

Queen number and the production of sexuals in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae)

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Summary. To investigate the possibility of queen control over the production of sexuals in polygyne colonies of the fire ant, *Solenopsis invicta*, large colonies were divided into polygyne (P) and monogyne (M) or queenless (Q-) halves. Sexual larvae were evident in the M and Q- halves 3 to 4 days after colony division, whereas sexual forms failed to develop in all but one of the 32 P halves examined. Both male and female sexuals were produced in abundance in all M ($n=25$) and Q- ($n=7$) halves. Evidently, individuals capable of sexualization are present in colonies with many functional queens but are normally prevented from developing. Electrophoretic and morphometric analyses indicated that both haploid and diploid males were produced in the Q- halves, although diploids far outnumbered haploids. It thus appears that queens exert control over all potential and genetically determined sexuals regardless of sex or ploidy. The timing of the appearance of sexual forms following colony division suggests that queen control may be pheromonally mediated and inhibits the growth of sexuals late in larval development. An experiment in which the queens from M and P halves of colonies were exchanged demonstrated the reversible nature of this inhibition within colonies, but also suggested that once individual larvae develop beyond a critical point they are no longer subject to queen control. Despite seasonal variation in the production of sexuals in the field, no substantial differences between colonies collected in the summer and fall were found in their response to colony manipulations. The interaction of colony weight and number of queens present prior to colony division was associated with the number of males produced in the Q- halves, but no factors examined were associated with the number of fe-

males produced in these halves, or with the number of males or females produced in the M halves.

Introduction

The evolution of sociality among insects has produced a variety of modes whereby primary reproductives inhibit reproductive development in nestmates. In some species of termites, the functional reproductive pair suppresses the differentiation of new reproductives, or sexuals, of both sexes (Wilson 1971; Brian 1979). In the social Hymenoptera, queens usually have some control over the reproductive development of nestmates (Fletcher and Ross 1985). Queen control over oviposition by workers has been reported in several species of ants, e.g., *Leptothorax unifasciata* (Bier 1954), *Leptothorax* (= *Temnothorax*) *recedens* (Dejean and Passera 1974), *Myrmica rubra* (Brian and Rigby 1978), and *Plagiolepis pygmaea* (Passera 1980). While workers of the genus *Solenopsis* are obligately sterile (Goetsch 1953), winged female sexuals of *S. invicta* are pheromonally prevented from de-lating and becoming reproductively active in the presence of a functional queen (Fletcher and Blum 1981, 1983), suggesting well-developed queen control over reproductives in this species.

In a few species of ants, queen control over the production of new female sexuals has been well-studied, e.g., *Myrmica rubra* (reviewed in Brian 1979), *Formica polyctena* and *F. pratensis* (Gösswald and Bier 1953, 1954a, b), and *Monomorium pharaonis* (Peacock et al. 1954; Petersen-Braun 1975, 1977). In addition, it has been anecdotally reported in a number of other species, e.g. *Aphaenogaster senilis* (Ledoux and Dargagnon 1973).

The fire ant, *Solenopsis invicta*, forms single queen (monogyne) colonies over most of its range in the southeastern United States, with multiple-queen (polygyne) colonies having been described from several locations (reviewed in Ross and Fletcher 1985a). While regulation of the production of sexuals has not been investigated in this species, we have observed in the field that polygyne colonies appear to produce far fewer sexuals than mature monogyne colonies. The objective of this study was to determine whether the development of sexuals in polygyne colonies of *S. invicta* is influenced by queen number, i.e. is under queen control. This was achieved by manipulating queen number in divided polygyne colonies in the laboratory and comparing the numbers of sexuals produced.

Methods

Ant colonies

Mounds of polygyne *S. invicta* (the population of a single mound will subsequently be referred to as a colony, although, at present, it is not clear if polygyne colonies occupy more than one mound) were collected in Walton County, Georgia in the summer (6 June, 1 and 14 August) and fall (2 and 25 October) of 1984, at which time numerous sexuals were reared in most monogyne and some polygyne colonies. Large colonies were selected in which there were few or no alates or sexual brood. Ants were separated from the soil by the method of Jouvenaz et al. (1977) and maintained in the laboratory as described by Fletcher et al. (1980). Air temperature was $29^{\circ} \pm 2^{\circ} \text{C}$ and illumination was provided for 14 h/day.

After one to two weeks in the laboratory, the colonies were sieved (No. 14 USA Standard Testing Sieve) to remove discernible immature and adult sexuals which were then counted. All sexual forms except dealate queens, most of which are inseminated egg layers (Fletcher et al. 1980), were discarded. The remaining workers and brood were weighed to the nearest 0.1 g. To standardize initial experimental conditions, only colonies containing fewer than 50 sexual larvae and less than 2.5 dealate queens/g of workers and brood were retained and divided as described below.

Monogyne/polygyne colony divisions

Colonies collected in summer ($n=18$) and fall ($n=12$) were divided into halves by weight, the workers and brood being distributed evenly between them. Each half received two nests (14 cm petri dishes half filled with damp castone) placed in plastic trays (48 × 58 × 7 cm) with Fluon-coated sides and given either one of the dealate queens collected with the colony (M treatment) or all of the remaining queens (P treatment). The numbers of sexual pupae and alates present were recorded without removal at weekly intervals.

At the end of each experiment, the queen in each M treatment, and at least 25% of the original number of queens in each P treatment were selected at random to determine whether they were inseminated. Spermathecae were examined for sperm with the aid of a microscope. The numbers of inseminated and uninseminated queens initially present in each colony were then

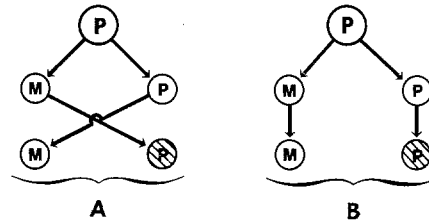


Fig. 1. Monogyne/polygyne reversal experiment. Polygyne (P) colonies ($n=16$) were divided into polygyne (P) and monogyne (M) halves. After 6 weeks all discernible immature and adult sexuals were removed. Queens of the M and P halves of each colony were either exchanged (A experimentals, $n=7$), or returned to the colony half from which they were removed (B controls, $n=9$). Treatments with diagonal lines correspond to those of Fig. 4

estimated by simple proportion. Colonies found to have an uninseminated queen in the M treatment ($n=2$ of 18 for summer colonies and $n=3$ of 12 for fall colonies) were excluded from all analyses.

The summer colonies had a mean weight of $94.1 \pm \text{SD } 15.2 \text{ g}$ (range 70.8–120.0 g) and a mean queen number of 101.7 ± 51.7 (25–187), while the fall colonies had a mean weight of $156.4 \pm 37.9 \text{ g}$ (96.7–207.6 g) and a mean queen number of 92.1 ± 41.2 (41–163).

Monogyne/polygyne reversal

To determine whether the difference in the production of sexuals between M and P treatments (see Results) could be reversed, colonies were manipulated as follows. Immediately following completion of the M/P experiments, some of the colonies collected in the summer ($n=7$) and fall ($n=9$) were sieved as before to remove all queens and discernible sexual forms. Colonies were randomly chosen to serve as experimentals ($n=7$) or controls ($n=9$). In the experimentals, the queens of the M and P treatments were exchanged, while in the controls they were not (Fig. 1). Sexuals were counted without removal for 6 weeks as in the previous experiments. Since alates persisted in the nest after eclosion and were recounted each week, the number of sexual pupae was a better indicator of any change in the production of sexuals over time, and was therefore used in the analyses.

Queenless/polygyne colony divisions

Seven colonies collected in summer (mean weight of $105.6 \pm 33.3 \text{ g}$ (45.6–143.4 g) were divided as described above except that one half of each colony received all of the queens (P treatment; mean queen number of 91.3 ± 50.2 (34–182), while the other half was made queenless (Q- treatment). The number of inseminated and uninseminated queens originally present in each colony was estimated in the manner described above.

To determine the ploidy of the males produced in the Q-treatment, 10% of the alate males present in each replicate were removed each week for morphometric and electrophoretic analyses. After removal from the colony, males were placed in a freezer at -40°C and held until electrophoresis. Since the mean number of male alates present was greatest on week six (see Results), the males removed on this week were chosen for study. The mesoscutal area for each male was determined by measuring its length and width at $\times 40$ with the ocular micrometer in a dissecting microscope and used as an indicator of size (Ross and Fletcher 1985b). Following size determina-

tion, standard horizontal starch gel electrophoresis was performed and the enzyme products of the diallelic loci *Alphaglycerophosphate dehydrogenase-1* (*Agp-1*) and *Esterase-4* (*Est-4*) were studied as genetic markers (Ross and Fletcher 1985a).

Determination of the sexual/worker brood ratio

The brood from each of the replicates of the Q-/P and summer M/P experiments was sampled weekly. The contents of the two artificial nests of each replicate was collected into a single pile, thoroughly mixed, and three 1 ml samples were taken at random. Individual larvae and pupae were classified by size as worker or sexual and counted. Sexual pupae are much larger than worker pupae and therefore easily distinguishable. Sexual larvae cannot be distinguished from worker larvae until the fourth and final instar when they exceed the maximum length of 2.4 mm attained by worker larvae (O'Neal and Markin 1975a). All larvae exceeding this length were considered sexual. No eggs or larvae smaller than 0.5 mm in length were included. The ratio of sexual/worker brood for each replicate was estimated by dividing the sum of the sexual larvae and pupae by the sum of the worker larvae and pupae.

Statistical analysis

All data were found to be normally distributed according to either the Shapiro-Wilk or Kolmogorov tests for normality, and the appropriate parametric tests were employed. The forward stepwise regression analysis of Hocking (1976) was performed to determine the association of initial colony weight, number of inseminated queens, and number of unseminated queens with the number of sexuals produced after colony division. For each experiment, the number of sexuals present at the week containing the greatest mean number of sexuals was used in the regression analysis.

Results

The ratio of sexual/worker brood exhibited similar patterns in the Q-/P and summer M/P experiments for the first 3 weeks (Fig. 2). In both experiments, significant differences between the P treatments and the Q- or M treatments were evident only one week following colony division. In the Q- and M treatments, there were many sexual larvae in the early-mid fourth instar (>2.4 mm long) after only 3–4 days, and by day 7 many had attained the prepupal stage. Due to the lack of queens in the Q-treatment, brood were too scarce to permit sampling beyond week 4.

The numbers of alates and sexual pupae reared in response to colony division and queen removal were similar in all three experiments (Fig. 3). While only one of the 32 P replicates produced any sexuals (3 females and 1 male), all of the Q- and M replicates produced both male and female sexuals in abundance.

Stepwise regression analysis of several independent variables with the number of sexuals produced after colony division indicated that the number of inseminated queens in the Q-/P experi-

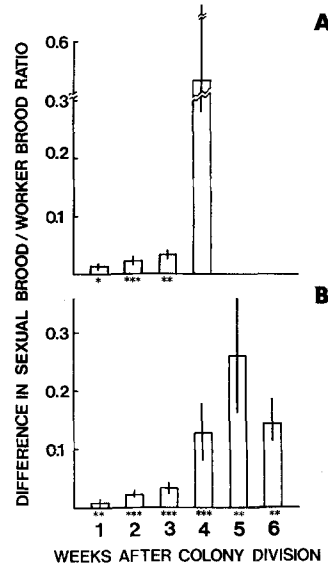


Fig. 2A, B. The difference in the sexual brood/worker brood ratio between paired halves of colonies following division. **A** Difference between queenless and polygyne halves ($n = 7$). **B** Difference between monogyne and polygyne halves ($n = 16$). Bars = ± 1 SE about mean. P -values indicate significance levels for differences using a two-tailed paired-sample t -test. * $P < 0.05$; ** $P < 0.025$; *** $P < 0.001$

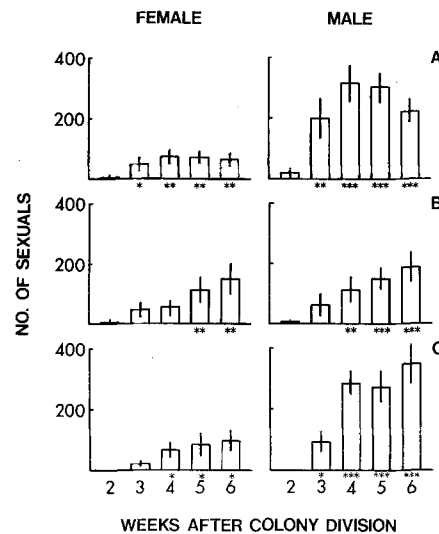


Fig. 3. The number of sexuals (alates + pupae) present in halves of divided polygyne colonies that were made: **A** queenless (collected in summer, $n = 7$); **B** monogyne (collected in summer, $n = 10$ for weeks 1–4, $n = 16$ for weeks 5–6); **C** monogyne (collected in fall, $n = 9$). Bars = ± 1 SE about mean. P -values indicate significance levels for $\bar{X} > 0$ (one-tailed one-sample t -test). See text for details. * $P < 0.05$; ** $P < 0.025$; *** $P < 0.005$

ment accounted for 67.5% of the variance in the number of males present in the Q- treatment ($F_{1,6} = 10.38$, $P < 0.02$), while the interaction of the number of inseminated and unseminated queens and colony weight accounted for 91.9% of the

variance in the number of males present ($F_{3,6} = 11.38$, $P < 0.04$). The effect of these variables on the number of females present in the Q- treatment at week 4 was not significant.

Since a t test indicated no significant difference between the summer and fall M/P experiments in either the mean number of males ($t_{23} = 2.03$, $P > 0.06$) or females ($t_{23} = 0.62$, $P > 0.54$) present at week 6, the data from these two experiments were pooled in the stepwise regression analysis. There were no significant effects of the independent variables examined on either the number of males or females present.

An ANOVA test on the number of males and females present each week in the Q-/P, summer M/P, and fall M/P experiments indicated significant differences only in the number of males present at two of the possible 5 weeks (week 4, $F_{2,25} = 6.22$, $P < 0.007$; week 5, $F_{2,31} = 3.52$, $P < 0.05$). A Duncan's multiple range test ($\alpha = 0.05$) indicated that at week 4 the summer M treatment had significantly fewer males present than either the Q- or fall M treatments, and at week 5, the summer M treatment contained significantly fewer males than the Q- treatment. Since the colonies used in the summer and fall M/P experiments did not differ in the number of females present at any week, and at only one of five possible weeks in the number of males present, we felt that the difference in their response was sufficiently small to pool colonies of each in the M/P reversal experiment.

Figure 4 (A and B) shows that the exchange of queens in the M/P reversal experiment produced a striking difference in the production of sexual pupae between the experimentals and controls. While the variance was too large with the sample size used to give statistically significant differences, a clear trend was evident. Compared to the M treatment of the controls (B), the production of sexuals (male and female) in the former M treatment made polygyne (A) decreased at a much faster rate and ceased altogether by the end of the experiment. Unlike the P treatment of the controls (B), both male and female sexuals appeared in abundance in the former P treatment made monogyne (A).

Based on the electrophoretic analysis of the males ($n = 333$) produced in the Q- treatment, individuals were divided into two groups: those heterozygous at both marker loci (confirmed diploids, $n = 190$) and those exhibiting single-band phenotypes (haploids or double homozygotes, $n = 143$). The frequency distributions of the mesoscutal area for the confirmed diploids was unimodal (mode = 2.14 mm^2 , range = $1.66\text{--}2.56 \text{ mm}^2$), while that of

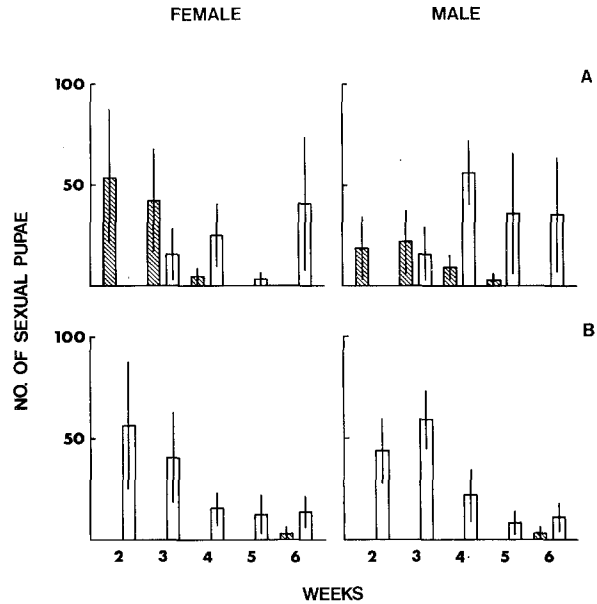


Fig. 4. The number of sexual pupae present in polygyne (diagonal lines) and monogyne halves of formerly polygyne colonies (see Fig. 1). Six weeks after polygyne colonies were divided into monogyne and polygyne halves, all discernible sexual forms were removed and the queens from the polygyne and monogyne halves were either exchanged (A experimentals, $n = 7$), or returned to the colony half from which they were removed (B controls, $n = 9$). Bars = ± 1 SE about mean.

the single-banded individuals was bimodal (modes = 2.07 and 1.56 mm^2 , range = $1.22\text{--}2.44 \text{ mm}^2$). This pattern closely resembles that found in a study of males taken from polygyne colonies of *S. invicta* in the field by Ross and Fletcher (1985b), in which haploids constituted a smaller size class than diploids with little overlap in mesoscutal area. In the present study there were 22 males (6.6% of total) with single-band phenotypes that were smaller than the smallest diploid (mesoscutal area $< 1.66 \text{ mm}^2$). These were distributed over six of the seven colonies examined and were assumed to be haploid.

Discussion

The inhibition of sexual development in the highly polygyne state suggests that potential female sexuals (caste-plastic brood) either develop into workers (if caste is determined in the larval stage) or they are eliminated (if caste is determined in the egg). Both haploid and diploid male larvae are selectively eliminated before the end of the fourth and final instar. Thus, either queens exert a direct and often fatal pheromonal influence on the development of larvae that is associated with queen number, or workers are able to recognize male and potential female larvae and either rear them or

eliminate them in response to queen influence. While there is no evidence for the former mechanism from any ant species, this mechanism cannot yet be ruled out for *S. invicta*. Further experiments are needed to distinguish between these two possibilities.

Two mechanisms are possible in the initiation and/or enhancement of sexual production in M and Q- halves of formerly polygyne colonies. 1. Queens may inhibit the production of sexuals pheromonally and reduction in queen number may result in disinhibition. 2. The increase in worker/larva ratio that inevitably follows queen removal may enhance the development of potential and genetically determined sexual larvae via increased individual care by workers. Bearing on these two hypotheses is the observation that the incubation period for eggs in *S. invicta* is 6 to 8 days under our laboratory conditions (unpublished data). For this period following colony division there is virtually no difference in the worker/larva ratio between the P and M, or Q- halves of a colony. Thus, the rapid appearance of discernible fourth instar sexual larvae (3 to 4 days) lends support to the pheromonal hypothesis. It is possible, however, that the colony may respond initially to a reduction in the level of pheromone(s) and that this is later reinforced by the increased worker/larva ratio. Conclusive evidence for the involvement of a pheromone(s) would, of course, be dependent upon the identification and synthesis of biologically active material.

The timing of the appearance of sexual forms following colony division and queen removal also suggests that queen control may halt the growth of sexuals late in larval development. At 32° C, the temperature at which larval development proceeds most rapidly, sexual larvae are in the third and fourth instars for ca 5 and 7 days respectively (O'Neal and Markin 1975 b). But these authors also showed that at 29° C, the temperature used in this study, developmental time is slower, so that the first discernible sexual larvae (>2.40 mm long) to appear (3–4 days) must have been in at least the mid-third instar at the time of colony division and queen removal. Since sexuals were not reared in the P treatment, they must have been either rerouted (in the case of females) or eliminated (in the case of both haploid and diploid males, and possibly in the case of females) at this time. This stands in sharp contrast to the early elimination of diploid male larvae in the honey bee, *Apis mellifera*, which are eaten by nurse bees within hours after hatching (Woyke 1963 a, b). Moreover, while diploid males are never reared to adulthood in col-

onies of *A. mellifera* under natural conditions, Ross and Fletcher (1985b) found that 89.8% of the males produced in four polygyne populations of *S. invicta* are diploid. Since only about 15% of the queens in these populations produce diploid males (Ross and Fletcher 1985b), polygyne workers of *S. invicta*, unlike workers of the honeybee, are either unable to distinguish diploid male larvae from other sexual larvae, or if they recognize them, do not discriminate against them to the same degree.

The continued appearance of sexual pupae in the P treatment of the M/P reversal experiment for several weeks following the exchange of queens suggests that once potential or genetically determined sexuals develop beyond some critical point they are caste-determined. This may help explain why sexuals can be found in some polygyne colonies of *S. invicta* in the field, although in reduced numbers compared to monogyne colonies (unpublished data). In this connection, the structure of the nest and the distribution of queens within it may be important. In several species of ants, the production of sexuals is known to occur in regions of the nest where queen control is inadequate to prevent it. For example, sexuals of the polygyne species *Formica pratensis* and *F. polyctena* are reared near the top of the nest, separated from the queens which remain lower down (Gösswald and Bier 1953, 1954a, b). In addition, the polydomous structure of many ant nests may provide regions in which queen control is reduced or absent (Fletcher and Ross 1985). Sexual potential larvae of *S. invicta* may be reared in the field only when they are not subject to queen control for a sufficient period to develop beyond the critical stage. In the laboratory, our artificial nests may not provide regions sufficiently free of queen control in highly polygyne societies, whereas in the field the large and extensive nests of mature colonies of *S. invicta* (Lofgren et al. 1975) probably contain such regions.

In the polygyne ant, *Monomorium pharaonis*, sexuals are produced cyclically. Removal of queens at any point in the cycle results in the production of both male and female sexuals from existing queen-laid eggs (Peacock et al. 1954, Petersen-Braun 1975). Mating apparently always takes place in the nest, and nuptial flights never occur (Wilson 1971). Thus, in *M. pharaonis*, the production of sexuals in response to queenlessness allows the colony to requeen itself. Whether colonies of *S. invicta* can respond in a similar manner is unknown. Although both male and female sexuals are known to take part in mating flights (Ross and Fletcher

1985a; D. Fletcher and S. Bradley, unpublished data), their fate, as well as the source of functional polygyne queens, has yet to be determined.

The numbers of sexuals produced by a colony under our experimental conditions might be influenced by a number of variables including colony size (as measured by colony weight) and the numbers of both inseminated and uninseminated queens it contains. The number of males produced in colony halves made Q- appears to be strongly dependent on the interaction of these factors. However, in view of our small sample size, this relationship should be treated with caution. Two important factors we were not able to take into account were the number of diploid male producing queens and the age of the queens present in each colony. Presumably, half of the fertilized eggs laid by a queen producing diploid males are destined to become diploid males (Ross and Fletcher 1985b). Therefore, the number of such queens present in a colony should profoundly influence the composition of the brood. Age has been shown to be an important factor in the ability of queens of both *Myrmica rubra* (Brian and Hibble 1964) and *Monomorium pharaonis* (Petersen-Braun 1977) to produce sexual potential eggs. In addition, halves of P colonies made M may be subject to differences in the ability of individual queens to inhibit sexual production, as found in *Myrmica rubra* and *M. scabrinodus* (Brian and Carr 1960), *Monomorium pharaonis* (Petersen-Braun 1975), and *Leptothorax nylanderii* (Plateaux 1971).

Our demonstration of a quantitative relationship between queen number and the inhibition of sexual production is unlike the situation found in *Myrmica rubra*, a polygyne species in which the presence of a single queen produces the full inhibitory influence on the production of sexuals in laboratory colonies (Brian and Carr 1960). Studies of possible queen control in other polygyne ant species, e.g. *Leptothorax* spp. (Plateaux 1971) and *Odontomachus insularis* (= *haematodes*) (Colombel 1978), have not been of sufficient scope to indicate how common such a quantitative relationship between queen number and the inhibition of the production of sexuals might be.

The origin and maintenance of polygyny in *S. invicta*, particularly in light of our findings, present a challenge to evolutionary theory. It is tempting to view queen control of the production of sexuals as the proximal mechanism by which initial colony growth is maximized by avoiding costly investment in sexuals during the critical early stages. If monogyny is the primitive condition in insect societies, as has been suggested (Hölldobler and Wilson

1977; Fletcher and Ross 1985), then the selective advantage of this form of queen control is readily apparent. Polygyne queens of *S. invicta*, and possibly other species, would appear to be at a distinct disadvantage compared to their monogynous counterparts, for not only are cohabiting queens likely to be subject to the reduction in fecundity associated with higher queen number (Michener 1964; Fletcher et al. 1980), but also to the strong inhibitory influence in the polygyne state which appears to yield a smaller proportion of sexuals from existing brood. On the other hand, sexuals are produced in sufficient numbers to sustain large polygyne populations, perhaps through reduced loss of queens during colony reproduction by budding. Detailed ecological and population genetic studies are needed before we can better assess the costs and benefits associated with monogyny and polygyny in this and other species.

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