

Social Control of Reproduction
in Fire Ant Colonies

E.L. Vargo

INTRODUCTION

The study of social control over reproduction occupies a key position in our attempt to understand the evolution and organization of insect societies. On one hand, colony-level selection can be expected to favor efficient cooperation of colony members to maximize the production of sexuals capable of founding new colonies (Oster and Wilson 1978). On the other, direct reproduction is generally dominated by only one or a few individuals in the colony, so that competition among nestmates for reproductive privileges is also a prominent feature of social life among the insects (West-Eberhard 1981; Fletcher and Ross 1985; Bourke 1988). The extent and means by which social factors regulate reproduction is determined by the interplay of these two evolutionary tendencies.

Social control of reproduction in the fire ant, *Solenopsis invicta*, has only recently been a focus of research, beginning with the discovery of pheromonal queen control over oogenesis in virgin queens (Fletcher and Blum 1981a). Progress has since been rapid, especially in the last two or three years, and a variety of reproductive processes in fire ant colonies are now known to be under social control.

CONTROL OVER OVIPOSITION

Alate Virgin Queens

Throughout most of its range in the southeastern U.S., *S. invicta* colonies produce sexuals in all but the coldest months (Markin and Dillier 1971). Both male and female alates reach sexual maturity in seven to 10 days (Lofgren et al. 1975); they then remain in the nest until favorable weather conditions bring about a mating flight. During this waiting period - which may last several weeks - female sexuals are prevented from ovipositing in the nest by means of a relatively nonvolatile primer pheromone produced by functional (egg-laying) queens (Fletcher and Blum 1981a, b). In addition to inhibiting oogenesis in virgin queens, this pheromone prevents histolysis of the flight muscles and dealation (shedding of the wings) which usually occur following disinhibition (Fletcher and Blum 1981a, 1983a). Study of this

pheromone has been greatly facilitated by the development of a bioassay in which queen corpses can be tested for their ability to inhibit dealation in sexually mature virgin queens (Fletcher and Blum 1981b; Fletcher et al. 1983).

The inhibitory power of different queens, as assessed by this bioassay, bears a positive relationship to the degree of ovarian development (Waller and Fletcher 1986; Obin et al. 1988), suggesting that the quantity of pheromone produced by a queen is correlated to her level of fecundity. This is not a simple relationship, however, as certain types of queens are more or less inhibitory than others. For example, Waller and Fletcher (1986) found that virgin queens which had dealated and taken over reproductive function in queenless colonies for only one week were significantly more effective than "low weight" inseminated queens of monogyne (single-queen) colonies, even though their ovaries were less developed. Incidentally, the rapid production of this inhibitory pheromone by such virgin replacement queens is evidence of strong reproductive competition to become the principal egg-layer in these colonies.

As a first step toward locating the glandular source of the pheromone, Fletcher and Blum (1981b) tested parts of queen corpses for their inhibitory capability. Gasters alone were about as effective as whole corpses, whereas heads and thoraxes together were only slightly inhibitory. These authors concluded that the pheromone is produced in the gaster, while the head and thorax become contaminated with it. This conclusion has been criticized by Vander Meer (1983) on the grounds that a queen attractant pheromone is produced in the venom gland located in the gaster (Glancey 1986). Thus, the gaster's strong inhibitory effectiveness may merely reflect the degree to which workers are attracted to this body region and thereby come into contact with substances on its surface, rather than indicate the site of production or storage of the inhibitory pheromone. Fletcher (1986a) has argued that as some gasters have remained inhibitory for a remarkably long period of time - more than three months - they must contain the source of the pheromone. In any event, dissemination of the nonvolatile inhibitory pheromone to virgin queens clearly depends on attractant pheromones, in so far as these mediate contact of the queen's body by workers. These two pheromones are, therefore, intimately related in the natural context, underscoring the complex nature of the pheromonal signals produced by the queen and the difficulties encountered when trying to sort them out experimentally.

Pheromonal inhibition of reproduction by virgin queens is remarkably effective, despite enormous colony size and complex nest structure. Mature monogyne colonies can contain 230,000 workers and tens of thousands of immature forms, all distributed over some 40 liters of nest (Markin et al. 1973). In addition, up to 5,000 alate queens may be present at any one time (Vargo and Fletcher 1987). Yet the queen produces enough pheromone to prevent these alates from producing males (see Ross and Fletcher 1985). Nevertheless, some female sexuals may oviposit if they remain in the nest for long periods. Fletcher and Blum (1983a) reported that despite having intact flight muscles, 68 of 300 (23%) female alates which overwintered in their parental monogyne nest had fully-developed ovaries and laid some eggs, although these eggs appeared to be nonviable.

The fact that flight muscle histolysis and dealation do not necessarily coincide with oviposition, raises the question of how many queen pheromones are involved in inhibiting reproductive activity of female sexuals. Fletcher

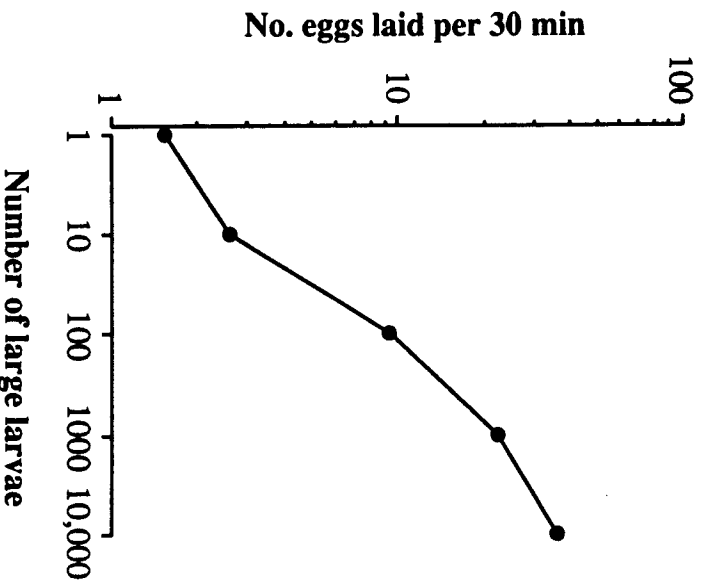


FIGURE 1. Effect of the number of fourth instar larvae on the egg-laying rate of queens. Each experimental colony contained about 3000 workers. $n=4$ in each case. (Redrawn with permission from Tschinkel 1988).

and Blum (1983a) have proposed that these different physiological events are controlled by a single pheromone which regulates the secretion and titer of juvenile hormone (JH). According to this hypothesis, oogenesis proceeds in the presence of low amounts of JH, while greater amounts are needed to effect histolysis of the flight muscles. These authors suggest that the pheromone does not inhibit JH production altogether, but reduces it to a degree permitting oogenesis through a continuous but low rate of vitellogenesis; a substantially higher titer is necessary to induce histolysis of the flight muscles. While this hypothesis is appealing, it has yet to be tested and the mode of action of this inhibitory pheromone remains uninvestigated.

Functional Queens

Monogyne Colonies. In a series of elegant experiments, Tschinkel (1988) investigated the role of workers and larvae in regulating queen oviposition in monogyne colonies. In ant colonies it is generally assumed that queens compete with larvae for food and worker attention, so that queen fecundity is correlated negatively with the number of larvae and positively with the

number of workers (Tschinkel 1988). These experiments revealed a very different relationship in *S. invicta*. Surprisingly, the queen's oviposition rate was highly correlated with the number of fourth (last) instar larvae (Fig. 1), whereas it was unaffected by the number of workers, at least not within the range tested (300-6,000). As the number of fourth instar larvae depends directly on the queen's egg-laying rate, these are linked in a positive feedback loop, such that fecundity is pushed to higher and higher levels as eggs develop into fourth instar larvae. This larval stimulation of the queen's egg-laying rate declines with increasing larval numbers, as indicated by the logarithmic nature of this relationship (Fig. 1). Thus, at high larval numbers - above 10,000 or 15,000 - each additional larva has very little effect on fecundity. As a consequence, the declining effect of larval numbers on queen fecundity may help determine maximum colony size by setting the upper limit on the queen's oviposition rate.

The precise nature of larval influence on queen fecundity is unknown, but probably involves nutritional factors, most likely proteins. Fourth instar larvae are the only colony members capable of ingesting and digesting solid protein (Petralia and Vinson 1978; Petralia et al. 1980). In addition, the labial gland secretions of these larvae contain high concentrations of protein and amino acids which appear to be collected by workers (O'Neal and Markin 1973; Sorensen et al. 1983a, b). Material can be transferred from larvae to queens; Tschinkel (1988) observed that dye fed to larvae rapidly appeared in worker crops and then in the queen and her eggs. Thus Tschinkel speculated that fourth instar larvae may be a "digestive metabolic caste that processes larvae on queen fecundity by the queen". A similar stimulating effect of *Monomorium pharaonis*, in which queens appear to feed directly on larval secretions (Bøtgeresen 1990).

Polygyne Colonies. In addition to the more common monogyne colonies, *S. invicta* forms polygyne (multiple-queen) colonies in both the U.S. and its native range in South America (Vargo and Fletcher 1987; K. G. Ross and J. C. Trager unpublished). In polygyne colonies the presence of other egg-laying queens strongly influences fecundity. Fletcher et al. (1980) were the first to report that queens from polygyne colonies are less physiogastric and lay fewer eggs per individual than queens from monogyne colonies, suggesting a negative relationship between fecundity and the number of colony queens. Greenberg et al. (1985) found supporting evidence in laboratory colonies where the number of queens was negatively correlated with the number of eggs laid per queen but positively correlated with the total egg number.

The relationship between colony queen number and fecundity in field and standardized laboratory colonies was recently studied by Vargo and Fletcher (1989). Queen weight, a reliable measure of ovarian development and oviposition rate in this species (Fletcher and Blum 1983a; Willeter and Fletcher 1986; Ross 1988; Tschinkel 1988, Vargo and Fletcher 1989), was used to assess the degree of fecundity. Although the fecundity of individual queens varied widely, the number of colony queens had a strong negative effect on mean fecundity in both field and laboratory colonies (Fig. 2). Uninseminated queens, which constitute a third or more of the functional queens in polygyne colonies (Lotgren and Williams 1984; Vargo and Fletcher 1987, 1989), were generally less fecund than their inseminated nestmates, weighing 5-25% less.

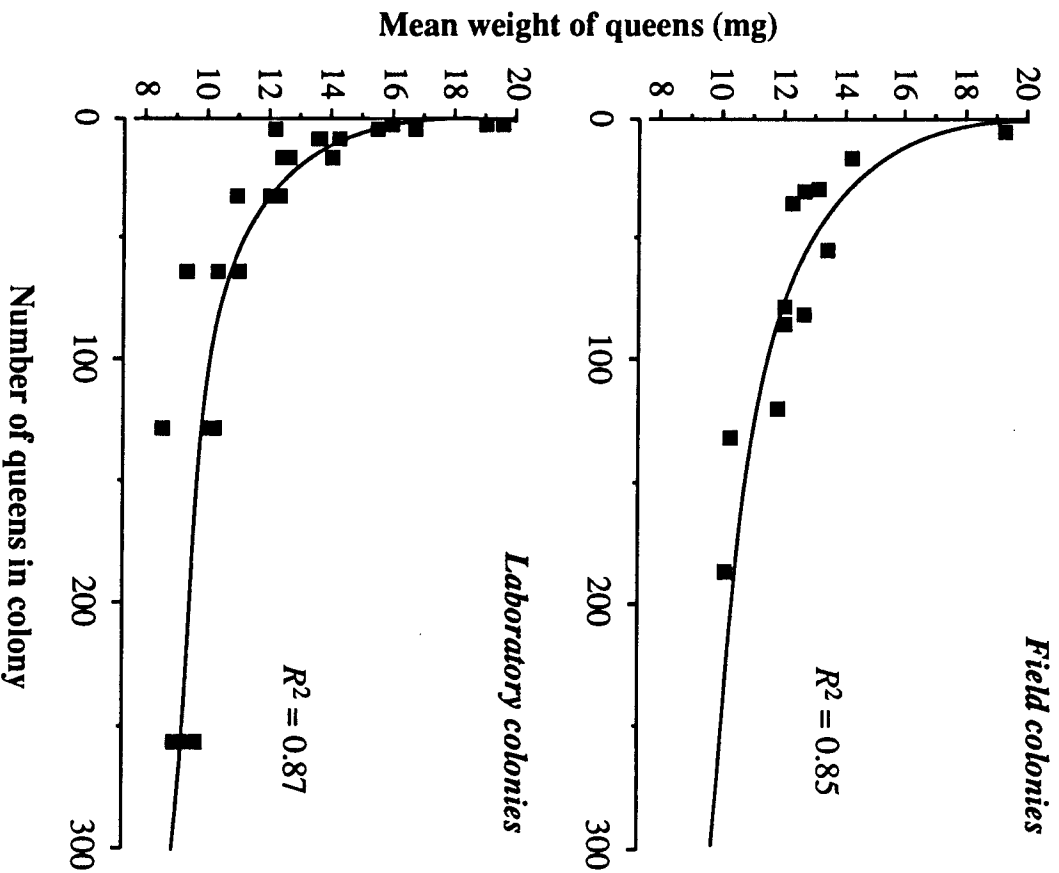


FIGURE 2. Relationship between queen number and mean queen weight in polygyne colonies of *S. invicta*. Queens placed in the standardized laboratory colonies were taken from a homogeneous pool and weighed after ca. nine weeks. (Adapted from Vargo and Fletcher 1989).

Colony size (total weight) was not significantly related to the mean weight of queens in either the field or laboratory colonies, suggesting that the number of workers or larvae bears little if any relationship to the fecundity of queens, at least within the range of colony size studied (12-265 g). While not specifically tested, it would seem that queen fecundity in polygyne colonies

is not strongly influenced by the quantity of nutritional or other factors provided by larvae, in contrast to the role of such factors in monogyne colonies. Thus an intriguing possibility for a regulatory mechanism is mutual pheromonal inhibition of fecundity among nestmate queens in polygyne societies. As discussed above, functional *S. invicta* queens produce a pheromone that inhibits reproductive activity in virgin queens, presumably by suppressing JH production. Perhaps mutual inhibition of fecundity among cohabiting polygyne queens is also effected by pheromones which regulate JH production.

PRODUCTION OF VIABLE EGGS

Nearly all eggs laid by the mother queen in mature monogyne colonies are viable, i.e., they form embryos and can presumably develop into larvae (Fletcher and Blum 1983a; Voss and Blum 1988), though some may be consumed by fourth instar larvae before hatching (Petraia and Vinson 1978). However, nonviable (so called "trophic") eggs may be produced in monogyne colonies under certain social and physiological contexts. Newly-mated queens engaged in colony founding lay some eggs which fail to form embryos and presumably serve as an important source of food for the larvae of young colonies (Glancey et al. 1973; Cherix and Fletcher 1982; Voss and Blum 1988). In addition, virgin queens from monogyne colonies removed from the inhibitory influence of the mother queen lay almost exclusively nonviable eggs (Voss 1981; Fletcher and Blum 1983a). However, if such disinhibited virgin queens are maintained in the presence of large numbers of workers and brood, or treated topically with JH, they produce some embryonated eggs (Voss 1981; Fletcher and Blum 1983a), suggesting that nutritional factors as well as endogenous JH titers influence egg viability.

The viability of eggs produced by polygyne queens has been studied by Vargo and Ross (1989). Surprisingly, the proportion of viable eggs produced by functional queens from field colonies was highly variable, but inseminated queens produced a higher proportion than uninseminated queens (top half of Fig. 3). This variability among queens was unrelated to queen weight (fecundity), indicating that the oviposition rate of queens in polygyne colonies does not necessarily reflect their individual contribution to the production of colony members.

Interestingly, polygyne queens placed in monogyne conditions - kept individually with workers and brood in laboratory rearing units (Vargo and Ross 1989) - laid almost exclusively viable eggs (bottom half of Fig. 3), as does the mother queen in a natural monogyne colony. In contrast, the proportion of eggs laid by uninseminated queens held individually differed very little from those taken directly from the field. Experimental manipulation of the quantity of workers and brood had a strong effect on fecundity, reflecting the dependence of fecundity on fourth instar larvae under monogyne conditions (Tschinkel 1988), but the presence of larvae did not influence the ability of a queen's eggs to form embryos. This suggests that the lower viability of eggs produced by inseminated queens in polygyne colonies may result from mutual inhibition. In other species, queens are known to influence the viability of eggs produced by workers (see Vargo and Ross 1989); it is possible that fire ant queens also influence each other in this way.

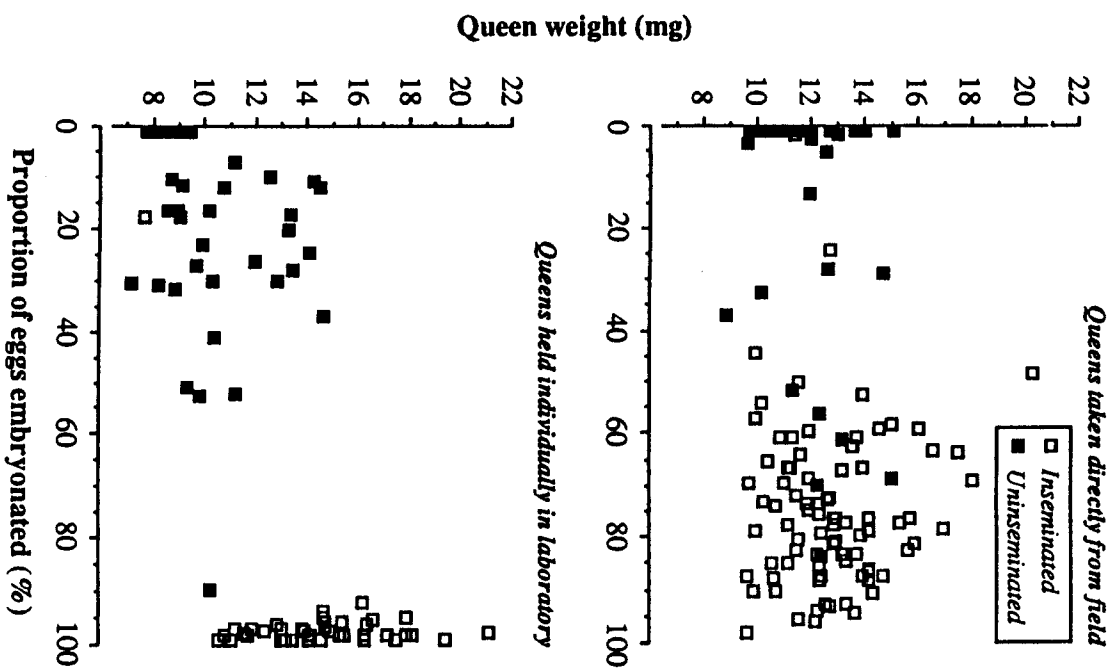


FIGURE 3. Proportion of viable eggs laid by polygyne queens of *S. invicta* in relation to insemination status and weight. Eggs were collected from individual queens, incubated with workers for 24-72 h, and then stained for chromatin (see Voss 1985). Eggs of queens held individually in the laboratory were sampled ca. six weeks after isolating the queens with nestmate workers and brood. (After Vargo and Ross 1989).

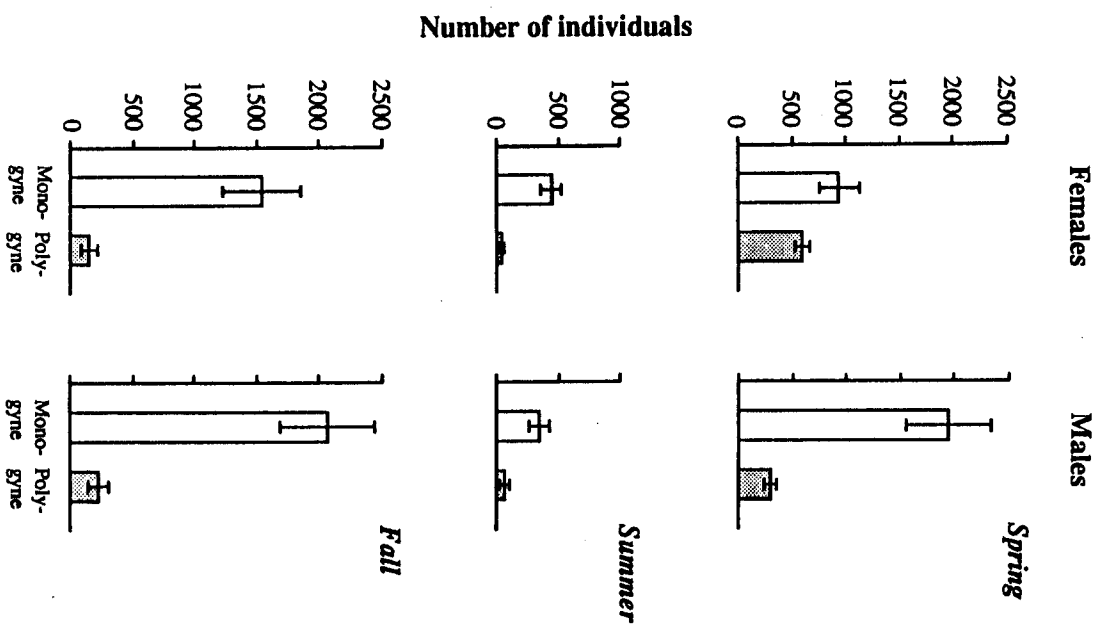


FIGURE 4. Numbers of sexuals (alates + pupae) present in monogyne and polygyne colonies of *S. invicta* from Georgia during three seasons of 1985. Bars=means±SE, n=25 in each case. Except for the number of females present in the spring sample, there were significantly fewer male and female sexuals present in the polygyne colonies during all three seasons ($P < 0.05$, t -test). (Adapted from Vargo and Fletcher 1987).

CONTROL OVER THE PRODUCTION OF SEXUALS

Vargo and Fletcher (1987) discovered that polygyne colonies in the field produce fewer male and female sexuals than monogyne colonies during all three seasons when sexuals are actively produced (Fig. 4), suggesting a negative relationship between queen number and production of sexuals in fire ant colonies. This hypothesis was supported by laboratory studies in which halves of divided polygyne colonies containing many queens failed to produce sexuals, while monogyne or queenless halves produced hundreds of both male and female sexuals (Vargo and Fletcher 1986a). The inhibitory influence was demonstrated to be mediated by a queen pheromone (Vargo and Fletcher 1986b); the daily addition of 10 corpses of functional queens inhibited the production of sexuals in small experimental units (5 g) of workers and brood, whereas an equal number of corpses of reproductively inactive virgin queens had no inhibitory effect (Fig. 5). This inhibitory pheromone appears to act indirectly by affecting the behavior of workers toward larvae in a sex-specific manner. In response to the pheromone, workers presumably restrict the quantity and/or quality of food given to female larvae resulting in their development as workers; in contrast, they kill young male larvae, which have no such alternative line of development. In addition to preventing the sexualization of larvae, workers may also respond to the pheromone by killing late instar larvae of both sexes after they have become sexualized (Vargo and Fletcher 1986b).

With the aim of providing a more sensitive test for the inhibitory pheromone, Vargo (1988) recently developed a bioassay in which individual queen corpses can be tested. With this procedure, the inhibitory activity of one queen equivalent or less can be detected in only two to three days, making it an exceptionally sensitive and rapid bioassay for a primer pheromone. Queen corpses - when placed in small cages which prevented direct contact by workers but through which volatile substances could readily pass - were not inhibitory. This suggests that this pheromone, like that inhibiting oogenesis and dealation, is relatively nonvolatile. Also, queen gasters were as effective as whole corpses, whereas heads and thoraces together were only slightly inhibitory. But as previously discussed, the effectiveness of gasters may relate to their attractiveness and not to the relative quantity of inhibitory pheromone they contain. Since the production of sexuals as well as oogenesis and dealation are under pheromonal inhibition in the fire ant, the same queen pheromone may mediate both responses. If so, this pheromone would be similar to the queen substance of the honey bee which, among other functions, inhibits both ovarian development in workers and the production of new queens (reviewed by Free 1987).

REGULATION OF QUEEN NUMBER

In the monogyne form of *S. invicta*, the presence of a single functional queen is usually enforced through execution of supernumerary queens by workers. There are, however, two conditions under which temporary polygyny is known. Monogyne colonies of this species are founded in a manner typical of many ants; after the mating flight, queens seal themselves in subterranean nest chambers and rear the first brood from their body

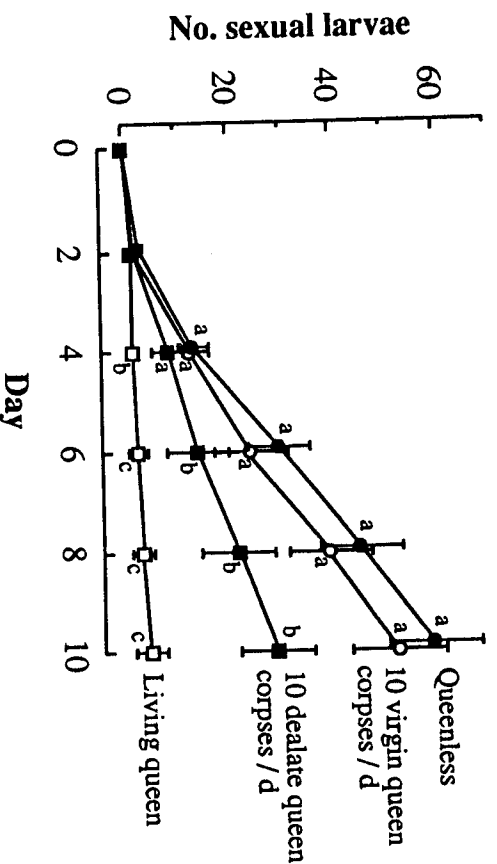


FIGURE 5. Numbers of sexual larvae produced in 5-g units of workers and brood. Shown are means \pm SE. Treatments with different lower case letters at a particular day differed significantly ($P < 0.05$, Newman-Keuls test, log transformation). $n = 20$ in each case. (From Vargo and Fletcher 1986b).

reserves (reviewed in Vinson and Greenberg 1986). In the field, newly-mated queens often associate in groups and cooperate in rearing the first brood. Such pleometrotically founded colonies always become monogyne when the first workers to emerge kill all but one queen (Markin et al. 1972; Tschinkel and Howard 1983; Fletcher 1986b).

In mature monogyne colonies, temporary polygyny may occur following removal or death of the mother queen. Once freed from her pheromonal inhibition, numerous virgin queens become reproductively active. However, the workers begin to execute them within 72 hours and continue until only one or two remain (Fletcher and Blum 1981a). How do workers choose among these virgin replacement queens? Fletcher and Blum (1983b) have proposed a multi-component hypothesis. They postulate that the quantity of pheromone produced by individual queens is positively correlated to fecundity, so that variable fecundity among coexisting queens forms the basis of a sort of pheromonal hierarchy. This hypothesis also holds that workers have a tolerance threshold for the level of some queen pheromone(s) in the colony and that they can distinguish individual queens according to the quantity of pheromone produced. Hence when the level of queen pheromone in the colony exceeds the tolerance threshold of workers, they begin to execute the poorest producers first and thereby retaining the most productive (i.e., most fecund) queen.

Results of experiments performed by these authors support such a mechanism (Fletcher and Blum 1983b). When queenless groups of workers were given the choice between two foreign queens, one highly fecund and the

other less so, they executed the queen of lower fecundity in 22 of 24 (92%) cases. As evidence of a positive correlation between fecundity and pheromone production, Fletcher and Blum (1983b) rely on the results of tests for the queen pheromone which inhibits oogenesis and dealation, though, as admitted by them, it is not known if this pheromonal signal is among those actually used by workers when they discriminate among queens under such conditions. The execution of foundress queens in pleometrotic associations may also be based on quantitative differences in pheromone production, but it has not been established whether the relative fecundity of queens is related to survival in such incipient colonies.

It has been suggested that in addition to the physogastric mother queen, monogyne colonies of *S. invicta* may contain one or more inseminated but reproductively inactive dealate queens. Tschinkel and Howard (1978) experimentally removed the mother queen from monogyne colonies in the field and reported that 27% of these nests possessed a functional inseminated queen when examined 8-10 weeks later. These authors hypothesized that such inseminated replacement queens were surviving foundresses from pleometrotic associations which had been reproductively inhibited by the previous queen. However, there has been no further evidence to support this hypothesis and it seems unlikely that monogyne colonies contain more than one inseminated queen. To my knowledge, not a single supernumerary dealate queen has been found among the thousands of monogyne colonies collected to date, and yet such queens should be present in more than one-quarter of these colonies if this hypothesis were true. The inseminated replacement queens found by Tschinkel and Howard may well have been adopted by the queenless colonies after a mating flight and/or the nests sampled after removal of the mother queen contained colonies other than those which were dequeenred, as monogyne colonies are known to change nest sites often (Hays et al. 1982).

Since workers normally enforce monogyny in *S. invicta*, how is it that they tolerate multiple queens in some colonies? Two mutually compatible possibilities come to mind. First, polygyne queens may produce relatively little pheromone, so that their combined production does not exceed the pheromonal tolerance threshold of the workers. Second, workers of polygyne colonies may have an elevated tolerance threshold or even lack one altogether. The current evidence tends to exclude the first possibility. When workers from both polygyne and monogyne colonies were presented with 25 foreign inseminated queens collected from a single mating flight, monogyne workers executed all but one in six of eight (75%) cases, whereas polygyne workers accepted nine or more in seven of eight (87.5%) cases (Fletcher and Blum 1983b). Since these queens all came from a single pool, the greater tendency of polygyne workers to tolerate multiple-queens in this case cannot be explained by abnormally low levels of pheromone production. Rather, it seems that compared to workers from monogyne colonies, polygyne workers have an elevated tolerance threshold for the queen pheromone(s) which elicits execution behavior. The circumstances under which this pheromone threshold changes, thereby permitting the coexistence of multiple queens, remain for future studies to determine.

CONCLUDING REMARKS

Our understanding of social control over reproduction in fire ant colonies has come a long way since it first became a subject of serious study only nine years ago. While this knowledge is far from complete, more is presently known about social regulation of reproduction in *S. invicta* than perhaps any highly eusocial species besides the honey bee. Queen pheromones appear to play a central role, underscoring the importance of chemical signals in regulating colony function in highly eusocial insects (Blum 1974). The number of distinct fire ant queen pheromones remains unknown, but three different aspects of reproduction are clearly under pheromonal control: oviposition by virgin queens, production of male and female sexuals, and control of queen number in monogyne colonies. While none of these pheromones has been chemically identified, the existence of bioassays for two of the three and the large number of queens provided by the abundance of polygyne colonies of this ant give much hope for progress along these lines. Other promising areas for future research include the interaction between the exocrine and endocrine systems of queen fire ants as well as the regulation of oviposition and egg viability in polygyne colonies.

The study of social factors regulating reproduction in *S. invicta*, as in other social insect pests, has obvious practical implications. Deliberate disruption of any one of the reproductive processes, e.g., the application of synthetic queen pheromones to prevent the production of sexuals, could offer efficient and environmentally safe avenues for control. It is too early to say whether such methods might prove feasible in the control of fire ant colonies. Clear evaluation must await chemical identification of the queen inhibitory pheromones coupled with a deeper understanding of their behavioral and physiological consequences.

ACKNOWLEDGMENTS

I thank Kenneth Ross for his helpful comments on the manuscript. This review was written while supported by a grant from the National Science Foundation (INT-8702250).

LITERATURE CITED

- BLUM, M.S. 1974. Pheromonal bases of social manifestations in insects, pp. 190-199. In M.C. Birch (ed.), Pheromones. North-Holland Publishing Co., New York.
- BØRGENSEN, L.W. 1990. A new aspect of the role of larvae in the pharaoh's ant society (*Monomorium pharaonis* (L.)), Formicidae, Myrmicinae): producer of fecundity-increasing substances to the queen. Insectes Soc. In Press.
- BOURKE, A.F.G. 1988. Worker reproduction in the higher eusocial Hymenoptera. Q. Rev. Biol. 63: 291-311.
- CHERIX, D. and D.J.C. FLETCHER. 1982. The eggs of founding queens of the imported fire ant, p. 249. In M. D. Breed, C. D. Michener and H. E. Evans (eds.), The biology of social insects, Westview Press, Boulder, Colorado. 419 pp.

- FLETCHER, D.J.C. 1986a. Perspectives on some queen pheromones of social insects with special reference to the fire ant, *Solenopsis invicta*, pp. 184-191. In C.S. Lofgren and R.K. Vander Meer (eds.), Fire ants and leaf-cutting ants: biology and management. Westview Press, Boulder, Colorado. 435 pp.
- FLETCHER, D.J.C. 1986b. Triple action of queen pheromones in the regulation of reproduction in fire ant (*Solenopsis invicta*) colonies. Adv. Invert. Repr. 4: 305-316.
- FLETCHER, D.C.J. and M.S. BLUM. 1981a. Pheromonal control of dealation and oogenesis in virgin queen fire ants. Science 212: 73-75.
- FLETCHER, D.C.J. and M.S. BLUM. 1981b. A bioassay technique for an inhibitory primer pheromone of the fire ant, *Solenopsis invicta* Buren. J. Ga. Entomol. Soc. 16: 352-356.
- FLETCHER, D.C.J. and M.S. BLUM. 1983a. The inhibitory pheromone of queen fire ants: effects of disinhibition on dealation and oviposition by virgin queens. J. Comp. Physiol. A 153: 467-475.
- FLETCHER, D.C.J. and M.S. BLUM. 1983b. Regulation of queen number by workers in colonies of social insects. Science 219: 312-314.
- FLETCHER, D.C.J., M.S. BLUM, T.V. WHITT and N. TEMPLE. 1980. Monogyny and polygyny in the fire ant, *Solenopsis invicta*. Ann. Entomol. Soc. Am. 73: 658-661.
- FLETCHER, D.C.J., D. CHERIX and M.S. BLUM. 1983. Some factors influencing dealation by virgin queen fire ants. Insectes Soc. 30: 443-454.
- FLETCHER, D.J.C. and K.G. ROSS. 1985. Regulation of reproduction in eusocial Hymenoptera. Ann. Rev. Entomol. 30: 319-343.
- FREE, J.B. 1987. Pheromones of social bees. Chapman and Hall, London. 218 pp.
- GLANCEY, B.M. 1986. The queen recognition pheromone of *Solenopsis invicta*, pp. 223-230. In C.S. Lofgren and R.K. Vander Meer (eds.), Fire ants and leaf-cutting ants: biology and management. Westview Press, Boulder, Colorado. 435 pp.
- GLANCEY, B.M., C.E. STRINGER and P.M. BISHOP. 1973. Trophic egg production in the imported fire ant, *Solenopsis invicta*. J. Ga. Entomol. Soc. 8: 217-220.
- GREENBERG, L., D.J.C. FLETCHER and S.B. VINSON. 1985. Differences in worker size and mound distribution in monogynous and polygynous colonies of the fire ant, *Solenopsis invicta* Buren. J. Kans. Entomol. Soc. 58: 9-18.
- HAYS, S.B., P.M. HORTON, J.A. BASS and D. STANLEY. 1982. Colony movement of imported fire ants. J. Ga. Entomol. Soc. 17: 266-274.
- LOFGREN, C.S., W.A. BANKS and B.M. GLANCEY. 1975. Biology and control of imported fire ants. Ann. Rev. Entomol. 20: 1-29.
- LOFGREN, C.S. and D.F. WILLIAMS. 1984. Polygynous colonies of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae) in Florida. Fla. Entomol. 67: 484-486.
- MARKIN, G.P., H.L. COLLINS and J.H. DILLIER. 1972. Colony founding by queens of the red imported fire ant, *Solenopsis invicta*. Ann. Entomol. Soc. Am. 65: 1053-1058.

- MARKIN, G.P., J.H. DILLIER and H.L. COLLINS. 1973. Growth and development of colonies of the red imported fire ant, *Solenopsis invicta*. Ann. Entomol. Soc. Am. 66: 803-808.
- MARKIN, G.P. and J.H. DILLIER. 1971. The seasonal life cycle of the imported fire ant, *Solenopsis saevissima richieri*, on the Gulf Coast of Mississippi. Ann. Entomol. Soc. Am. 64: 562-565.
- OBIN, M.S., B.M. GLANCEY, W.A. BANKS and R.K. VANDER MEER. 1988. Queen pheromone production and its physiological correlates in fire ant queens (Hymenoptera: Formicidae) treated with fenoxycarb. Ann. Entomol. Soc. Am. 81: 808-815.
- O'NEAL, J. and G.P. MARKIN. 1973. Brood nutrition and parental relationships of the imported fire ant *Solenopsis invicta*. J. Ga. Entomol. Soc. 8: 294-303.
- OSTER, G.F. and WILSON E.O. 1978. Caste and ecology in the social insects. Princeton University Press, Princeton, New Jersey. 352 pp.
- PETRALIA, R.S. and S.B. VINSON. 1978. Feeding in the larvae of the imported fire ant, *Solenopsis invicta*: behavior and morphological adaptations. Ann. Entomol. Soc. Am. 71: 643-648.
- PETRALIA, R.S., A.A. SORENSEN and S.B. VINSON. 1980. The labial gland system of larvae of the imported fire ant, *Solenopsis invicta*: ultrastructure and enzyme analysis. Cell Tiss. Res. 206: 145-156.
- ROSS, K.G. 1988. Differential reproduction in multiple-queen colonies of the fire ant *Solenopsis invicta*. Behav. Ecol. Sociobiol. 23: 341-355.
- ROSS, K.G. and D.J.C. FLETCHER. 1985. Comparative study of genetic and social structure in two forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. 17: 349-356.
- SOERENSEN, A.A., R.S. KAMAS and S.B. VINSON. 1983a. The influence of oral secretions from larvae on levels of proteinases in colony members of *Solenopsis invicta* Buren (Hymenoptera: Formicidae). J. Insect Physiol. 29: 163-168.
- SOERENSEN, A.A., T.M. BUSCH and S.B. VINSON. 1983b. Behaviour of worker subcastes in the fire ant, *Solenopsis invicta*, in response to proteinaceous food. Physiol. Entomol. 8: 83-92.
- TSCHINKEL, W.R. 1988. Social control of egg-laying rate in queens of the fire ant, *Solenopsis invicta*. Physiol. Entomol. 13: 327-350.
- TSCHINKEL, W.R. and D.F. HOWARD. 1978. Queen replacement in orphaned colonies of the fire ant, *Solenopsis invicta*. Behav. Ecol. Sociobiol. 3: 297-310.
- TSCHINKEL, W.R. and D.F. HOWARD. 1983. Colony founding by pleometrosis in the fire ant, *Solenopsis invicta*. Behav. Ecol. Sociobiol. 12: 103-113.
- VANDER MEER, R.K. 1983. Semiochemicals and the red imported fire ant (*Solenopsis invicta* Buren) (Hymenoptera: Formicidae). Fla. Ent. 66: 139-161.
- VARGO, E.L. 1988. A bioassay for a primer pheromone of queen fire ants (*Solenopsis invicta*) which inhibits the production of sexuals. Insectes Soc. 35: 382-392.
- VARGO, E.L. and D.J.C. FLETCHER. 1986a. Queen number and the production of sexuals in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. 19: 41-47.

- VARGO, E.L. and D.J.C. FLETCHER. 1986b. Evidence of pheromonal queen control over the production of male and female sexuals in the fire ant, *Solenopsis invicta*. J. Comp. Physiol. A 159: 741-749.
- VARGO, E.L. and D.J.C. FLETCHER. 1987. Effect of queen number on the production of sexuals in natural populations of the fire ant, *Solenopsis invicta*. Physiol. Entomol. 12: 109-116.
- VARGO, E.L. and D.J.C. FLETCHER. 1989. On the relationship between queen number and fecundity in polygynous colonies of the fire ant, *Solenopsis invicta*. Physiol. Entomol. 14: 223-232.
- VARGO, E.L. and K.G. ROSS. 1989. Differential viability of eggs laid by queens in polygynous colonies of the fire ant *Solenopsis invicta*. J. Insect Physiol. 35: 587-593.
- VINSON, S.B. and L. GREENBERG. 1986. The biology, physiology and ecology of imported fire ants, pp. 193-226. In S. B. Vinson (ed.), Economic impact and control of social insects. Praeger, N.Y. 421 pp.
- VOSS, S.H. 1981. Trophic egg production in virgin fire ant queens. J. Ga. Entomol. Soc. 16: 437-440.
- VOSS, S.H. 1985. Rapid, simple DNA staining for fire ant eggs. J. Entomol. Sci. 20: 47-49.
- VOSS, S.H. and M.S. BLUM. 1988. Trophic and embryonated egg production in founding colonies of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). Sociobiol. 13: 271-278.
- WEST-EBERHARD, M.J. 1981. Intragroup selection and the evolution of insect societies, pp. 3-17. In R. D. Alexander and D. W. Tinkle (eds.), Natural selection and social behavior. Chiron Press, New York. 532 pp.
- WILLER, D.E. and D.J.C. FLETCHER. 1986. Differences in inhibitory capability among queens of the ant *Solenopsis invicta*. Physiol. Entomol. 11: 475-482.