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# THE EFFECT OF MULTIPLE QUEENS IN SMALL GROUPS OF *Myrmica rubra* L.

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SUMMARY

The results from three experiments, designed to test the effect of multiple queens upon the productivity of small cultures of *Myrmica* ants, show that under laboratory conditions there is no advantage for a large queen pool. In fact there is a clear indication that surplus queens reduce the productivity of their worker group, this is true both under conditions of abundant food and starvation.

Surplus queens therefore act as parasites on the workers. This contention is discussed briefly in terms of kin selection. The conclusion is that high levels of polygyny persists because *Myrmica*, both queens and workers, are relatively short lived and have low average relatedness so that both attempt to maximise their individual fitness through worker produced males. Polygyny therefore has ecological advantages that are balanced by the tendency of the whole system to produce true social parasites.

RESUME

Les résultats obtenus dans trois expériences entreprises pour mesurer les effets de la polygynie sur la productivité de petits élevages de fourmis du genre *Myrmica*, montrent que dans des conditions de laboratoire, un grand groupement de reines ne présente pas d'avantages. De fait, il apparaît clairement qu'un nombre excessif de reines réduit la productivité de leur groupe d'ouvrières que ce soit dans conditions d'alimentation abondante ou de disette.

Les reines surnuméraires se comportent donc en parasites de leurs ouvrières. Cette affirmation est discutée brièvement dans le cadre de la théorie de la sélection de parentèle. On aboutit à la conclusion que de hauts degrés de polygynie ont été retenus par l' Evolution parce que chez *Myrmica* à la fois les reines et les ouvrières ont une durée de vie plutôt brève et un faible degré de parenté si bien que toutes deux s'efforcent de maximaliser leur aptitude individuelle à travers la production de mâles issus d' ouvrières. La polygynie présente donc des advantages écologiques qui sont compensés par la tendance du système entier à produire de vrais parasites sociaux.

## INTRODUCTION

*Myrmica rubra* is the most polygynous of all the western palaearctic *Myrmica* species; densities greater than 1 queen per 20 workers are often found in natural colonies (Elmes 1973). Yet, laboratory studies show that one queen is capable of maintaining a colony of at least 250 workers. Why then do many wild colonies have so many surplus queens?

I offer three explanations: 1. Surplus queens enable the colony to respond very quickly to bonanza years, allowing it to produce many new workers. 2. They offer no advantage in good or average years but during periods of hardship the workers may select a few of the best queens and eliminate older or inferior ones, ensuring a quick recovery of the worker population. 3. In this species the surplus queens act as social parasites on the worker population.

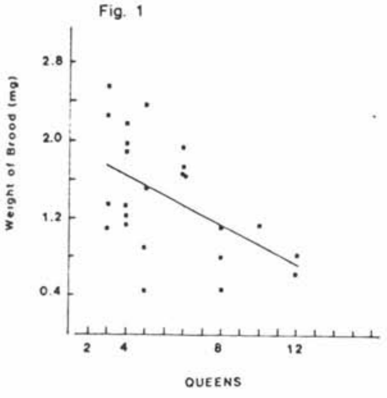
All of these ideas imply selection for polygyny by improved worker fitness, through their production of sons. It is hard to see any advantage for individual queens in being part of a large group, other than during the colony founding stage. This will be taken up in the discussion.

In order to test some of these ideas I have started a series of rearing experiments, using small cultures of workers with differing densities of queens and different levels of feeding. The results of the first of these are reported in this paper.

## METHODS

All experiments were started immediately after hibernation. Artificial colonies, being fragments of larger natural ones, were maintained at 20° C in plastic Janet type nests. Results are thus comparible with similar earlier studies made by M.V.Brian and G.W.Elmes. A difficulty was that earlier experiments have shown huge variation in productivity between different wild colonies which often masks the effects of the experimental treatments. Normally this is countered by taking each set of treatments from the same wild colony. However, it was not always possible to obtain the large numbers of queens required from a single colony. In every case the total brood produced was recorded at the end of the summer period, when some of the larvae naturally enter a diapause in anticipation of the winter. Queens were also weighed individually at this time.

Experiment 1: The first replicate comprised 3,6 or 12 queens with 60 workers given three levels of food (ample, adequate & low) making a total of 9 cultures all taken from the same wild colony. Ample food ensured that each week, each worker had at least 1 *Drosophila melanogaster* larva and 1mg of sucrose, adequate food was 0.25 *Drosophila* larva and 0.25 mg. sucrose, low food was 0.07 *Drosophila* and 0.07mg. sucrose. These amounts were calculated from the data given by Brian & Abbott (1977). A second replicate comprised 6 queens + 30 workers, 3 queens + 30 workers and 3 queens + 60



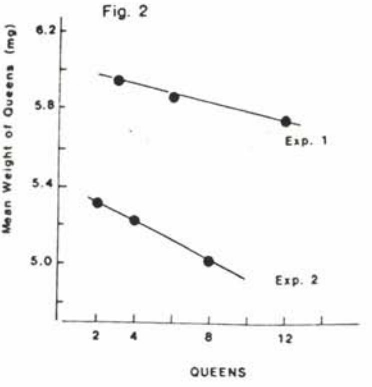




*Fig. 1. Weight of over-wintering brood per worker plotted against the number of queens, combining Exps. 1 & 2.*
*Fig. 2. The mean weight of queens plotted against number of queens. The regression lines are significant but different for Exps. 1 & 2.*

workers, giving the same worker queen ratio as replicate 1. however, several different wild colonies were needed to cross replicate the treatments so that the results were confounded both by worker numbers and source colony.

Experiment 2: Only the effect of multiple queens was tested by giving cultures of 32 workers and 32 small over-wintered larvae either 2,4 or 8 queens, with ample food. Four different wild colonies were used as replicates.

Experiment 3: Here the effect of groups of young freshly mated queens was tested. *Myrmica scabrinodis* Nyl. queens were used because newly mated *M.rubra* were not available. Four replicates of 12, 6 and 3 queens, taken from a mating swarm, were set in Janet type nests to over-winter. In the following spring these were given with ample food because colony foundation in *Myrmica* is not claustral.

RESULTS

Experiment 1 (Table 1): Consider the fresh weights of queens at the end of the experiment; replicate 2 can be ignored because it is confounded by colony variation (ie. different colonies provided stock for different treatments). Although the queens in the low food treatment were lighter on average than the other two food treatments this was not significant, however, the differences between the queen number treatments are significant ($P = 0.02$), showing that queens are not as well nourished in large groups as in small ones.

TABLE 1. Experiment 1: Summary of the state of the experimental cultures at the end of the first year.

Initial number of workers per queen

| FOOD | | 5 | | | 10 | | | 20 | | | Mean | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | W | B | Q | W | B | Q | W | B | Q | W | B | Q |
| Ample | R1 | 0.67 | 0.80 | 5.90 | 0.43 | 1.65 | 5.83 | 0.93 | 2.17 | 6.06 | 0.68 | 1.54 | 5.89 |
| | R2 | 0.96 | 1.73 | 6.08 | 1.16 | 1.23 | 5.88 | 1.38 | 1.90 | 5.74 | 1.17 | 1.62 | 5.94 |
| Adequate | R1 | 0.60 | 0.62 | 5.79 | 0.58 | 1.65 | 6.03 | 0.58 | 1.33 | 5.98 | 0.59 | 1.20 | 5.88 |
| | R2 | 0.87 | 1.93 | 6.34 | 0.73 | 1.97 | 6.03 | 0.73 | 1.13 | 5.88 | 0.77 | 1.68 | 6.15 |
| Low | R1 | 0.07 | 0 | 5.43 | 0.17 | 0.10 | 5.84 | 0.10 | 0.33 | 6.54 | 0.11 | 0.14 | 5.70 |
| | R2 | 0.03 | 0 | 5.06 | 0.07 | 0 | 5.42 | 0.25 | 0 | 6.23 | 0.12 | 0 | 5.44 |
| Mean | R1 | 0.45 | 0.47 | 5.73 | 0.39 | 1.13 | 5.89 | 0.53 | 1.28 | 6.15 | | | |
| | R2 | 0.62 | 1.83 | 5.83 | 0.65 | 1.07 | 5.78 | 0.78 | 1.01 | 5.95 | | | |

*The three levels of queen density used are shown against the three feeding treatments, the column and row means are also given. R1 and R2 are the results for replicates 1 & 2, W = the number of workers surviving as a proportion of the original number, this includes any new workers produced. B = the weight of over-wintering brood (mg) per worker originally given. Q = the average fresh weight of queens (mg), the means for this have been adjusted for the numbers of queens given.*

TABLE 2. Experiment 2: Summary of the state of the experimental cultures at the end of the year.

Initial number of workers per queen

| REPLICATE | 4 | | | 8 | | | 16 | | | Mean | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | W | B | Q | W | B | Q | W | B | Q | W | B | Q |
| R1 | 1.03 | 1.09 | 4.86 | 0.63 | 0.43 | 5.32 | 0.88 | 2.22 | 5.68 | 0.85 | 1.25 | 5.11 |
| R2 | 0.53 | 0.78 | 4.83 | 1.06 | 1.50 | 4.74 | 1.06 | 2.53 | 5.39 | 0.88 | 1.60 | 4.88 |
| R3 | 1.53 | 1.13 | 4.61 | 0.69 | 2.25 | 4.80 | 1.00 | 1.34 | 4.90 | 1.07 | 1.57 | 4.71 |
| R4 | 1.69 | 0.44 | 5.78 | 1.47 | 0.88 | 6.04 | 1.72 | 1.09 | 5.32 | 1.63 | 0.80 | 5.79 |
| Mean | 1.19 | 0.86 | 5.02 | 0.96 | 1.26 | 5.22 | 1.16 | 1.80 | 5.32 | | | |

*The three levels of queen density used are shown against the four replicates R1-R4. The column and row means are also given. W = the number of workers surviving as a proportion of the original number, this includes any new workers produced. B = the weight of over-wintering brood (mg) per worker originally given. Q = the average fresh weight of queens (mg), the means for this have been adjusted for the numbers of queens given.*

Fig. 3

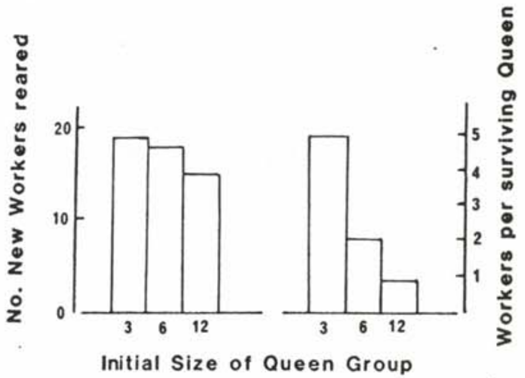



*Fig. 3. The total number of workers and number per surviving queen, produced by three different sized groups of young newly mated Myrmica scabrinodis queens, in Exp. 3.*

The number of workers at the end of the summer (= old workers + new production) varies significantly between the food treatments, most being due to the very low survival the low food treatments. Although there is an indication that there were fewer workers surviving or reared with the higher queen numbers, this relationship is not statistically significant. Both effects are more marked when the weight of over-wintering larvae is considered, there being a strong indication of an effect of queen number in replicate 1 ($p = 0.05$).

Experiment 2 (Table 2): Note here the considerable variation between the different colonies (replicates). The differences between the queen number treatments are not statistically significant, nevertheless, like experiment 1, there is a strong indication that queens are less well nourished and that fewer over-wintering larvae are reared with high queen numbers.

When the results of Exp.1 & 2 are taken together there is a clear correlation between the numbers of surviving workers and the weight of brood left to over-winter ( $P < 0.01$). Regardless of subsequent treatment, the cultures can be divided into two classes, those that were originally given about 60 workers and those given about 30 workers. The former reared an average of 42mg and the latter 84mg. of over-wintering brood. When the weight of brood/worker reared is plotted against the actual number of queens in the culture, a significant negative regression is obtained ($r= -0.53$ $P= 0.02$ Fig.1).

Likewise, if the weights of queens are plotted against the actual number of queens (Fig.2) significant but different relationships are obtained from the two experiments ($P<0.05$).

Experiment 3: By the end of the summer period about 65% of all the queens had died, mortality appeared to be random; no differences could be detected for size of founding group. In every culture, young workers were reared but there was no over-wintering brood. No significant difference was noted between the treatments for the number of workers produced but if these are expressed as number per surviving queen then clearly the queens in small groups have more workers available to them than those in large groups (Fig.3).

## DISCUSSION

These experiments show that there is huge colony variability to be contended with when trying to isolate the effects of caste numbers on productivity. The variation between queens is related to size, ovaries and age, even so we have little idea how much of this is genotypic and how much is phenotypic. We have even less idea why workers from different colonies and from different areas work at different rates, this might be a phenotypic conditioning to an environmental factor such as temperature, so that when they are all reared at a constant 20 °C in the laboratory, some do better than others. This needs more study.

Nevertheless, there is a strong consistency between the three experiments. First, production depends on worker number, eg 60 workers averaged 84mg over-wintering larvae whereas 30 workers averaged only 42mg regardless of the number of queens they were given. In future experiments the number of workers should be constant and variation in queen density induced by varying queen numbers.

Secondly, the food levels in experiment 1 gave rather surprising results, ample food treatments did little better, in terms of survival and brood production, than adequate food. There was no evidence that a culture with a large pool of queens could use the surplus to produce more ants than a similar sized one with few queens, showing that production is limited by the worker pool's capacity to work and not the fecundity of the queens. This is contrary to the prediction of hypothesis 1 (see introduction). Under starvation or low food the workers died rather than allow the queens to die, and there was virtually no production of brood, contrary to hypothesis 2.

This leaves the third possibility that queens merely parasitize the worker pool. These experiments tend to support this. There is a clear and consistent indication that surplus queens actual reduce the capacity of their worker pool to produce brood. The simplest interpretation is that each queen takes the full attention of say 2-3 workers. Under ideal conditions roughly 1.5 new ants are produced per worker so that each queen actual prevents the production of 3-5 new workers.

*Myrmica rubra* colony. Here, the assumption holds in the experimental situation and agrees with field observations, where queen number has a negative and worker numbers a positive effect on both the size and numbers of workers and larvae in the nest (Elmes 1974).

High levels of primary polygyny have been assumed to be an advantage in a colony founding situation and persistent secondary polygyny is explained by colonies being in a permanent founding condition. However, experiment 3 suggests that in *Myrmica*, a large group of queens does no better in absolute terms and far worse in terms of production per queen than a small group. This can be explained if there are two types of queen, analagous to the microgyne and macrogyne of *Myrmica ruginodis* Nyl. There may be "foundresses" that can cope with no workers and "joiners" that need worker help to rear brood. Experiment 3 may then be artificial in that any foundress effect might have been inhibited by the inclusion of "joiners" due to queen groups being a random selection rather than self chosen.

If "joiner" queens act as parasites on the workers then clearly there are the normal competitive interactions between them and the density effects associated with overburdening the host population. However, the system can not evolve simply as a parasitic one because of the paradox that the parasites are also progenitrix of the host population. Ruling out a group selection type hypothesis such a system could only arise if it gave increased fitness to individual workers. Given that in highly polygynous colonies there is low relatedness (Pearson 1983), the benefit an individual worker can only be by her producing sons.

All *Myrmica* workers can lay male eggs and in *M. rubra* these can be numerous (Brian 1969, Smeeton 1982). A worker lives about a year and her eggs take about a year to develop into mature males. Therefore an average worker depends upon the next generation of workers to complete the development of her sons. Thus she must offset a possible advantage in "cheating" her fellow workers and co-operate in rearing some of the queens eggs to produce new workers and it does not really matter if the queen is related or not. If queens are short-lived, as seems likely in the genus *Myrmica*, then the queen also benefits because she obtains grandsons from the following generation of workers.

Under this hypothesis gynes should only be produced when there are few queens and the workers are more likely to be related to the gynes. My opinion is that in the habitats where *Myrmica* specialise, gyne production is regulated by so many chance environmental factors that any selective manipulation of sexual investment is mostly on the male numbers. Gyne production being merely opportunistic. This both accommodates the queen effect shown in the laboratory and the very highly male biased sex-ratios shown in field populations.

To summarize, I think that the whole social system of the genus *Myrmica* is worker driven. High polygyny is a product of short lived queens (Elmes 1980) specialising on unstable, transient and harsh habitats which cause frequent colony fragmentation. This strategy has the high risk of "joiner-cheating" where some of the surplus queens lay eggs that have much higher "queen potential" and reduced "plasticity" or worker potential (see Brian's Caste Determination series 1-9: Brian & Kelly 1967).

Such "cheats" are in effect social parasites on the other queens who themselves are exploiting the workers. In general cheating should be an unsuccessful strategy but occasionally, if there is inbreeding between the "cheats" progeny combined with reduced size and fecundity of queens, then a new sibling social parasite might be evolved very quickly. This might explain the high incidence in the genus *Myrmica* of social parasites, such as *M. rubra microgyna* and *Myrmica hirsuta* Elmes, which are closely related to their host (Elmes 1978).

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