

On the relationship between queen number and fecundity in polygyne colonies of the fire ant *Solenopsis invicta*

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ABSTRACT. The reproductive status of individual queens in relation to the number of queens in polygyne colonies of *Solenopsis invicta* Buren was investigated under both field and laboratory conditions. In field colonies, the weight of individual queens is inversely related to the number of resident queens present. The weight of a queen is positively correlated with fecundity, as measured by the number of eggs laid in 5 h in isolation. Thus increasing queen number has a strong negative effect on the fecundity of individual queens in these colonies. A similar relationship was established in standardized laboratory colonies using queens from a single experimental population. Colony size by itself had no significant effect on queen weight in either the field or laboratory colonies, suggesting that the inverse relationship between queen number and fecundity results from mutual inhibition among queens, possibly involving pheromones, rather than reduced nutrition through lower worker/queen ratios. While uninseminated queens can comprise up to 50% of the functional (i.e. egg-laying) queens in polygyne colonies of this ant, they tend to be less fecund than their inseminated nestmates; uninseminated queens within a given colony generally weigh 5–25% less.

Key words. Social insects, fire ants, polygyny, queen number, fecundity.

Introduction

The fire ant, *Solenopsis invicta* Buren, is native to South America and was inadvertently introduced to the United States c. 1940 (Lofgren *et al.*, 1975). From its initial point of introduction, this ant rapidly expanded its distribution to include virtually all of the southeastern and

south-central U.S., where it has attained pest status. Within this range, *S. invicta* typically forms single-queen (monogyne) colonies, but populations of multiple-queen (polygyne) colonies have also been described from several locations. Polygyne colonies were first reported from Mississippi by Glancey *et al.* (1973, 1975), and have since been found in Texas (Hung *et al.*, 1974; Miranda & Vinson, 1982), Florida (Morrill, 1974; Lofgren & Williams, 1984), Georgia and Louisiana (Fletcher, 1983) and Alabama (D. Fletcher and K. Ross, unpublished data). In addition to possessing a distinctive social structure, polygyne colonies differ from monogyne

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colonies in having smaller workers (Greenberg *et al.*, 1985) and in the close spacing of mounds consistent with budding as a means of colony reproduction (Fletcher, 1983; Greenberg *et al.*, 1985; Vargo & Porter, 1988).

By means of oviposition tests (isolating queens in vials to count the number of eggs laid) and direct observation of oviposition, Fletcher *et al.* (1980) demonstrated that polygyny in *S. invicta* is indeed functional, that is more than one queen lays eggs. These authors found that both inseminated and uninseminated queens from polygyne colonies are functional. That the latter may comprise up to 50% of the functional queens in a colony (see, e.g., Lofgren & Williams, 1984; Vargo & Fletcher, 1987) is a peculiar feature of polygyny in this ant. Evidence from genetic studies corroborates that the offspring of many females are being reared in polygyne colonies of *S. invicta* (Ross & Fletcher, 1985a).

Fletcher *et al.* (1980) found that queens from polygyne colonies are less physogastric and lay fewer eggs per individual than queens from monogyne colonies, suggesting a negative relationship between queen number and fecundity of individual queens in this species. Evidence supporting such a relationship was obtained in laboratory colonies by Greenberg *et al.* (1985) who found that the number of queens was correlated negatively with the number of eggs laid per queen, but correlated positively with the total egg number. However, the fecundity of individual queens in relation to queen number as it exists under field conditions has not been investigated in detail in *S. invicta*, nor has it been studied experimentally. Therefore, to fill this gap as well as to determine the relative reproductive status of cohabiting inseminated and uninseminated queens, we investigated the relationship between queen number and fecundity in both field and standardized laboratory colonies.

Methods

Laboratory colonies

Twenty polygyne colonies of *S. invicta* were collected in Walton Co., Georgia, on 25 and 27 July 1986. [For convenience, the inhabitants of a single mound of this species will be referred to as a colony, although it seems likely, but has not

been established, that mounds in a given area are interconnected (Greenberg *et al.*, 1985; Bhatkar & Vinson, 1987).] The ants were removed from the soil by flooding (Jouvenaz *et al.*, 1977) and maintained in the laboratory at $29 \pm 2^\circ\text{C}$ and 14 h light/day. On 8 August the colonies were sieved to remove all sexual forms (Vargo & Fletcher, 1986a), including dealate queens, most of which are inseminated egg-layers (Fletcher, 1983; Vargo & Fletcher, 1987). The colonies had a mean weight of 152.5 ± 34.2 g (\pm SD, range 87.1–215.1 g) and contained 103.7 ± 105.1 queens (range 25–452). The dealate queens from all of the colonies were pooled into a single container. The workers and brood from the colonies were mixed together to form a homogeneous source for the experimental colonies which consisted of 75 g of workers and 25 g of brood of all stages, a weight ratio of workers/brood close to that found in the source colonies at the time of set-up (0.26 ± 0.09). The experimental colonies were housed in plastic trays ($40 \times 25 \times 8.5$ cm) equipped with four nests (14 cm diameter Petri dishes half filled with damp plaster). Each colony was given 2, 4, 8, 16, 32, 64, 128, or 256 queens taken at random from the single pool of queens. The mean weight of 100 such queens was 9.5 ± 1.6 mg. There were three replicates of each treatment, for a total of twenty-four experimental colonies. The ants were fed a copious diet of pureed beef, eggs, sugar and multiple vitamins in an agar base. This was supplemented by crickets, mealworms, pureed vegetables, and whipped eggs.

On 8–12 October 1986, c. 9 weeks after set-up, the experimental colonies were weighed and then sieved to remove all sexual forms, which included dealate queens, female and male alates, sexual pupae, and sexualized larvae (larvae >4 mm long). The numbers of each sexual form were counted and the dealate queens were weighed individually. All dealate queens were dissected and their spermathecae checked for sperm. Of the 1530 queens placed in the colonies at the beginning of the experiment, 1447 (94.6%) survived and were recovered at the end. The loss of queens was fairly uniform among the replicates, with no particular replicate losing more than 12.5% of the original queens.

Field colonies

Twelve polygyne colonies were collected at the Brackenridge Field Laboratory of the

University of Georgia, on 14 May 1986. The colonies were collected from 14 May queen fecundity (unpublished) obtaining all queens collected at the top of the mounds in the tops of the mounds on a sunny morning. Immediately after collection the ants were spread out on a tray and searched for dealate queens present in the colonies individually, more than ten queens per colony). To determine the remaining queens, the colonies had to be flooded (range 5–186 g) (11.8–266.5 g).

Results of the experiment suggested that there was a good indication of polygyny (Fletcher 1987). The relationship between queen number and maximum number of functional virgin queens (Fletcher & Blum 1987) was determined by per ovariole dissection. The functional virgin queens were determined by dissection of queens of known age and oviposition technique. Queens with less than one functional ovariole were placed in a layer of damp plaster for 5 h, the queen was weighed, the eggs laid by the queen were weighed, and the spermathecae examined to determine whether they

Results

The weight of the colonies was a good indicator of polygyny, as shown by the relationship between the weights of qu

University of Texas at Austin in Austin, Texas, from 14 May to 6 June 1987, a time of year when queen fecundity reaches a maximum (unpublished data). To maximize the chances of obtaining all members of a colony, the ants were collected at times when they were concentrated in the tops of the mounds, generally on warm sunny mornings following a relatively cool night. Immediately after collection, the soil containing the ants was taken to the laboratory where it was spread out in a thin layer and thoroughly searched for dealate queens. All dealate queens present in each colony were then weighed individually, with an upper limit of 100 queens if more than this number were present (three colonies). To determine the weight of each colony, the remaining ants were separated from the soil by flooding as above and then weighed. These colonies had a mean queen number of 70.9 ± 54.0 (range 5–186) and weighed 81.7 ± 75.1 g (range 11.8–266.5 g).

Results of previous studies of *S. invicta* have suggested that the weight of a functional queen is a good indicator of relative fecundity. Willer & Fletcher (1986) found a strong positive correlation between the weights of egg-laying queens (both inseminated and uninseminated) and the maximum number of oocytes per ovariole, and Fletcher & Blum (1983) found a positive correlation between the maximum number of oocytes per ovariole and the number of eggs laid by functional virgin queens. In the present study, to determine whether the weight of a queen was indeed indicative of her relative fecundity, queens of known weight were subjected to an oviposition test (Fletcher *et al.*, 1980). Within 1 h of collection, ten queens from each colony [or all queens if less than ten were present (one colony)] were placed in small cups containing a thin layer of damp plaster and held at $30 \pm 1^\circ\text{C}$. After 5 h, the queens were removed and the number of eggs laid by each queen was counted. All of the weighed queens were dissected and their spermathecae examined for sperm to determine whether they were inseminated.

Results

The weight of a queen appears to be a relatively good indicator of fecundity for *S. invicta*, as shown by the linear relationship between the weights of queens and the numbers of eggs laid

in the 5 h oviposition test (Fig. 1). This relationship seems to apply equally well to both inseminated and uninseminated queens; when plotted separately and 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 weights of queens are not fixed in relation to the number of resident queens, e.g. due to differ-

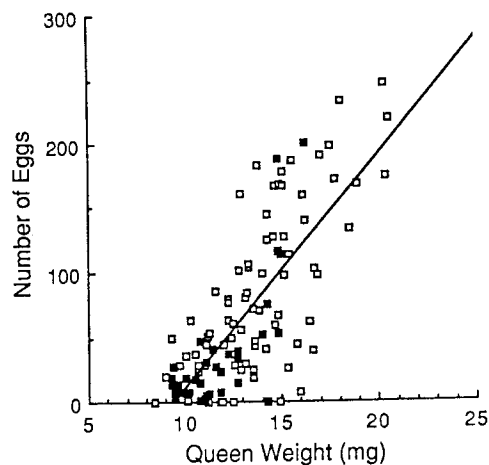


FIG. 1. Relationship between the weight of dealate queens and their fecundity as measured by a 5 h oviposition test. Open squares represent inseminated queens ($n=80$) and solid squares represent uninseminated queens ($n=35$). The line shown is fitted to both inseminated and uninseminated queens pooled and is described by $y = -169.77 + 18.07x$ ($R^2 = 0.57$; $F_{1,113} = 149.53$, $P < 0.0001$).

ences in overall body size as may occur in some species of *Myrmica* (Elmes, 1974), but rather that they reflect the degree of fecundity which changes in response to queen number.

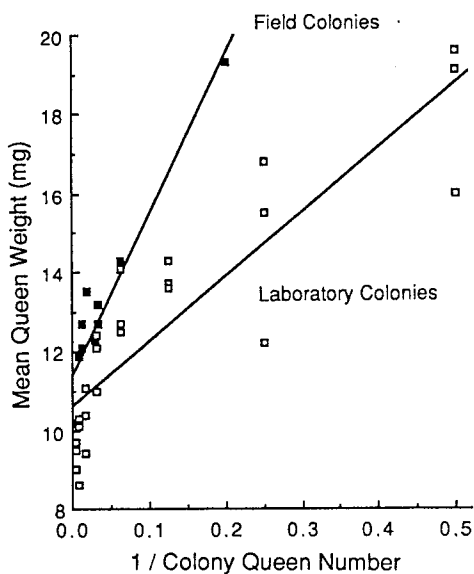


FIG. 2. Relationship between number of dealate queens in a colony and mean queen weight. Solid squares represent field colonies ($n=12$) and open squares represent laboratory colonies ($n=24$). The lines are described by the equations $y=11.41+40.66/x$ ($R^2=0.88$; $F_{1,11}=76.34$, $P<0.0001$) for field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

A reciprocal function relating queen number and mean queen weight was chosen based on visual inspection of the data and because it might be expected that colony resources are being divided more ways as queens are added, although evidence presented below suggests that mutual inhibition among queens may be much more important in determining fecundity. However, it should be noted that when the mean queen weights were regressed against the log of the number of colony queens, the results were very similar (both $R^2 \geq 0.82$, $P < 0.0001$).

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 ($R^2=0.15$; $F_{1,23}=0.51$, $P>0.48$). Moreover, when colony size was added to the regression for the lines shown in Fig. 2, it failed to explain significantly any additional variation in mean queen weight in either the field or laboratory colonies.

Queen number by itself did not affect the growth of laboratory colonies, calculated as the difference between the final weight and the initial weight of 100 g (range -43.8 – 87.1 g), as there was no significant effect of either the total number of queens or the number of inseminated queens on this value (both $R^2 \leq 0.07$; $F_{1,23} \leq 1.54$, $P > 0.22$). However, a more important relationship in this regard might be a measure of the total fecundity of all colony queens. Based on the results of the 5 h oviposition test of field-collected individuals, queens weighing 9.4 mg or less can be expected to lay negligible quantities of eggs. Therefore, if this weight is taken as a baseline, any weight above 9.4 mg can be considered 'fecundity'. When summed over all queens in a colony, this fecundity accounted for 69% of the variation in colony growth ($F_{1,23}=48.49$, $P<0.0001$); this relationship was even stronger when inseminated queens only were included ($R^2=0.74$; $F_{1,23}=44.87$, $P<0.0001$), since unseminated queens do not contribute directly to worker production.

In the case of the field colonies, colony weight was not significantly related to queen number or summed fecundity; this applied to analyses involving all colony queens as well as those involving inseminated queens only (all $R^2 \leq 0.42$; $F_{1,10} \leq 6.53$, $P > 0.05$). However, the relationship between queen number and colony size in the field may be blurred if extensive movement of workers and brood occurs among neighbouring mounds of the polygyne form (see, e.g., Bhatkar & Vinson, 1987).

Unseminated queens constituted a substantial proportion of the functional queens in both the laboratory and field colonies. Excluding the treatment receiving two queens, in which both queens were inseminated in all three replicates, the mean proportion of unseminated queens in the laboratory colonies was 0.21 ± 0.11 (range 0.06–0.37), a proportion close to that found in the same Walton Co., Georgia, population the previous summer (0.26 ± 0.14 ; Vargo & Fletcher, 1987). In the field colonies from Texas,

which were collected in spring, the mean proportion of unseminated queens was 0.30 ± 0.19 [range 0 (in the colony containing only five queens) to 0.51], values nearly identical to those obtained in spring 1985 for colonies of the Walton Co., Georgia, polygyne population (0.30 ± 0.18 ; Vargo & Fletcher, 1987). Thus colonies of these two distant polygyne populations appear not to differ appreciably in the proportion of unseminated queens they contain.

Within the same colony, inseminated queens were generally more fecund than their unseminated nestmates, weighing 5–25% more (Fig. 3). This difference was most striking in the field colonies; excluding the one colony in which only five inseminated queens were found, the mean weight of inseminated queens was higher than that of their unseminated nestmates in all eleven colonies, and these differences were significant ($P < 0.05$, two-tailed *t*-test) in eight (73%) cases. Moreover, the heaviest queen was

inseminated in ten (91%) of the eleven colonies and the lightest queen was unseminated in ten cases. This same trend held for the laboratory colonies, but here it was not as pronounced; excluding all of the replicates in the two and four queen treatments and one replicate of the eight queen treatment in which there were either none or only one unseminated queen present, the mean weight of inseminated queens was higher than that of their unseminated nestmates in sixteen (94%) of the seventeen colonies, and in six (35%) cases these differences were significant. The heaviest queen was inseminated in sixteen (94%) and the lightest queen was unseminated in ten (59%) of the seventeen laboratory colonies.

The frequency distributions of queen weights for four representative colonies are shown in Fig. 3. In general, the distributions were continuous with no clear gap between the heaviest queen or queens, suggesting that there is no

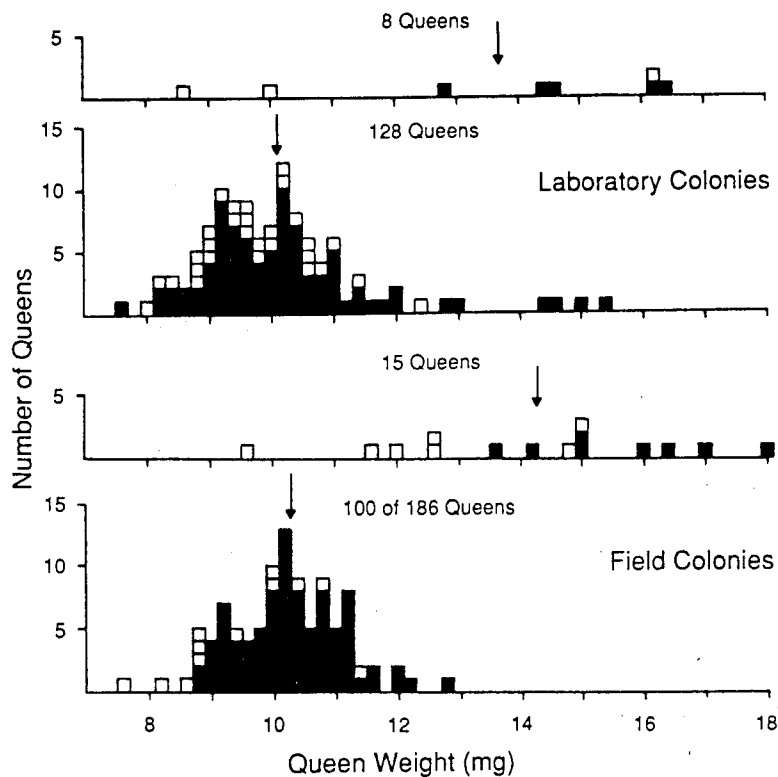


FIG. 3. Frequency distributions of queen weights in representative laboratory and field colonies containing low and high queen numbers. Solid squares represent inseminated queens and open squares represent unseminated queens. Arrows indicate the mean queen weight for each colony.

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obvious domination of reproduction in a colony by one or a few individuals. For example, using the relationship between queen weight and relative fecundity above, the heaviest 10% of the queens of the four colonies shown in Fig. 3 are predicted to lay only c. 25% of the total eggs.

Analysis of the frequency distributions of queen weights suggested a relationship between high queen number and positive skewness. Of the eighteen laboratory colonies with at least eight queens, six (33%) had queen weight frequency distributions which deviated slightly but significantly from the normal ($P < 0.05$, Kolmogorov-Smirnov goodness of fit test); all of these contained sixty-four or more queens and all had distributions skewed significantly to the right [$P < 0.05$, test of symmetry (Zar, 1984)]. In the case of the field colonies, this tendency was weaker; seven (64%) of the twelve colonies had distributions which deviated significantly from the normal, and all of these had thirty-five or more queens. However, the distributions in only two of these seven were significantly skewed, both to the right.

As suggested by Fig. 3, there was a negative relationship between the number of queens and the variance in queen weight for both the field

($R^2 = 0.56$; $F_{1,10} = 12.82$, $P < 0.005$) and laboratory colonies ($R^2 = 0.29$; $F_{1,22} = 7.80$, $P < 0.02$), suggesting that the distribution of queen weights is more dispersed when queen number is low than when it is high. However, the lack of a significant correlation between queen number and the range of queen weights in either the field or laboratory colonies (both $R^2 = 0.05$, $P > 0.4$) shows that a wide range of queen weights was present at all queen numbers. Apparently, some queens are able to attain relatively high levels of fecundity no matter how high the queen number.

The number of queens had a strong negative effect on the production of sexuals in the laboratory colonies (Fig. 4), supporting previous findings that queens of this species inhibit the production of sexuals pheromonally, with more queens resulting in stronger inhibition (Vargo & Fletcher, 1986a, b, 1987). The relationship between queen number and the production of sexuals found in the present study was a logarithmic one, indicating that the presence of additional queens has a greater effect on the intensity of inhibition at low queen number (fewer than fifty) than at high queen number. Although this was not investigated in the field colonies in the present study, a negative correlation between queen number and the production of sexuals was found previously (Vargo & Fletcher, 1987) for field colonies in the Walter Co., Georgia, population in two of three seasons.

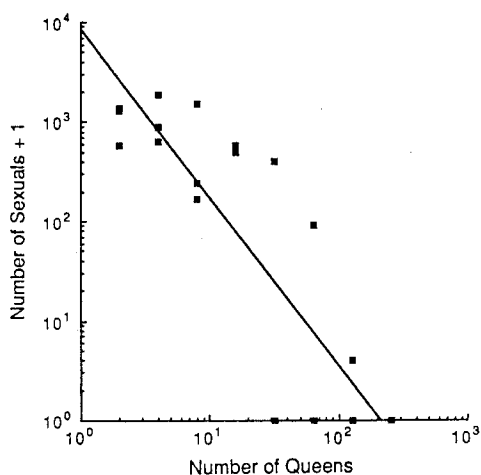


FIG. 4. Relationship between the number of queens in laboratory colonies and the number of sexuals (alates, pupae, and sexualized larvae) produced after c. 9 weeks. The line shown is described by $\log(y+1) = 3.93 - 1.69 \log x$ ($R^2 = 0.73$; $F_{1,22} = 60.08$, $P < 0.0001$). All replicates began with equivalent amounts of workers and brood drawn from a single homogeneous source.

Discussion

These results provide a detailed look at the negative relationship between queen number and the relative reproductive competence of individual queens in the polygyne form of *S. invicta*, and give some insight into the possible mechanisms involved. In noting the low degree of physiological variation in queens of polygyne colonies compared to the highly physiogastric queens of conspecific monogyne colonies, Fletcher *et al.* (1980) hypothesized that polygyne queens are either fed by the workers (presumably due to low worker/queen ratios), or, alternatively, that they experience a reduction of oviposition via mutually inhibitory pheromones. The lack of a significant effect of colony size on the fecundity of queens in the present study rules out an exact

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sive 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 & Blum, 1981, 1983) and larvae (Vargo & Fletcher, 1986b) are known to occur in this species would seem to implicate mutual inhibition via pheromones as the most likely mechanism involved. Functional queens of *S.invicta* inhibit ovarian development in winged virgin queens pheromonally (Fletcher & Blum, 1981, 1983; Willer & Fletcher, 1986) presumably by suppressing the production of Juvenile Hormone, which is known to stimulate vitellogenin synthesis and ovarian development in a variety of insects (Engelmann, 1983). Possibly, the mutual inhibition of ovarian development among cohabiting functional queens in polygyne colonies of this ant is also mediated by pheromones which affect Juvenile Hormone production.

The fact that the range of weights spanned by queens is independent of queen number suggests that some queens are not inhibited, no matter how high the number of queens, and therefore how strong the inhibitory influence. One possible explanation is that it is the older queens that are able to overcome this control. Fletcher & Blum (1983) found that some virgin queens of *S.invicta* which had overwintered in monogyne colonies and were therefore several months old showed signs of ovarian development, whereas younger spring-reared virgin queens did not. As pointed out by these authors, this finding is consistent with the hypothesis that the inhibitory pheromone produced by functional queens does not inhibit Juvenile Hormone production altogether, but rather reduces it to a degree permitting a continuous but low rate of vitellogenesis. If a similar phenomenon takes place in the mutual inhibition among functional queens, then it may be the older queens that have sufficiently high titres of Juvenile Hormone for extensive ovarian development. If this is true, then perhaps the uninseminated functional queens in polygyne colonies, which generally have less-developed ovaries than inseminated ones, are younger and represent an earlier stage in the ontological development of polygyne queens in this species. Finally, differences in reproductive competence may relate to varying

conditions in which the queens were reared or individual genetic endowment.

The strong negative correlation between queen number and fecundity of individuals illustrates the 'reproductivity effect', first recorded in the social bees and wasps (Michener, 1964; Wilson, 1971) and reported previously for polygyne colonies of *S.invicta* in the laboratory (Greenberg *et al.*, 1985). In a different context, Tschinkel & Howard (1978) noted a similar effect in this ant. These authors removed queens from monogyne colonies in the field; whereas most colonies so manipulated contained a single replacement queen (usually uninseminated) when sampled 8–10 weeks later, some had numerous uninseminated replacement queens (up to ninety-nine). In the latter case there was an inverse relationship between the weight of replacement queens and the number of such queens in a colony.

A negative relationship between queen number and individual reproduction has been found in other polygyne ants. In *Plagiolepis pygmaea*, a negative correlation between the number of queens in a nest and their fecundity exists under both field and laboratory conditions (Passera, 1969; Mercier *et al.*, 1985). In field colonies of *Lasius sakagami*, Yamauchi *et al.* (1982) reported an inverse relationship between ovarian size and the density of queens in the nest. In a facultatively polygyne species, *Leptothorax curvispinosus*, Wilson (1974) found no apparent effect of queen number on oviposition rate (as measured by the quantity of eggs in the standing crop), but the proportion of eggs developing into larvae decreased with increasing queen number. Recently, Keller (1988) has shown that queens of the highly polygyne ant, *Iridomyrmex humilis*, are more fecund when maintained individually in rearing units in the laboratory than in groups of five to eight.

While polygyny in termites has received detailed attention only recently, similar findings have been reported. In *Nasutitermes princeps*, a paleotropical species, Roisin & Pasteels (1985) found that 60% of the nests examined in the field were polygyne; all of the queens within a polygyne nest exhibited nearly the same level of physogastry and the degree of physogastry was negatively correlated with the number of queens in the colony. In the neotropical termite, *N. corniger*, the weights of individual queens in colonies with more than two queens tend to be

lower than when one or two queens are present (Thorne, 1985).

Our results provide a basis for a comparison of the relative fecundity of queens in monogyne and polygyne societies of *S. invicta*. The mean number of queens in the field colonies was seventy-one. According to the relationships among queen number, queen weight, and oviposition rate determined in this study, the average queen from such a colony weighs 12 mg and has a relative oviposition rate of 47 eggs/5 h. In contrast, queens of mature monogyne colonies in the field are predicted to weigh 22.7 g and have a relative oviposition rate of 240 eggs/5 h, over 5 times the reproductive output of the average polygyne queen. This inequality in individual reproduction is almost certainly greater, since the actual weight attained by monogyne queens can be as high as 29 mg (Tschinkel, 1988; unpublished data), although, on average, the combined egg production of all queens in a polygyne colony is expected to be some 10–15 times that of a monogyne queen (see also Greenberg *et al.*, 1985). In addition to this large disparity in individual fecundity, a smaller proportion of eggs laid by queens in polygyne colonies develop into sexuals, the ultimate measure of reproductive success, presumably due to higher levels of inhibitory pheromones in these colonies (Vargo & Fletcher, 1986a, b, 1987). Thus the relative individual reproductive success of polygyne queens appears to suffer substantially on two counts.

This large reproductive disadvantage to queens in polygyne colonies raises the question of the selective forces, if any, promoting polygyne in this species. Ross & Fletcher (1985a) found that cohabiting queens of *S. invicta* exhibit exceptionally low levels of relatedness, indicating that the lower direct reproductive success of queens in polygyne colonies is not offset by inclusive fitness effects. Thus these authors suggest that mutualism, rather than kin selection, may be the primary force mediating stable queen associations in *S. invicta*. For mutualism to operate in the evolution and maintenance of permanent polygyne, the lifetime benefits to a queen of associating with unrelated queens must outweigh the loss in personal reproduction. While such advantages have yet to be identified in this and other polygyne forms, Ross & Fletcher (1985a) suggest that in the case of *S. invicta* the genetic load associated with a high frequency of

diploid male production (Ross & Fletcher, 1985b, 1986) may be involved.

Permanent polygyne in many ants appears to be an adaptation to particular ecological conditions (Hölldobler & Wilson, 1977; Brian, 1983). *S. invicta* seems to be an exception in this regard in that polygyne colonies do not appear to occupy habitats distinctive from those of monogyne colonies (Greenberg *et al.*, 1985; unpublished data). Detailed comparative studies of contrasting social structures within species and among closely related species will no doubt provide crucial insights into the evolution and maintenance of polygyne in social insects. Further studies of the physiological, ecological and genetic correlates of monogyne and polygyne in *S. invicta*, together with parallel studies of congeners, such as *S. geminata* and *S. xyloni*, which are typically monogyne but known to form polygyne colonies on occasion (Banks *et al.*, 1973; Adams *et al.*, 1976; Summerlin, 1976), should be a valuable contribution to this end.

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