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Research article

Relationship of queen number and worker size in polygyne colonies of the fire ant *Solenopsis invicta*

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Summary

We examined the relationship between queen number and worker size in colonies of the fire ant *Solenopsis invicta*. Worker size in monogyne colonies was significantly greater than in polygyne colonies; furthermore, polygyne colonies showed a strong negative linear relationship between queen number and worker size. Higher queen pheromone level and/or decreased food availability accompanying an increase in queen number likely play important roles in producing the observed patterns.

Introduction

Size variation in ants is believed to reflect both the heritable products of past selection for colony efficiency and the nonheritable effects of present environmental conditions. Examples of nonheritable effects of the extranidal environment are numerous. Factors such as food availability, climatic conditions, colony stress, and interspecific competition all have been found to affect worker size (Hölldobler and Wilson, 1990). The intranidal environment also is likely to influence worker size in ants. For example, the social environment in monogyne colonies (those with a single reproductive queen) is likely to differ from that in polygyne colonies (those with multiple reproductive queens) in ways that may affect worker size.

In the fire ant *Solenopsis invicta*, intraspecific size variation often has been ascribed to differences in colony social structure that presumably correspond to distinctive social environments. For instance, reproductive queens in monogyne colonies are heavier than those in polygyne colonies (Vargo and Fletcher, 1989). Furthermore, Greenberg et al. (1985) found that worker head width in monogyne

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colonies is significantly greater than that in polygyne colonies. We were interested in examining the relationship between worker size and colony queen number in fire ants in greater detail. Specifically, we wished to determine if there was an association between worker size and queen number within the polygyne social form.

Materials and methods

We collected 39 presumed polygyne *S. invicta* colonies in Walton County, Georgia, USA, from a site that previously has been shown to contain only polygyne colonies. An attempt was made to collect colonies exhibiting a wide range of sizes, while choosing mounds that were fairly isolated from one another. As many individuals as possible were collected from each colony using the method of Jouvenaz et al. (1977). Colony inhabitants were placed in large trays and all dealate queens were collected. Colonies were considered polygyne if they contained more than one dealate queen.

Monogyne samples also were obtained from Walton County, Georgia, USA, at a site approximately 20 km from the polygyne site that previously was found to be free of polygyne colonies. We collected monogyne workers and sexuals from 13 large, mature colonies by collecting individuals that climbed onto a shovel inserted into the mound. To confirm monogyny, the multilocus genotypes of eight sexuals from each colony were examined at four polymorphic allozyme loci (*Est-4, G3pdh-1, Pgm-1, Pgm-3*) using starch gel electrophoresis (Shoemaker et al., 1992). We considered colonies monogyne if the genotypes of these sexuals were consistent with their being the offspring of a single, once-inseminated queen (Ross, 1993).

We obtained the wet weight of twenty samples of 25 randomly chosen workers from each study colony (500 workers/colony). The mean mass of workers from each individual sample was then calculated. The distribution of the 20 means was used to find the approximate mean and standard deviation for worker mass from a given colony by employing the central limit theorem. The standardized coefficient of variation (s.d./$\bar{x}$) was used to quantify within-colony variation in worker mass. Statistical estimates were obtained using the statistical software package SPSS.

Results

Thirty-five of the 39 colonies collected from the polygyne site could be confirmed as polygyne. Queen number in the confirmed polygyne colonies ranged from 2 to 143 ($\bar{x}$ = 32.3, s.d. = 32.2). The mean worker mass in each polygyne colony ranged from 0.45 to 0.71 mg, with an overall mean of 0.56 mg. A strong negative linear relationship was found between colony queen number and mean worker mass for the polygyne colonies ($F_{1, 33} = 10.14$, $p = 0.003$, $r^2 = 0.24$) (Fig. 1). The coefficient of variation for worker mass in each colony spanned from 0.92 to 4.03, with a mean value of 1.69, and it was not related to colony queen number ($F_{1, 33} = 0.33$, $p > 0.5$).

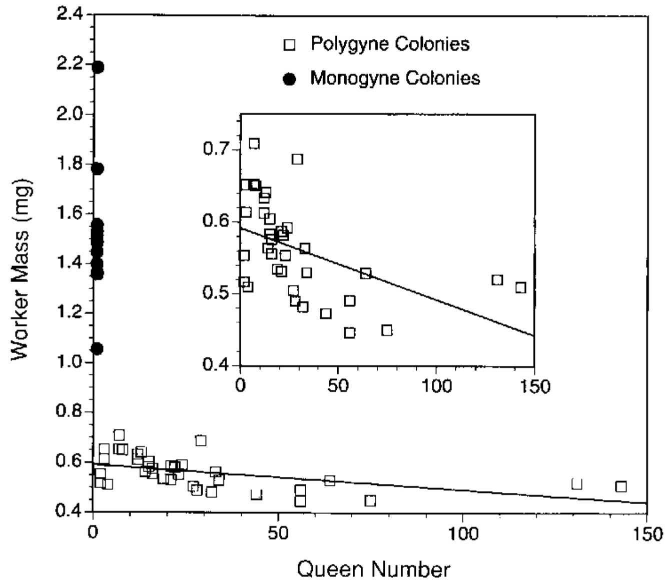

Figure 1. Relationship of queen number and mean worker mass in monogyne and polygyne colonies of *Solenopsis invicta*. Inset shows data from polygyne colonies only. We can describe the linear relationship in polygyne colonies as $y = -0.001x + 0.592$, where y is mean worker mass in mg and x is queen number

All samples collected from the putative monogyne site were confirmed by the genetic data as coming from colonies headed by a single queen (data not shown). Mean worker mass in each monogyne colony ranged from 1.06 to 2.19 mg, with an overall mean of 1.50 mg. The coefficient of variation for monogyne colonies ranged from 1.01 to 1.86, with a mean of 1.29, which was significantly lower than that in polygyne colonies ($F_{1,46}=5.33$, $p=0.026$). Thus, for their size, monogyne workers are less variable than polygyne workers.

The mean worker mass in any monogyne colony was found to be significantly higher than that in any polygyne colony (Student-Newman-Keuls procedure, $\alpha=0.05$) (Fig. 1). Furthermore, the mean mass of workers in monogyne colonies clearly does not fall on the regression line fitted to the polygyne data. The probability that all of the monogyne data points would lie above the regression line, if the values for monogyne worker mass were described by the same regression line as that fitted to the polygyne data, is approximately 0.0001 (one-tailed binomial test).

Discussion

The major finding of this study is that a negative linear relationship exists between queen number and worker size in polygyne *S. invicta* nests. Thus, increasing queen number in multiple-queen colonies apparently changes the intranidal environment in some way that inhibits the growth potential of worker larvae. The trend in worker size observed in polygyne colonies is accentuated greatly in monogyne colonies, leading to a striking disparity in worker size between the social forms. This difference has been documented previously in this species (Greenberg et al., 1985), and similar differences have been reported in *Myrmica* and *Formica* (Elmes, 1974; Pisarski, 1981). Although the difference in worker size between the monogyne and polygyne social forms is considerable, it is consistent with the negative relationship between queen number and worker size observed in the polygyne colonies. Thus, the same factors may affect worker size in both social forms.

Pisarski (1981) argued that the difference in worker size between monogyne and polygyne nests of *Formica* species is due to a higher larva to worker ratio in multiple-queen colonies as compared to that in single-queen colonies. This high ratio could cause an imbalance in trophic conditions in polygyne colonies, leading to underfed larvae and subsequently to smaller workers. Such a difference in larva to worker ratio between monogyne and polygyne colonies has been found in *S. invicta* (Porter et al., 1991). Furthermore, experimental studies have demonstrated that an increased brood to worker ratio in artificial colonies leads to a decrease in the size of worker pupae produced (Porter and Tschinkel, 1985a).

Elmes (1974) cited a possible "queen effect" as leading to a decrease in worker size with increasing queen number in *Myrmica* species. Such an effect has been shown to influence certain aspects of *S. invicta* reproductive biology. For instance, the lower number of sexuals produced, as well as the decreased fecundity of reproductive queens in polygyne colonies, has been found to be related to a higher pheromone level accompanying increased queen number (Vargo and Fletcher, 1986, 1989). It is possible that such a queen pheromone also accounts for the variation in worker size either by acting directly as a primer pheromone that affects larval development or indirectly as a releaser pheromone that alters worker treatment of larvae.

It is unlikely that the small workers found in polygyne *S. invicta* colonies are produced as an adaptation related to the different environments experienced by the two social forms. Small workers are more competent than large workers at certain tasks, such as brood rearing (Porter and Tschinkel, 1985b), but a polymorphic worker force is likely to be more effective when other factors such as colony defense, foraging, and energetics are considered (Porter and Tschinkel, 1985a, 1985b). The variation in worker size observed in this study is a product of the altered environment created by increased queen number, and in itself does not appear to have a positive or negative effect on colony survival. Rather, the success of the polygyne form is related to other aspects of its social biology, such as the rapid colony growth and dominance of local habitats associated with colony budding as a means of reproduction (Vargo and Porter, 1989).

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