constituent jusqu' à 50% de l'effectif des reines pondeuses des sociétés polygynes de cette espèce - émettent en général de 5 à 25% d'oeufs de moins que leurs compagnes inséminées. La proportion des oeufs fertiles émis par les reines, determinée après incubation et coloration de la chromatine, varie considérablement d'un individu à l'autre. En général, les reines inséminées produisent une proportion d'oeufs fertiles beaucoup plus grande que ne le font les reines non inséminées. Il n'y a pas de corrélation entre la proportion des oeufs fertiles émis et la fécondité chez les reines récoltées dans la nature. Ainsi, le succés reproductif réel d'une reine issue d'une société polygyne de cette espèce et peut-être d'autres espèces d'insectes sociaux, apparaît être un phénomène plus complexe que ne le laisse supposer l'étude de sa simple fécondité comme on le pense habituellement.

Mots clés: *Fourmis, polygynie, fécondité, fertilité des oeufs, variabilité reproductrice*

INTRODUCTION

Although the occurrence of multiple-queen colonies (polygyny) is common in ants, there have been few detailed investigations of the reproductive structure of polygyne colonies. Information of how reproductive effort is distributed among nestmate queens is important to our understanding of social organization in these colonies and can be expected to play an important role in testing hypotheses concerning the evolution and maintenance of polygyny in social insects (see ROSS, 1988).

Recent studies have begun to examine closely the reproductive roles of individual queens in polygyne *Solenopsis invicta*. Based on the types of eggs laid, polygyne colonies of this ant contain 3 distinct reproductive classes of functional (egg-laying) queens. Uninseminated queens comprise about 30% of all functional queens in a colony (FLETCHER *et al.*, 1980; VARGO and FLETCHER, 1987, 1988). Among inseminated queens, some 15-20% are diploid-male-producing queens in which about half of the diploid offspring develops into sterile males, whereas non-diploid-male-producing queens produce normal diploid females (for details, see ROSS and FLETCHER, 1985).

As part of a series of studies on the reproductive structure of polygyne colonies of *S. invicta*, the present study was conducted to determine whether and to what extent polygyne queens differ in fecundity and the proportion of viable eggs produced, with particular attention paid to variability among individuals and between inseminated and uninseminated queens.

METHODS

Relationship between queen number and fecundity
Laboratory colonies

Experimental colonies consisted of 75 g of workers and 25 g of brood drawn from a mixture of 20 different polygyne colonies collected near Athens, Georgia, U.S.A. in July 1986. Each colony was given 2, 4, 8, 16, 32, 64, 128, or 256 dealate queens taken at random from a single pool of queens coming from the 20 original colonies. There were 3 replicates of each treatment, for a total of 24 experimental colonies. Colonies were maintained in the laboratory as described by VARGO and FLETCHER (1988).

Nine weeks after set-up, the experimental colonies were weighed and all sexual forms were removed and counted; these included dealate queens, female and male alates, sexual pupae, and sexual larvae. All dealate queens were weighed individually and their spermathecae checked for sperm to determine whether or not they were inseminated.

Field colonies

Twelve polygyne colonies were collected at the Brackenridge Field Laboratory of the University of Texas at Austin in Austin, Texas in spring of 1987. Immediately after collection, dealate queens were removed from the soil and then weighed individually. The weight of each colony was determined by weighing all ants after separating them from the soil by flooding (JOUVENAZ *et al.*, 1977). These colonies had a mean (±SD) queen number of 70.9 ± 54.0 (range = 5-186) and weighed 81.7 ± 75.1 g (range = 11.8-266.5 g).

To determine whether the weight of a queen was indicative of her relative fecundity as suggested but not demonstrated by previous studies (FLETCHER and BLUM, 1983; WILLER and FLETCHER, 1986), queens coming directly from the field were weighed and then subjected to a 5-h oviposition test (FLETCHER *et al.*, 1980). All of the tested queens were dissected and their spermathecae examined for sperm to determine whether they were inseminated.

Viability of eggs laid by individual queens

Polygyne colonies were collected during the summer of 1987 at the Brackenridge field laboratory at the University of Texas at Austin. Queens were removed immediately from the soil, weighed and then placed in a small cup for 24 h with 5-10 nestmate workers. Upon removal from the cup, all queens were dissected to determine their insemination status and the eggs were incubated for 72 h at 30° C with workers and then stained for chromatin using the method of VOSS (1985). In all, the eggs of 119 queens (8.5 ± 6.5 queens/colony) were investigated, of which 84 queens (70.6%) were inseminated and 35 were uninseminated. A mean of 118.9 ± 55.5 eggs per queen was examined.

RESULTS

Relationship between queen number and fecundity

The weight of a queen appears to be a relatively good indicator of fecundity for *S. invicta* (fig. 1). This relationship seems to apply equally well to both inseminated and uninseminated queens; when plotted separately and
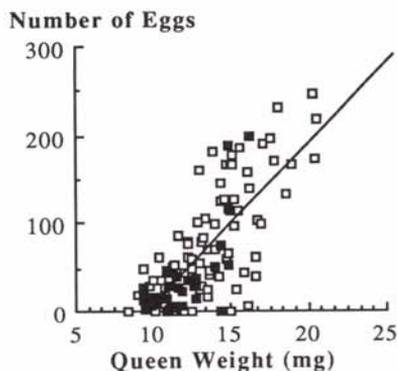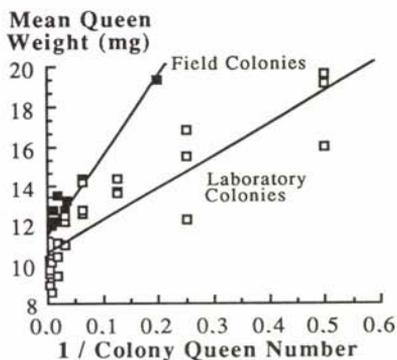
Fig. 1. - Relationship between the weight of dealate queens and their fecundity as measured by a 5 h oviposition test. Open squares represent inseminated queens ($n = 80$) and solid squares represent uninseminated queens ($n = 35$). The line shown is fitted to both inseminated and uninseminated queens pooled and is described by $y = -169.77 + 18.07x$ ($R^2 = 0.57$; $F_{1,113} = 149.53$, $P < 0.0001$).

Fig. 1. - Relation entre le poids des reines désailées et leur fécondité au cours d'un test d'oviposition de 5 heures. Les carrés blancs représentent les reines inséminées ($n = 80$) et les carrés noirs représentent les reines non inséminées ($n = 35$). La droite de régression est calculée pour l'ensemble des reines inseminées et non inséminées. Son équation est: $y = -169.77 + 18.07x$ ($R^2 = 0.57$; $F_{1,113} = 149.53$, $P < 0.0001$).

Fig. 2. - Relationship between number of dealate queens in a colony and mean queen weight. Solid squares represent field colonies ($n = 12$) and open squares represent laboratory colonies [$n = 8$ treatments (2, 4, 8, 16, 32, 64, 128, and 256 queens) x 3 replicates = 24]. The lines are described by the equations $y = 11.41 + 40.66/x$ ($R^2 = 0.88$; $F_{1,11} = 76.34$, $P < 0.0001$) for field colonies and $y = 10.62 + 16.32/x$ ($R^2 = 0.78$; $F_{1,23} = 76.90$, $P < 0.0001$) for laboratory colonies.

Fig. 2. - Relation entre le nombre des reines désailées présentes dans une colonie et leur poids moyen. Les carrés noirs représentent les colonies provenant de la nature ($n = 12$) et les carrés blancs représentent les colonies maintenues en élevage au laboratoire [$n = 8$ traitements (2, 4, 8, 16, 32, 64, 128 et 256 reines) x 3 répétitions = 24]. Les droites de régression sont données par les équations: $y = 11.41 + 40.66/x$ ($R^2 = 0.88$; $F_{1,11} = 76.34$, $P < 0.0001$) pour les colonies provenant de la nature et $y = 10.62 + 16.32/x$ ($R^2 = 0.78$; $F_{1,23} = 76.90$, $P < 0.0001$) pour les colonies maintenues en élevage au laboratoire.

compared, neither the slopes nor the elevations of the two lines differed significantly (both $t_{112} \leq 1.63$, $P > 0.1$).

In both the laboratory and field colonies, the number of colony queens and mean queen weight were inversely related (*fig. 2*), indicating that increasing queen number has a negative effect on the fecundity of individual queens. The reciprocal of colony queen number accounted for 88% and 78% of the variation in mean

queen weight in field and laboratory colonies, respectively. The reciprocal nature of this relationship suggests that the effect of increasing queen number is strongest when queen number is low (< 50). The slopes of the lines fitted to the field and laboratory colonies differed significantly $(t_{32} = 118.37, P < 0.0001)$, possibly reflecting differences between field and laboratory conditions and/or between colonies in the Texas and Georgia populations. Nonetheless, that this negative relationship holds equally well for the laboratory colonies where the queens were taken from a single pool demonstrates that the fecundity of queens changes in response to queen number.

There was no significant effect of colony size (total weight) on mean queen weight in the field colonies $(R^2 = 0.15;\ F_{1,10} = 0.20, P > 0.66)$, despite the large range in colony size, suggesting that colony size by itself bears little if any relationship to the weights of queens. Similarly, there was no significant effect of final colony size on mean queen weight in the laboratory colonies $(R^2 = 0.15;\ F_{1,23} = 0.51, P > 0.48)$.

Uninseminated queens constituted a substantial proportion of the functional queens in both the laboratory and field colonies. Excluding the treatment receiving 2 queens, in which both queens were inseminated in all 3 replicates, the mean proportion of uninseminated queens in the laboratory colonies from Georgia was 0.21 ± 0.11, whereas the field colonies from Texas contained a mean proportion of 0.30 ± 0.19 uninseminated queens.

Within the same colony, inseminated queens were generally more fecund than their uninseminated nestmates, weighing 5-25% more. This difference was most striking in the field colonies; excluding the one colony in which only 5 inseminated queens were found, the mean weight of inseminated queens was higher than that of their uninseminated nestmates in all 11 colonies, and these differences were significant ($P < 0.05$, two-tailed t-test) in 8 (73%) cases. Moreover, the heaviest queen was inseminated in 10 (91%) of the 11 colonies and the lightest queen was uninseminated in 10 cases. This same trend held for the laboratory colonies, but here it was not as pronounced.

Viability of eggs laid by individual queens

Both inseminated and uninseminated queens produced a surprisingly variable proportion of nonviable eggs, but this proportion was considerably higher in uninseminated queens (fig. 3; $t_{117} = 16.26$, $P \ll 0.0001$; angular transformation). Of the 84 inseminated queens examined, 80 (95%) had over 50% embryonated eggs, whereas only 7 (20%) of the 35 uninseminated queens were in the same category. Moreover, 20 (57%) of the uninseminated
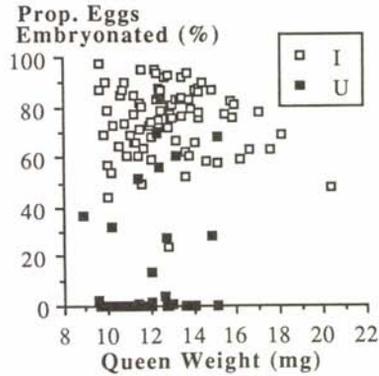
queens had no embryonated eggs at all.

There was no significant correlation between queen weight and the proportion of embryonated eggs for either inseminated or uninseminated queens (r_{83} = -0.11 for inseminated and r_{34} = 0.16 for uninseminated queens, both $P > 0.5$; angular transformation of proportions; see *fig. 3*), suggesting that oviposition rate and egg viability are independently regulated phenomena.

DISCUSSION

Under field conditions, functional queens in polygyne colonies of *S. invicta* may exhibit high variability in fecundity and the proportion of their eggs forming embryos. Much of this variablity is related to insemination status, with uninsemi-

Fig. 3. - Relationship between queen weight, proportion of eggs forming embryos, and insemination status in field collected queens. Inseminated (I): $n = 84$; uninseminated (U): $n = 35$.

Fig. 3. - Relation entre le poids des reines et la proportion de leurs oeufs qui se révèlent embryonnés chez les reines inséminées (I; $n = 84$) et non inséminées (U; $n = 35$), provenant directement de la nature.

nated queens being less fecund and laying a far lower proportion of viable eggs than their inseminated counterparts. Even among inseminated nestmate queens, there is high variability in fecundity and the proportion of viable eggs laid. Thus it seems reasonable to expect that these differences in reproductivity will translate into short and long term differences in realized reproductive success. Recent genetic evidence of differences in short term reproductive success among cohabiting queens in polygyne *S. invicta* has been obtained by ROSS (1988) who found considerable variability in relative production of female offspring, especially sexuals.

The strong negative correlation between queen number and fecundity of individual queens of *S. invicta* illustrates the 'reproductivity effect' first recorded in the social bees and wasps (MICHENER, 1964). In addition, the finding that the oviposition rate of queens changes in response to queen number demonstrates that queen fecundity in polygyne colonies of *S. invicta* is under social control. The lack of a significant effect of colony size on the fecundity of queens rules out an exclusive effect of decreased nutrition through low worker/queen ratios or the presence of proportionately fewer

fourth instar larvae which are known to affect the fecundity of monogyne *S. invicta* queens (TSCHINKEL, 1988). Rather, that well-developed pheromonal queen control over both adults (FLETCHER and BLUM, 1981, 1983) and larvae (VARGO and FLETCHER, 1986) are known to occur in this species would seem to implicate mutual inhibition via pheromones as the most likely mechanism involved. Recent evidence (VARGO and ROSS, unpublished) suggests that the viability of eggs laid by queens is also under social control.

A surprising result is that oviposition rate and proportion of viable eggs laid are independent in field-collected queens. This indicates that fecundity alone is not an accurate measure of reproductive success in polygyne *S. invicta*. Rather, realized reproductive success of individual queens appears to involve an unsuspected degree of complexity, and it is possible that a similar degree of complexity in reproductive activity exists in other species of social insects. Thus caution should be exercised in equating fecundity with reproductive success, as is commonly assumed in studies of reproductive roles in social insect colonies.

The results of this study give us important insights into the reproductive structure of polygyne *S. invicta*. Nevertheless, we are far from a complete understanding of the reproductive role played by individual queens. Further studies along these lines, especially those concerning the physiological basis of differential reproduction and the social factors influencing it, will no doubt prove rewarding.

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