

Short communication

**Unmated Queens in the primitively eusocial wasp
Ropalidia marginata (Lep.) (Hymenoptera: Vespidae)**

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Summary

In the primitively eusocial tropical wasp *Ropalidia marginata*, five out of eleven colonies studied had an unmated female as their queen. In two colonies this was the case despite the presence of another mated individual in the colony. We found no detectable differences between colonies with unmated queens and those with mated queens. We argue that in species such as *R. marginata*, where intra-colony relatedness is expected to be low and where sociality is likely to be maintained because several individuals have opportunities for direct reproduction in the future, individual selection is likely to override “the good of the colony” and lead to such phenomena as that of unmated queens.

Introduction

In the Hymenoptera, females mate with one or more males and store a lifetime's supply of sperm in their spermathecae. However, both fertilized and unfertilized eggs are laid; the former develop into females and the latter into males. Queens are defined as mated females who spend little time away from the nest and do most of the egg laying, while workers are defined as unmated females who undertake such tasks as foraging, nest building and brood care (Wilson, 1971). These definitions of “queen” and “worker” are borrowed from the literature on highly eusocial insects and are often not suitable for primitively eusocial species. For instance, West-Eberhard (1969) found that 13 out of 51 foundresses in *Polistes canadensis* were unmated and that three of these had mature eggs and were the sole occupants of their nests. Similarly, Dropkin and Gamboa (1981) found that 4 out of 15 queens in multiple-foundress nests and 6 out of 24 queens in single-foundress nests were unmated in *Polistes metricus*. Pardi and Marino Piccioli (1970) found that in *Belonogaster grisea*, at least some unmated females can reach a level of fertility equal to or surpassing that of fertilized females, attain high dominance ranks and even found

nests alone. We report here that unmated females are the sole egg layers in a substantial proportion of nests of the primitively eusocial wasp *Ropalidia marginata*.

Materials and Methods

This study was conducted on 11 naturally occurring post-emergence colonies of the primitively eusocial tropical wasp, *Ropalidia marginata* between January 1986 and May 1987. Seven of the 12 colonies were located in Bangalore (13°00' N and 77°32' E) and five were in Mysore (12°25' N and 76°50' E) in India. Data pertaining to size of the nest and behaviour, morphology and anatomy of the wasps were obtained as described elsewhere (Gadagkar and Joshi, 1983; Chandrashekara and Gadagkar, 1991). The spermatheca of each wasp was examined under the microscope to ascertain whether she had mated.

We compared nests having mated queens with those having unmated queens by four methods. In the first method we performed parametric (*t*-test) and non-parametric (Mann-Whitney *U*-test) comparisons of means using 41 variables. In the second method, we considered the probability of a colony having a mated or unmated queen as the binary dependent variable and performed a logistic regression analysis as described in Chandrashekara and Gadagkar (1991). In the third method, colonies with mated queens and those with unmated queens were compared by one-way ANOVA using one variable at a time. In the fourth method, we performed a nested ANOVA where each animal is nested in any one colony and each colony is nested in any one of the two colony types namely, those with mated queens and those with unmated queens. For ANOVA, data were subjected to arcsin or logarithmic transformation as appropriate.

Results

Our results are three-fold. First, each colony observed had only one egg layer who also was the only female who had mature eggs; she was therefore designated as the queen.

Second, five out of 11 colonies had an unmated queen. Two out of these five colonies also had one mated individual each but these animals had very poorly developed ovaries. Of the six colonies that had mated queens, three had one additional female each who was also mated, but had rather poorly developed ovaries. Of the five mated non-queens, one was a Sitter, one was a Fighter and three were Foragers, according to the behavioural caste differentiation described for these colonies (Chandrashekara and Gadagkar, 1991).

Third, colonies with unmated queens appeared to be no different from those with mated queens. We had no hint of the unmated status of their queens or of any other abnormality of these colonies during the observations. Social organisation and division of labour based on a behavioural caste differentiation that is normally seen in *R. marginata* was evident in all colonies (Chandrashekara and Gadagkar, 1991). The colonies with unmated queens were present in both the localities of our study. We

were unable to detect any significant differences between colonies with mated queens and those with unmated queens by the comparison of the variables mentioned in materials and methods by parametric and non-parametric tests, ($p > 0.05$). Logistic regression analysis, did not yield any regression coefficient that was significantly different from zero ($1.0 > p > 0.13$). We also failed to find any significant added component of variance between colony types (one-way ANOVA, $0.94 > p > 0.08$). The proportion of variance "within colony types" ranged from 65.2% to 100% and that "between colony types" only from 0 to 34.8%. In the nested ANOVA, the proportion of variance "within colonies" ranged from 46.5% to 99.8%, that "within colonies of a type" ranged from 0 to 53.5% and that "between colony types" ranged only from 0 to 5.8%. While the added component of variance "within colonies of a type" was significant for several variables, in no case was there a significant added component of variance "between colony types" ($0.99 > p > 0.11$).

Discussion

The results reported in this paper suggest that in *R. marginata*, mating is not only unnecessary for the development of a female's ovaries but is also unnecessary for an individual to assume the role of the queen of a colony, prevent all other individuals from laying eggs and maintain normal social organisation. The fact that three out of five mated non-queens seen were Foragers (who are expected to have the least chance of direct reproduction, unpublished observations), strengthens the idea that mating is unrelated to caste. Mating has however been said to be crucial in caste determination in the primitively eusocial bee *Halictus rubicundus* (Yanega, 1989), but the caste that is apparently determined here by mating is that of "gynes" who necessarily mate, diapause, disperse and initiate new colonies. But even in *H. rubicundus* there are replacement queens and there is no evidence that mating is necessary for their differentiation.

Queens in *R. marginata* seldom leave their nests but on more than one occasion, we have seen replacement queens leave their nests for several hours in the first few days of taking over the role of the queen. Colonies with such replacement queens have then been seen to produce both male and female offspring, suggesting that replacement queens may mate after taking over the role of queen (unpublished observations). Even if such replacement queens do not mate, they should get some fitness for the haploid eggs they lay during their tenure as queens. We suggest therefore that parthenogenesis may be a significant, as yet underestimated avenue for obtaining fitness in primitively eusocial species.

R. marginata queens are known to mate multiply (Gadagkar, 1991) and queen replacements are common (Gadagkar et al., 1990a). Workers in *R. marginata* therefore often rear mixtures of full-sisters, half-sisters, nieces, daughters, brothers, nephews, sons and cousins (Gadagkar et al., 1990) and probably do so without the ability to discriminate on the basis of genetic relatedness (Gadagkar, 1991). For this reason it has been argued that group life in this species is unlikely to be maintained because of indirect fitness gained by sterile workers but because many workers are hopeful reproductives who often have opportunities to gain direct fitness (Gadagkar,

1991). It is in such species that one would expect individual fitness considerations to override what is "good for the colony" and lead to such phenomena as an unmated individual taking over the role of the queen even in the presence of a mated individual who may make a better queen for the colony.

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