CASTES AND ROLES IN REPRODUCTION AMONG SOCIAL INSECTS

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Résumé: Les castes et leurs rôles dans la reproduction chez les insectes sociaux.

Certaines sociétés d'insectes sont monogynes (une seule reine pondeuse) alors que d'autres sont polygynes (plus d'une reine pondeuse). La polygynie ne peut pas être simplement interprétée à la lumière de l'une ou de l'autre des principales théories concernant l'origine et l'évolution de la socialité chez les insectes ("kin selection" et manipulation parentale) à moins d'être considérée comme une adaptation secondaire. Si la monogynie est apparue premièrement dans l'évolution, elle aurait évolué à travers la compétition entre les reines, mais chez quelques insectes sociaux, les ouvrières tuent les reines surnuméraires. Chez l'abeille du Cap,*Apis mellifera capensis* les ouvrières pondeuses sont plus semblables aux reines que celles des autres sous-espèces d'abeilles et leurs descendants sont toutes des femelles. Toutefois, dans les colonies orphelines, ces ouvrières pondeuses ne sont pas agressives les unes envers les autres. Leurs nombres sont contrôlés par les ouvrières plus âgées, qui sont les plus "ouvrières" dans une colonie. Comparativement, dans les colonies de la fourmi de feu *Solenopsis invicta*, les ouvrières tuent la majorité des reines vierges devenant reproductivement actives, lorsque les colonies sont rendues orphelines. Elles tuent aussi les reines surnuméraires durant la fondation pléométrotique.

Les expériences décrites ici suggèrent que les ouvrières réagissent à la quantité de phéromone royale présente dans une colonie lorsqu'elles exécutent des reines et qu'elles sont capables de distinguer les reines sur la base de la quantité de phéromone produite par chaque reine. La quantité de phéromone inhibitrice produite par une reine de fourmi de feu est positivement corrélée avec sa production d'oeufs. Ainsi les ouvrières tuent les reines faiblement fertiles pour commencer et conservent la reine la plus productrice. La quantité de phéromone inhibitrice secrétée peut être corrélée avec les quantités d'autres phéromones produites par les reines, ou dans le cas de l'abeille du Cap, par les pseudoreines. La meilleure interprétation de la régulation du nombre de reines par les ouvrières est que, comme la polygynie, il s'agit d'une adaptation évolutionnaire secondaire.

Mots-clés: *monogynie, polygynie, castes, sélection parentale*, Apis, Solenopsis, *colonies orphelines, pléométrose, reines vierges, phéromone inhibitrice, colonies orphelines, comportement agressif*.

Summary: Some insect societies are monogynous (have only one egg-laying queen) and other are polygynous (have more than one egg-laying queen). Polygyny cannot readily be interpreted in the light of either of the main theories concerning

the origin and evolution of insect sociality (kin selection and parental manipulation) unless it is a secondary adaptation. If monogyny is primary evolutionarily, it could have evolved through competition between queens, but in some social insects workers kill supernumerary queens. In the Cap bee, *Apis mellifica capensis*, laying workers are more queenlike than those of other subspecies of honey bees and their offspring are all female. However, in queenless colonies these laying workers are not aggressive towards one another. Their numbers are controlled by older bees, which are the most workerlike bees in a colony. Similary, in colonies of the fire ant, *Solenopsis invicta* workers kill most of the virgin queens that become reproductively active when colonies are made queenless. They also kill supernumerary queens during pleometrotic colony founding.

Experiments are described that suggest that workers respond to the quantity of queen pheromone present in a colony when they execute queens, and that they also discriminate among queens on the basis of the quantity of pheromones each queen produces. The amount of inhibitory pheromone produced by a queen fire ant is positively correlated with her egg production. Thus, workers kill poor egg producers first and retain the most fertile queen. The amount of inhibitory pheromone secreted may be correlated with the amounts of other pheromones produced by queens, or in the case of Cap bee, by pseudoqueens.

The best interpretation of the regulation of queen number by workers is that, like polygyny, it is a secondary evolutionary adaptation.

Key-words: *monogyny, polygyny, castes, kin selection, Apis ,Solenopsis, virgin queens, aggressive behaviour, inhibitory pheromone, pleometrosis, queenless colonies.*

I do not inted to review much literature concerning the role of different castes in the regulation of reproduction in social insects, because I propose to concentrate on an aspect that seems to have received little attention, namely, the role of workers in the regulation of queen number.

It has been estimated that there are more than 20,000 species of social insects (WILSON. 1982). We really know very little about any of these, but the best known among them is surely the honey bee, Apis mellifica L., which has been studied for generations, because of its economic importance to humankind, and because its societies have long had intrinsic fascination for us. Thus, the social structure of the honey bee colony seems to serve as a paradigm that influences many of our assumptions about other social insects. One of the most conspicuous features of honey bee societies is that they almost always have only one queen, that is, they are rather strictly monogynous. It is not surprising, therefore, that one of the most common assumptions about other social insects is that their colonies are also monogynous, with certain notable exemptions. of course. However, an increasing number of examples of polygyny are now coming to light, even in groups where one might least axpect it, as for example in Macrotermes spp. (R. LEUTHOLD, pers. comm.).

I believe that it is important to question whether polygyny in various species is a primary evolutionary trait,

or whether it is a secondary adaptation. It is importante because it has a strong bearing on the two main theories concerning the evolution of eusociality among insects, that is, on theories concerning the origin of a sterile worker caste. These theories are: 1) that workers evolved through a process of kin selection in which nonreproducing females increase their inclusive fitness by helping to rear the offspring of a close relative instead of rearing offspring of their own; and 2) that workers evolved through parental manipulation, that is, they are females in which the reproductive function has been suppressed, or severely reduced, as a result of the manipulation of parental investment. For a review of these theories see STARR (1979).

The term *"altruism"*, applied to the first theory is curiously inappropriate. It is defined by WILSON (1975) as, "Self-destructive behavior performed for the benefit of others". Clearly, the cost of an altruistic act exceeds the benefit, whereas by definition in kinship theory the inclusive fitness of an individual is increased only when benefits exceed the costs. An individual invests something, mostly labor, and receives interest on that investment, so altruism, as applied to the evolution of sociality, is really capitalism in disguise.

Queen number is important to kinship theory because the coefficient of relationship between cooperating individuals is greatest in monogynous colonies in wich the queen is inseminated by a single male, and it is diminished both by polygyny and by the number of males with which a queen mates if this is more than one. It is also important to the theory of parental manipula-pulation, because the investment interests of all the queens must somehow be reconciled. Do queens in functionally polygynous colonies compete? No clear general answer to this question has been obtained. Some evidence suggests that they do compete and some that they do not.

Perhaps the main problem with both the kin selection and parental manipulation models is that each attempts to explain too much. I agree with the view that they are not mutually exclusive (MICHENER and BROTHERS, 1974 ; CROZIER, 1979) and I believe that both will encounter an increasing number of difficulies if exclusivity is maintained. This is not to say that a synthetic theory will resolve the difficulties either, although it may help. What is needed is a great deal more information about individual species of social insects, as this will probably show an even wider diversity of phenomena to be explained. Certainly, much of the new information we are deriving from our studies of the fire ant, *Solenopsis invicta* Buren, do not seem to fit comfortably into either theory.

Let us assume that in evolutionary terms monogyny is primary. How could it have evolved? WILSON (1971) suggested that it evolved through competition between queens, and there is plenty of evidence from monogynous insect societies to support this hypothesis. In primitively eusocial bees, e.g. *Lasioglossum* , *Bombus*, and in primitively eusocial wasps, e.g. *Polistes*, females com pete directly by behaving aggressively towards one another. This results in the formation of dominance hierarchies and regression of the ovaries of subordinate individuals (MICHENER, 1974;

FREE , 1955; PARDI, 1948; WEST-EBERHARD, 1969). In many highly eusocial species, queens are also highly antagonistic towards one another. For example, in the honey bee, queens usually fight to the death, as first reported by HUBER in 1792 . So too do queens of the ant *Camponotus ligniperda*, which in oligogynous colonies, normally occupy different territories within the nest (HOLLDOBLER, 1962). However, in many species of social insects workers participate in the elimination of supernumerary queens. For example, LUSCHER (1952) reported that this occurs in the termite *Kalotermes flavicollis*, and it also occurs in colonies of stingless bees, (KERR, 1969; SILVA et al., 1972), and even in the honey bee as reported by DARCHEN and LENSKY (1963). This behavior does not seem to be in accord with the hypothesis that monogyny evolved through competition between queens. WILSON 's tentative solution was that workers may remove those queens with the last familiar odor if some of the odor differences are genetic in origin. It seems to me that there must be more to it than that, and my interest in the problem began some years ago while I was still in South Africa.

It had been reported by ANDERSON (1963, 1968) that when a colony of Cape bees. *Apis mellifica capensis*, is made queen-less, severe fighting breaks out among the workers and many fo them are stung to death. Earlier, SAKAGAMI (1958) had reported that aggression also occurs among queenless workers of the Italian honey bee, *Apis mellifera ligustica* , although the aggression was . of a milder nature than in the Cape bee. Here too, no clear association was found between the level of aggression and degree of ovary development. I reinvestigated the nature of this aggressive behavior using the Cape bee.

The Cape bee is much darker than the adansonii bee, which is essentially a yellow race. The color difference is especially well marked between queens. There is no geographic barrier between the two subspecies, but the Cape bee is confined to a small area within the winter rainfall region of South Africa (RUTTNER, 1977). It is exeptional among honey bees, because it is the only subspecies in which the eggs of laying workers give rise obligatorily to females (workers or queens) instead of to males as in other subspecies. including the adansonii bee. In other words they reproduce by thelytokous parthenogenesis.

Functional laying workers develop in 4-8 days after queen loss, and at first they lay eggs in a haphazard way, as do other subspecies, but as their ovaries develop and the abdomen elongates, they lay more like true queens, placing a single egg at the bottom of a cell. Since all their offspring are female, the cappings over worker cells are flat instead of dome-shaped. Workers of the capensis bee are also more queenlike than those of adansonii. They have many more ovarioles per ovary and some have a well-developed spermatheca. The degree of ovary development attained by fonctional laying workers is substantial, but is nevertheless much less than that a normal queen.

To investigate the nature of the reported aggressive behavior among queenless workers, I installed 3 colonies in observation hives that had rows of windows through which individual bees could easily be captured, marked with different colored paints and returned to the colony. I also fitted each hive a dead bee trap, so that I could record any mortality that might occur. To leave the hive, workers had to pass throught small holes that would not permit them to take dead bees with them.

When released dead bees dropped down a tube about 0.8 m long into a darkened bottle from which they could be removed as required without disturbing the colony.

In each of the 3 colonies the first signs of agression appeared less than 24 hours after dequeening. It became apparent very quickly that among the bees that appeared to be fighting there were two distinct behavioral categories, aggressors that mauled, bit, and/or stung others, and victims that seldom retaliated but were either very submissive, or attempted to escape, often successfully. The overwhelming majority of bees originally marked as aggressors remainded aggressors thereafter, and hardly any victims, among those that survived, subsequently displayed aggressive behavior (Table 1). Thus, the aggression cannot really be described as fighting. In each colony about 2000 bees out of a total of 7000 were stung to death during the first 10 days of the experiment when aggression was at its most intense.

	Behavior subsequent to marking			
	attacking		being attacked	
	n	%	n	%
Aggressors	1678	98.5	25	1.5
Victims	49	2.8	1691	97.2

Table 1. *Behavioral attributes of the Cape honey bee workers involved in aggressive interactions during 22 days in a queenless condition.*

Some victims became functional laying workers. Of these 78 were given individual recognition marks. On 156 occasions thereafter physical contacts between marked pairs were observed, but they were not aggressive towards one another.

To determinate whether there was a relationship of any kind between behavior and degree of ovarian development, 3 new colonies were installed in the observation hives, and on day 3, 6, and 9 after dequeening, i.e. during the period when aggression was most severe, 20 aggressors and 20 victims were captured from each colony to determine their degree of ovarian development. This amounted to a total of 180 aggressors and 180 victims.

The results showed that there was a general increase in ovarian development through time, but that this increase was much greater among victims than among aggressors. In fact, 40% of the victims captured on day 9 were functional laying workers, but no aggressor attained that status. When the ages of aggressors and victims were determined in a third experiment, I found that victims were mainly yong bees, whereas aggressors

were mostly bees older than about 18 days, that is, they were essentially comprised of foragers. Frequent aggression was displayed towards functional laying workers, but this was, for the most part, of a mild nature. When they were eventually killed, the workers tended to ball them in the manner of true queens rather than stinging them as they did victims with less well developed ovaries.

Clearly, aggression among queenless workers of the Cap bee does not consist of attempts by ovary developed individuals to either dominate each other behaviorally, as in primitively eusocial insects, or to eliminate each other in the manner of honey bee queen. Since aggressors are older bees that remain more workerlike with regard to their degree of ovary development, and victims are mostly younger bees become more queenlike with time, the behavior closely resembles the elimination of supernumerary queens by workers as in the examples given earlier. Evidently, many young bees signal their developing reproductive capability, before their ovaries are well developed, and hence the attacks upon them. Recent studies on the pheromones of Cap bees (HEMMLING et al., 1979; CREWE and VELTHUIS, 1980) support this conclusion.

To determine what specific mechanisms are involved in the regulation of queen number by workers, I used the fire ant, *Solenopsis invicta*, as the experimental animal, after I had moved to the United States of America

The fire ant was introduced into the United States in about 1940 through the port of Mobile, Alabama (BUREN, 1972). It spread extraordinarily rapidly, and is now present in 9 southeastern states from North Carolina to Texas, covering an aera that is approximately the size of France. It is still spreading. The main reasons it is considered a pest are: Firstly, when colonies are disturbed, thousands of workers respond very quickly and administer very painful stings. Hence the name "fire ant". Within 24 hours a sterile pustule appears on the site of each sting, which becomes itchy and leaves an unsightly red lesion for several weeks. A small percentage of people are highly allergic, and there have even been a few deaths. Large number of people are stung, because the ants nest in open, sunny area, and are therefore common on lawns and in recreation areas. A second reason the fire ant is considered a pest is that its earthen mounds cause damage to farm machinery on croplands, and they are very numerous. There may be a many as 300 per hectare. Mature colonies may contain upwards of 200.000 ants (LOFGREN et al., 1975).

We keep colonies in the laboratory in large trays, the sides of which are treated with fluon (a teflon suspension) to prevent escapes. In the tray are several Petri dish nests each about 16 cm in diameter and containing a hard, damp plaster. We feed these colonies on an artificial diet consisting mostly of ground beef, eggs, and vitamins, and we supplement this liberally with mealworms and crickets. These colonies rear numerous sexual forms, both male and female, which assures us they are in exellent condition for experimental work.

Fire ant colonies are usually monogynous. The queen becomes physogastric, but remains mobile. She can weight up to 27 mg, but more usually 22-24 mg, and lays about 1000 eggs per day. The ovaries of workers are too vestigial ever to become functional, so the question of queen control over worker reproduction does not arise. On the other hand, mature colonies can produce three to four thousand female reproductives each year, and while they remain in the parental

nest, they are prevented from becoming reproductively active, that is, from laying eggs, by an inhibitory primer pheromone produced by the mother queen of the colony (FLETCHER and BLUM, 1981 a). Previously, it was thought that,in ants, stimuli derived from mating during a nuptial flight, or flight itself, were necessary for ovary development to occur in young queens. Current investigations being carried out by mycolleagues and myself with other species of ants, suggest that such inhibition of virgin queens is probably common in the Formicidae.

If one removes the mother queen from a colony of fire ants containing virgin queens, some of the virgins dealate and their ovaries develop rapidly. However, within a few days the workers begin to kill some of the dealates, and they usually retain only 1-4, from whose eggs many males are reared before the colony dies out. This behavior is very similar to the killing of potential and actual laying workers by nonlaying workers in colonies of the Cape bee, except that there is no ambiguity whatever about the role of the workers. They clearly exercise control not only over queen number, but also over which individual queens will be permitted to lay eggs. They also exercise similar control in a completely different context.

In common with many other species of ants, such as *Lasius flavus*, fire ant colonies are established claustrally either by single queens (haplometrotically) or by a number of queens together (pleometrotically). During pleometrosis some fighting occurs between queens, but the first workers that they rear are mainly responsible for the elimination of supernumerary queens. For three years we started large number of colonies with 5, 10, or 15 newly mated queens each, and in every case the first workers reared (minims) progressively killed queens until each colony became monogynous. They seized queens by the appendages and held them down while others dismembered them.

In my investigations into the mechanisms involved in the regulation of queen number by workers, I made use of the fact that polygynous colonies of fire ants sometimes occur in North America. I tested the responses of workers from both monogynous and polygynous field colonies to foreign queens from each of these two types of colonies. I did this first while the workers were queenright and then again afterthey had been queenless for 48 hours. There were 22 replications of each treatment. When queenright, workers from monogynous colonies killed foreign queens from both monogynous and polygynous colonies and when they were queenless they accepted queens from monogynous colonies but still killed most of these from polygynous colonies (Table 2).

Workers from polygynous colonies also killed queens from monogynous colonies when they were queenright, but they accepted the queens from polygynous colonies. When they were queenless they accepted queens from both types of colonies (Table 2).

Based on these results I predicted that if I introduced multiple, recently mated queens to queenless workers, the monogynous colonies would kill all but one of them, and those from polygynous colonies would retain more than one. There were 3 replications of each of the two treatments and 25 queens from a single mating flight were introduced to each of these. The result, assessed

Source of	Source of workers			
foreign	Monogynous colonies		Polygynous colonies	
queens	Queenright	Queenless	Queenright	Queenless
Monogynous colonies	1	19	0	19
Polygynous colonies	0	8	21	22

Table 2. Rejection of foreign queens by workers fire ants.
There were 22 test units per treatment and the number that accepted the introduced queens was recorded. Each unit consisted of approximately 5000 workers and 5 cc of worker brood.

6 weeks later, were essentially in accord with the prediction. The mean number of queens retained by the workers from monogynous colonies was 1.8, with 6 of these re-establishing monogyny and two others retaining 2 and 6 queens respectively. The mean number of queens retained by the workers from polygynous colonies was 10.7 with only one colony becoming monogynous and the other 7 retaining 9-15 queens each.

An obvious difference between the queens of monogynous and polygynous field colonies is their degree of physogastry. As I have already indicated, queens of monogynous colonies are physogastric. Most of their body weight is, therefore, made up of their greatly enlarged ovaries. Queens in polygynous colonies on the other hand, are relatively nonphysogastric. Their fertility is correspondingly lower. I had previously shown this for queens collected in the field by means of a simple oviposition test (FLETCHER et al., 1980). This consists of temporarily removing queens from their colonies and isolating them on damp plaster for a period of 5 hours. During this time they continue to lay eggs and the number they lay is proportional to their degree of ovarian development, as measured by the maximum number of oocytes per ovariole (FLECHTER and BLUM, in press).

I confirmed this difference in fertility between the queens of monogynous and polygynous colonies by subjecting the queens in the experiment, in which multiple queens were introduced to queenless workers six weeks after the introduction. The queens in the colonies that became monogynous laid a mean of 104 eggs, and those in colonies that became polygynous laid a mean of only 41 eggs during the 5 hours of the test.

From the result I had obtained in the experiments with both the Cape bees and the fire ants, I formulated an hypothesis concernig two pheromonal mechanisms that seemed to me to be involved in the regulation of queen number by workers (FLETCHER and BLUM, 1983). The hypothesis has four parts as follows:

(i) Workers recognize queens by means of pheromones produced only by female reproductives. The exocrine secretion (or secretions) consists of a number of compounds forming a mixture that is characteristic of a species. Hence, queenless workers are able to recognize and accept foreign queens of their own species.

(ii) The various constituents of this pheromonal complex are produced in different proportions by different queens, thereby providing each queen with a unique odor. Workers recognize the singular pheromonal blend of their own queen and can therefore distinguish her from all other queens of the same species. Hence, the same pheromonal mixture permits both species and individual recognition of queens by workers.

(iii) Queens also produce other pheromones, such as the inhibitory pheromone, and the quantity of queen pheromones circulating in a colony is maintained within some optimal range. Wide deviations in the amount of these pheromones cause changes in worker behavior that tend to restore the level to within the optimal limits. Queenlessness causes a pheromonal deficit, resulting in the production, or acceptance, of a replacement queen, whereas the presence of supernumerary queens raises the level above a tolerance threshold and causes workers to behave aggressively towards some queens.

(iv) Queens produce different amounts of pheromones and there is a positive correlation between amount and fertility. Selection of queens by workers depends on their position in the pheromonal hierarchy; the poorest queen is destroyed first and the most productive queen is left unharmed.

To determine whether workers do, in fact, discriminate among queens in a manner consistent with the hypothesized quantitative pheromonal mechanism, I designed several experiments. Dr. Daniel CHERIX helped me to carry out these experiments. In the first one, we divided each of 12 monogynous colonies containing 30,000 to 40,000 workers and a physogastric queen (minimum weight = 21.7 mg) into two. The queenright half was discarded. After 72 hours, pairs of physogastric and relatively nonphysogastric queens foreign to the workers were introduced together into the queenless half, and the responses of the workers were recorded. The use of exclusively foreign queens ensured that the workers would not be able to discriminate between pairs on the basis of familiar or unfamiliar odors, i.e. a qualitative pheromonal mechanism. Moreover, to eliminate any possible effects of age on pheromone production, all the queens were from a mating flight that had occured 2.3 years previously. A reduction in food supply was used as the means of obtaining relatively nonphysogastric queens, which were, however, still laying eggs. The mean weights of the queens in the two categories were 24.2 mg and 16.2 mg.

The workers killed the relatively nonphysogastric queen in 10 of the 12 replicates, in one they killed both, and in one they retained the relatively nonphysogastric queen. This experiment was then repeated with queens of unknow age but with somewhat greater difference in degree of physogasty. Here, the mean weights of the two categories were 23.2 and 15.4

mg . The workers killed the relatively nonphysogastric queen in all 12 replicates.

To test whether the fertility of a queen, as measured by body weight, is related to pheromone production, the inhibitory pheromone content of physogastric and relatively nonphysogastric queens was compared. Newly mated queens from a single mating flight were put into artificial nests where they established new colonies haplometrotically. After 10 weeks, 14 of them were introduced into large queenless colonies to make them physogastric (first to only a small part of each colony, so that the workers would not kill them) and 14 others were left in their colonies, which were still too small for the queens to become physogastric. After a further 5 weeks, when the mean weights of the two groups of queens were 20.1 and 10.7 mg, all the queens were killed by freezing and their corpses were assayed for their inhibitory pheromone content. The method used was described by FLETCHER and BLUM (1981 b). The physogastric queens were found to contain appreciable quantities of the pheromone, and the relatively nonphysogastric queens very little, if any. I cannot say, of course, that the inhibitory pheromone is definitively involved in the quantitative pheromonal mechanism, but it is the only fire ant queen pheromone that can be assayed quantitatively.

Next, to test the hypothesized quantitative pheromonal effect on workers at the level of the colony, 12 monogynous colonies were divided into two, as before, and two physogastric foreign queens (minimum weight = 21.7 mg) were introduced simultaneously into each queenless half after 72 hours. With this arrangement, the workers could not discriminate between the queens on the basis of either the qualitative or quantitative mechanisms, yet the hypothesis predicted that they would have to kill one of them, because too much queen pheromone would be present. They, in fact, killed one queen in 11 of the 12 replicates, and both queens in the twelfth. It is of interest that the queens usually lost weight before they were killed, that is, their pheromone production, according to the hypothesis, was reduced.

The results of these experiments are evidently consistent with a quantitative pheromonal mechanism for the discrimination among queens by workers of monogynous fire ant colonies. On the other hand, the workers of polygynous colonies appear to have a highter threshold of tolerance for the queen pheromone(s) involved. This difference is probably not great, however, since each of the queens in a polygynous colony, being of lower fertility than the physogastric queens of monogynous colonies, produce less of the pheromone(s). We have recently confirmed this, at least in the case of the inhibitory pheromone (WILLER and FLETCHER, unpublished data).

The discrimination of queens by workers on the basis of quantitative pheromonal effect is not inconsistent with WILSON 's hypothesis that monogyny evolved through competition between queens. Instead of engaging rivals in direct combat, a queen may simply outcompete them pheromonally, since workers kill the poor pheromone producers first (young Cape bees with poorly developed ovaries, and the less physogastric fire ant queens). There is, of course, a chicken-and-egg problem regarding

the ability of a queen to compete successfully for the food resources in the first place. Possibly, the workers feed her more in response to a pheromone output that is already higher than that of the other queens present.

These investigations with Cape bees and fire ants show that both the queen and worker castes play important roles in the regulation of reproduction in colonies of social insects. In honey bees it is the queens themselves that play the main role in the maintenance of monogyny, but functional laying workers in queenless colonies are not mutually aggressive and their numbers are regulated by workers. Each laying worker, being of lower fertility than a queen, presumably produces less queen pheromones, so that a colony will tolerate a number of them and becomes temporarily polygynous. In fire ants, on the other hand, the regulation of queen number is almost exclusively the role of the workers. There is some, but not much, animosity among queens during pleometrotic colony founding, but the queens of mature colonies are not aggressive towards one another (FLETCHER and BLUM, unpublished data).

The implications of the regulation of queen number by workers for theories concerning the evolution of insect sociality will require detailed analysis, but if monogyny is indeed primary evolutionarily, this mode of regulation almost certainly represents a secondary adaptation.

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