is that in the United States, 80% of the males produced by polygyne colonies are diploid and, therefore, sterile. This situation arose as a result of the loss of sex-determining alleles at the time *S. invicta* was introduced (Ross and Fletcher 1986). In hymenoptera, individuals who are hemizygous (haploid) or homozygous at the sex-determining locus (or loci) become males, whereas heterozygotes become females. In Argentina's native populations of *S. invicta*, the very large number of different alleles at these loci make homozygous diploids very rare, but the reduction of the allelic diversity through the recent founder event in the United States has raised the probability of matched matings to approximately 15–20%. Thus, half of the offspring of a queen mating with a male that carries the same sex-determining allele(s) are diploid homozygotes, which develop into large, sterile males. Of course, such diploid male-producing queens occur in both monogyne and polygyne populations with equal frequency. When such a queen attempts to found a colony

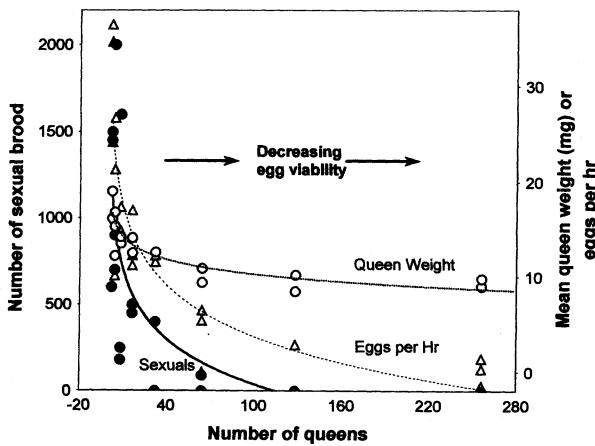


Figure 9. The multiple queens in polygyne colonies suppress the production of alates, eggs laid per queen, queen body weight, and egg viability in proportion to their number. These effects are all dependent on the levels of queen pheromones in the nest. The rate of egg laying was calculated from queen body weight using the linear equation in Vargo and Fletcher (1986). Data from Vargo and Fletcher (1986).

independently, she will invariably fail because much of her reserves are invested in useless sterile males. However, should she become adopted into a polygyne colony, workers cannot tell that she is match-mated and cannot discriminate haploid and diploid male larvae, so she survives and happily churns out large numbers of diploid males, creating a genetic and economic burden on the colony.

The combination of producing very few, and mostly sterile males ensures that female alates from polygyne populations will often be unable to mate. Indeed, approximately 30% of the egg-laying queens in polygyne colonies are uninseminated, possibly because they failed to mate on a nuptial flight. Interestingly, most of the successful matings taking place in the polygyne enclaves are with males flying in from the surrounding monogyne populations (Shoemaker and Ross 1996), creating unidirectional gene flow (see below).

Mating, adoption, growth, and budding. In many ant species that exhibit monogyny and polygyny, alates from monogyne colonies tend to mate and disperse considerable distances, whereas those from polygyne colonies tend to mate on or near the natal nest and do not disperse very far (Bourke and Franks 1995). Alates from polygyne *S. invicta* colonies

may behave the same way (Christopher J. DeHeer, University of Georgia, 1997, personal communication). Because they cannot found colonies independently, probably the only option for newly mated polygyne queens is to be adopted into a polygyne nest, which is what happens. Queens are accepted whether they are related to the adopting colony or not, but only a small fraction survive for long (Porter 1991).

New queens thus probably regularly enter polygyne colonies after mating flights, and even unmated queens are accepted. Here they join the competition for reproduction (see below), mostly laying worker-producing eggs. Together, these queens produce far more eggs than does a

monogyne queen (Vander Meer et al. 1992), causing their colony to grow rapidly. New "colonies" of the polygyne form are subsequently founded by budding off a part of the worker population and some of the queens, who emigrate through underground tunnels to form a new mound some distance away (Vargo and Porter 1989). A single mound may proliferate into as many as eight in just four to five months. Queens do not move freely among nests but are limited to those that were previously connected. As a result, the genetic variation among nestmate workers can be predicted from the queen number (Ross 1993), and there is a strong correlation between queen number and worker size (Goodisman and Ross 1996).

Because polygyne colonies invest so little in alate production, they invest heavily in worker production, resulting in very high colony growth rates (fourfold in six months; Porter 1991). For the same reason, the size of polygyne colonies varies much less seasonally than that of monogyne colonies: The small allocation to alate production results in only minor reduction of worker production (and therefore in continued colony growth; Vargo and Fletcher 1987). Following through the "weedy" analogy suggests that polygyne colonies have carried weediness one step fur-

ther than monogyne colonies by emphasizing "vegetative" rather than sexual reproduction. Because colonies reproduce by budding, variation of size through the life cycle is also much smaller than the five orders of magnitude variation seen in monogyne colonies.

As a consequence of the high rates of egg (Vander Meer et al. 1992) and worker production, ratios of workers to worker larvae are high in polygyne colonies. Consequently, the pupae reared by these workers are distinctly smaller and less variable in size than those in monogyne colonies (Porter and Tschinkel 1985, Vargo 1997). In fact, smaller, less variable workers are one of the ways in which polygyne colonies can be recognized in the field.

Reproductive competition within the nest. An obvious reproductive consequence of polygyny in both *S. invicta* and *S. geminata* (and probably other *Solenopsis* species) is that the more queens there are, the less fecund each queen is, as measured in eggs laid in a five-hour oviposition test (Figure 9; Vargo 1993, 1997, Vargo and Fletcher 1989). Vargo (1997) ascribed this mutual inhibition to a queen pheromone because corpses of queens also have an inhibitory effect. The more fecund a queen, the greater her inhibitory powers, presumably because she secretes more pheromone. The pheromone, which is thought to work by suppressing endogenous juvenile hormone titers (Vargo and Fletcher 1989, Vargo 1997), may be the same pheromone that prevents dealation of virgin alates in monogyne colonies. Lower levels of this pheromone in monogyne colonies may also explain why monogyne colonies produce so many more alate offspring than polygyne colonies. The connection between fecundity and inhibitory pheromone may also explain why monogyne colonies produce alate brood following periods of low queen fecundity—that is, why the spring alate brood follows the winter low in queen fecundity and why the small number of fall alates follow the midsummer low in queen fecundity (Tschinkel 1993a).

It was once thought that each queen of a polygyne society contrib-

utes more or less equally to reproduction, but this is clearly not the case. In fact, it appears that an intense competition for reproduction is played out within polygyne nests. Because queens in polygyne colonies are unrelated, they cannot benefit from reproduction of close relatives and thus must achieve their fitness by direct reproduction, that is, by rearing their own offspring as alates. Some queens are more successful at doing so than others. Ross (1988, 1993) showed that 26% of the queens in polygyne colonies in the lab produced 84% of the female alates, and 16% produced none at all, although all lived at least 117 days. Three of 32 queens managed to have 70–85% of their offspring reared as alates. All queens contributed to worker production, and they did so much more equally. The apportionment of alates and workers was not strongly related to egg-laying rate, that is, it was not achieved simply by laying more eggs. Rather, it was based on the greater ability of some queens to have workers rear their eggs as alates or to bias their eggs toward sexual development.

Complicating this picture and further contributing to variation in apportionment of alate production is the great variation in the viability (i.e., the capability to form an embryo) of the eggs laid by inseminated polygyne queens—from approximately 50% to 100% (Vargo and Ross 1989). The proportion of a queen's eggs that form an embryo is not related to her fecundity (as estimated by weight) or to the amount of brood in the nest. Thus, a queen's realized reproductive success is not a simple reflection of her fecundity. When queens taken from the field were held individually with workers in lab nests, the viability of their eggs increased to more than 95% in most cases (Vargo and Ross 1989). This observation suggests that the multiple queens in polygyne nests mutually suppress the embryonation of each other's eggs, as well as fecundity.

Uninseminated queens fare even less well in terms of reproduction. Over half of the uninseminated queens taken directly from the field laid no viable eggs at all, although for a few, up to 80% of the eggs were viable. Viability of the eggs increased

after these queens were maintained for some time in the laboratory, especially among those who originally had the lowest proportion of viable eggs, but it was always much lower than that of inseminated queens. The lower fecundity and viability of eggs of uninseminated queens led Vargo and Ross (1989) to question whether they reproduce successfully to any significant extent. When isolated from other queens, uninseminated queens are sometimes capable of producing males, showing that their low success in nests cannot be ascribed entirely to the reduced viability of haploid eggs but may be related to the ambient queen pheromone milieu.

Although polygyne colonies adopt newly mated queens indiscriminately, as soon as they start reproducing, workers invariably kill all those queens that are homozygous for the *a* allele at a locus that encodes phosphoglucomutase (*pgm-3*). Ross et al. (1996b) and Ross (1997) proposed that because *pgm-3* produces the enzyme in common to glycogen metabolism, glycolysis, and the pentose phosphate shunt, it may not be merely a marker but may directly affect queen fecundity. Thus, the *pgm-3^{aa}* genotype may directly increase fecundity. This genotype also leads to slightly heavier alate pupae (Keller and Ross 1993). Selection against this genotype is complete in all polygyne populations, both native and introduced, so that only *pgm-3^{ab}* and *pgm-3^{bb}* are found among reproductive polygyne queens, with a frequency that differs strongly from the expected frequencies calculated from the frequencies of the *a* and *b* alleles in the population.

By contrast, these genotypes occurred with the expected frequency among nonreproductive queens and alates and in monogyne populations, showing that the selection occurs only in polygyne populations and only after queens begin to lay eggs. The *pgm-3* locus is also closely linked to another protein-encoding locus, *Gp-9*, for which selection is more complex. The queens killed by polygyne workers are the most fecund initially; perhaps the selection against more fecund queens prevents reduction to monogyny. The more fecund genotype (*pgm-3^{aa}*) is the most com-

mon one among functional queens of monogyne colonies. However, it is not clear whether or not the initially higher fecundity of the *pgm-3^{aa}* queens is maintained throughout life.

In spite of the intense selection against *pgm-3^{aa}* in polygyne colonies, the *a* allele persists in polygyne populations because of gene flow from surrounding monogyne populations. Of the four possible routes of gene flow (through polygyne males, polygyne females, monogyne males, and monogyne females), only one is functional—males from monogyne populations mating with polygyne queens (Shoemaker and Ross 1996)—creating unidirectional gene flow. The other three routes are ineffective because polygyne colonies produce mostly diploid males and their newly mated queens are neither accepted into monogyne colonies nor capable of independent founding. Monogyne queens are incapable of independent founding in polygyne-occupied territory and mostly incapable of being accepted by polygyne colonies because polygyne workers kill queens with high fecundity.

Origin of polygyne from monogyne colonies. Monogyne and polygyne populations are genetically almost identical, making it possible that the latter arose from the former after arrival in the United States (Ross and Fletcher 1985). Ross et al. (1996b) argue that several factors have selected for polygyne colonies: the combination of the reduction of colony recognition signals resulting from the loss of genetic diversity following the founder effect; the skewing of the operational sex ratio through the production of diploid males; and the very high population densities achieved in the United States, which have decreased the success of a queen founding independently and improved her reproductive chances on returning to the nest. The crucial change that would have allowed polygyne colonies to form would appear to be that workers suddenly tolerated more than one reproductive queen, but how this tolerance arose is unknown.

Most other differences between monogyne and polygyne colonies are a consequence of this single change,

whose identification might well be a suitable Holy Grail of myrmecology. Ross suggested that the first polygyne colonies may have arisen by the re-adoption of mated nestmates by monogyne colonies and that these adoptions may have gradually weakened the workers' ability to discriminate nestmates from non-nestmates (Vander Meer et al. 1990). As the number of queens increased, this reduced discriminatory ability would eventually lead to the adoption of even unrelated alates. Once the polygyne syndrome was established, it was perpetuated "culturally" (Keller and Ross 1993).

More recently, Ross and his colleagues have found that one of the alleles at the *Gp-9* locus is associated with the main features that distinguish polygyny from monogyny: worker tolerance of multiple queens, low queen weight, and limited queen dispersal (Kenneth G. Ross, University of Georgia, 1997, personal communication). This finding suggests that polygyny has a genetic basis and that the lack of relatedness among queens in polygyne nests in the United States may be a consequence of large numbers of alates seeking readoption, a process that will eventually eliminate the ability to distinguish nestmates. The lower queen numbers and smaller populations in Argentina would allow this ability to persist.

Conclusion

A female fire ant's reproductive options are many, depending on the milieu in which she develops (Figure 2). She may be a sterile worker in a monogyne or polygyne colony helping to rear alate sisters and brothers or unrelated alates, or she may be an alate female. In the latter case, if she is the offspring of a monogyne queen, she may attempt either dependent or independent founding. If she founds independently of workers, she may do so alone or in groups with other alates. Success during the founding period is followed by the intense competition for reproductive primacy in a surviving colony.

If the female developed in a polygyne colony, she may mate and be readopted successfully into a colony, or she may be adopted with-

out mating, relegated to laying few and nonviable eggs. Mated or unmated, her chances of surviving in the polygyne colony depend on her genotype and fecundity. As a mated queen, the female joins a competition for having her offspring reared as alates, a competition whose weapons are probably the secretion and responsiveness to queen pheromones and the acquisition of ovary-stimulating material from metamorphosing larvae.

The complexity of this reproductive biology emphasizes the multiplicity of routes through which fitness can be achieved under various contingencies. Many interesting evolutionary, physiological, and ecological questions have been addressed, and are continuing to be addressed, by research on fire ant reproductive biology. The fire ant is richly compensating us for the aggravation it continues to cause.

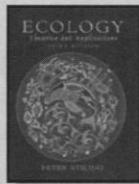
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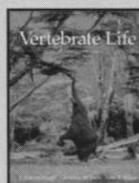


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