Do Social Wasps Choose Nesting Strategies Based on Their Brood Rearing Abilities?

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Primitively eusocial wasp nests may be founded by one or a group of females. The solitary foundress builds a nest, lays eggs, defends her brood from parasites and predators, and forages to feed her growing larvae, all by herself, at least until the eclosion of her first daughter. In multiple-foundress nests, only one individual normally assumes the role of dominant queen or egg layer while the remaining cofoundresses act as subordinate workers, building the nest and foraging for food and building material and laying few or no eggs [1, 2]. An obvious question is why the subordinate cofoundresses do not leave to start their own solitary-foundress nests and rear their own offspring. In most species studied, the per-capita productivity of nests does not increase as a function of the number of foundresses [3–6]. This makes the altruism on the part of the cofoundresses even more paradoxical because it appears that subordinate cofoundresses gain no particular advantage by joining another individual's nest rather than initiating their own. This argument makes the assumption, however, that the subordinate cofoundresses would have achieved the same productivity as the solitary foundresses do, had they themselves chosen the solitary nesting strategy. If, however, the individuals who chose to become subordinate cofoundresses fare very poorly as solitary foundresses, then one must compare their contribution in multiple-foundress nests with (1) what they might have achieved if they them-

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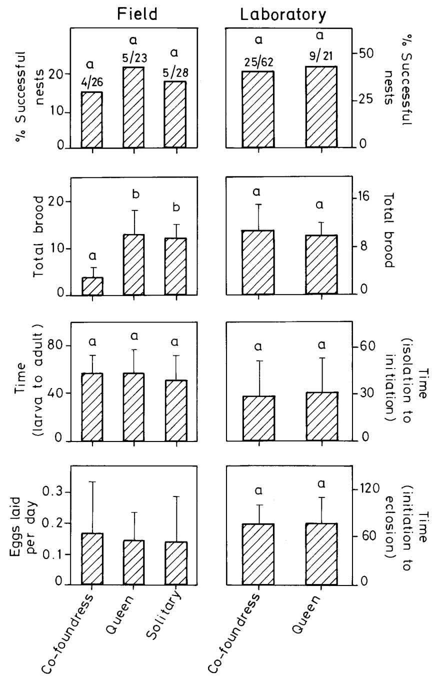

Fig. 1. Comparison between randomly chosen cofoundresses forced to nest alone, queens of multiple foundresses nests forced to nest alone, and naturally occurring solitary foundresses. *Laboratory* Comparison between cofoundresses and queens from naturally occurring multiple-foundress nests isolated individually in laboratory cages. *Bars* means; *lines above them* standard deviations. Except in the case of brood in the field experiment (p<0.01), all comparisons are insignificant (p>0.05) by the Kruskal-Wallis test. Within each *box*, *bars carrying different alphabets* are significantly different from each other by the Mann-Whitney U-test (p=0.05). Brood produced by the cofoundress forced to nest alone in the field was also significantly less than the brood produced by isolated cofoundresses and queens in the laboratory cages (Mann-Whitney U-test, p=0.05). Brood produced by the isolated queens and the solitary foundresses in the field were not significantly different from the brood produced by the cofoundresses and queens isolated into laboratory cages (Mann-Whitney U-test, p>0.05). Since *R. marginata* follows a perennial indeterminate nesting cycle, all nests could not be monitored until they were abandoned. Besides, there is no strict demarcation between potential workers and potential reproductives, so that one cannot measure productivity as the number of new reproductives produced. Nests were therefore monitored until the eclosion of the first adult offspring or until they were abandoned, whichever was earlier [16]. Identical results were obtained when cells, eggs, larvae, and pupae were analyzed separately. For brevity, only results with total brood are shown. Since the time of hatching of the first egg was known more precisely than laying of the first egg under field conditions, brood developmental time was measured as the time between the production of the first larva and the eclosion of the first adult offspring

selves had chosen the solitary-nesting strategy rather than with (2) the productivity of individuals who naturally opt for the solitary-nesting strategy.

It has been hypothesized that individuals opting for subordinate worker roles may be subfertile and may be making the best of a bad job [7, 8]. In the primitively eusocial wasp. *R. marginata*, there is evidence for a larval nutrition based preimaginal caste bias such that relatively better-nourished larvae develop into egg layers and relatively poorly nourished larvae develop into nonegg layers [9–11], but in *Polistes bellicosus* there is no significant difference in the productivities of small and large wasps [12]. There has, however, been no direct test of the hypothesis that subordinate cofoundresses might fare much more poorly compared to solitary nesters, if they themselves had chosen the solitary-nesting strategy. Such a test would require that individuals that have naturally chosen to become subordinate cofoundresses in multiple-foundress nests be forced to nest alone.

Seventy-seven naturally initiated nests of *R. marginata* located in the Indian Institute of Science, Bangalore (13°00′N and 77°32′E), were used in this study. Of these, 28 were natural single-foundress nests and they were not manipulated in any way. Of the remaining 49 multiple-foundress nests, 26 were randomly chosen, to force cofoundresses to nest alone; the queen and all but one cofoundress (chosen randomly) were removed on the day each nest was located. To control for the disturbance caused by such manipulation, the remaining 23 nests were manipulated such that all the cofoundresses were removed and the queen was forced to nest alone. In *R. marginata* at any given time, only one individual is the egg layer, who was unambigously identified by behavioral observations. All manipulations were performed in the very early egg stage of the nesting cycle and the total brood present at the time of manipulation was not significantly different between the different categories of nests (t-test, p>0.05, df=47 to 52). For successful nests, namely those that produced at least one adult offspring, productivity was measured as the total brood (eggs+larvae+pupae) present at the time of eclosion of the first adult offspring.

The proportions of successful nests ranged from 15% to about 22% and did not differ significantly between nests with cofoundresses forced to nest alone, queens of multiple foundress nests forced to nest alone, and naturally occurring solitary foundresses (Fig. 1, field). However, the productivity of cofoundresses forced to nest alone was significantly less compared to both the productivity of queens forced to nest alone and naturally occurring solitary foundresses. The productivity of queens forced to nest alone was not significantly different from that of naturally occurring solitary foundress nests (Fig. 1, field; Mann-Whitney U-test, multiple comparisons with Bonferroni corrections). The time taken from the hatching of the first larva to the eclosion of the first adult was not significantly different for the three classes of nests (Fig. 1, field).

Why did the cofoundresses that were forced to nest alone have such low productivity as compared to naturally initiated single-foundress nests and queens forced to nest alone? One possibility is that they were incapable of laying enough eggs. Another possibility is that they might have been incapable of sufficient foraging to permit productivities on a par with naturally initiated single-foundress nests and queens forced to nest alone. The first possibility is unlikely for two reasons. One, cofoundresses forced to nest alone, queens forced to nest alone, as well as naturally occurring solitary foundresses had similar rates of egg-laying during the observation period (t-test, p>0.50, df=47 to 52;

Fig. 1, field). The second reason comes from the laboratory experiments. The 62 cofoundresses and 21 queens that were removed from the field colonies in order to force one of the cofoundresses or the queen to nest alone were isolated into individual laboratory cages and provided with an ad libitum supply of food and building material. Under these conditions, the wasps can initiate single-foundress nests and produce offspring [9–11]. In the laboratory cages, about 40% of the isolated cofoundresses and about 43% of the isolated queens successfully produced at least one offspring. Not surprisingly, success rate in the field (Fig. 1, field) was lower than that in the laboratory for both queens and subordinate cofoundresses (Fig. 1, laboratory). As in the field, the success rate did not differ significantly between the isolated cofoundresses and the isolated queens. However, unlike in the field, there was no significant difference between the isolated cofoundresses and the isolated queens in their total brood production (Fig. 1, laboratory). No significant difference was observed between the isolated cofoundresses and the isolated queens in the time required for nest initiation and eclosion of the first offspring (Fig. 1, laboratory). Cofoundresses forced to nest alone in the field, but not queens forced to nest alone in the field or naturally occurring solitary nesters, had significantly lower brood compared to cofoundresses and queens isolated in laboratory cages (Fig. 1). Their similar rates of egglaying in the field and identical productivities in the laboratory suggest that cofoundresses are as fertile as queens and solitary nest foundresses. The significantly lower productivity of cofoundresses forced to nest alone in the field thus seems to arise not from their inability to lay enough eggs, but perhaps from their inability to forage for as large a quantity of brood as the other two categories of individuals and at the same time have the same probability of survival (which they do). In the field, cofoundresses forced to nest alone, but not queens forced to nest alone, lost or destroyed most of the eggs laid prior to the experimental manipulation and maintained substantial numbers of empty cells (data not shown). *R. marginata* females thus appear to choose their nesting strategies based on their abilities to rear brood, the relatively "inferior" subordinate cofoundresses may prefer not to initiate their own nests as the "superior" solitary foundresses and queens of multiple foundress nests do. When they find themselves in a multiple-foundress nest, however, the subordinate cofoundresses appear to be able to rear as much brood as solitary foundresses and queens forced to nest alone because the per-capita productivity remains more or less constant with increasing group size in multiple-foundress nests [6]. How the same individuals manage to rear more brood when working in multiple-foundress nests, however, remains to be understood.

The experiments reported here indicate that the productivity of joiners increases by a factor of 2.9, from about 4.2 if they nest alone to about 12.3 if they become subordinate cofoundresses (assuming that each additional individual contributes as much as a single foundress does, leading to a constant per-capita productivity in multiple-foundress nests). This means that the subordinate cofoundresses would break even in their inclusive fitness even if they reared brood in multiple-foundress nests, that are related to them 2.9 times less than the brood in their own single-foundress nests would have been. Solitary foundresses rear their own offspring, who, in outbred populations, are expected to be related to them by 0.5. Thus, as subordinate cofoundresses, they obtain as much inclusive fitness as they would in the solitary state, even if they rear brood related to them by $0.5/2.9=0.17$. On account of polyandry and serial polygyny that result in the presence of multiple patrilines and matrilines in colonies of *R. marginata*, female offspring have been estimated to be related to each other by values ranging from 0.22 to 0.46 [13, 14]. If new colonies are founded by groups of female wasps eclosing from the same nest, then subordinate cofoundresses rearing brood produced by one of them must therefore rear brood related to them by values ranging from (0.22 to 0.46) x 0.5=0.11 to 0.23. Thus, the lower efficiency of subordinate cofoundresses in rearing brood as solitary foundresses substantially compensates for the cost of not reproducing and, instead, rearing brood of low genetic relatedness in multiple-foundress nests.

At this stage we are, however, unable to entirely rule out an alternative interpretation of our results, namely that cofoundresses forced to nest alone in the field may be unwilling to rather than incapable of rearing as much brood as naturally occurring solitary foundresses and queens forced to nest alone can; the unwillingness potentially arising from the expected lower genetic relatedness of the cofoundress nesting alone to brood in the nest, because the latter belongs to the queen which was removed. However, not all the brood reared by the cofoundress forced to nest alone belonged to the previous queen; often, these cofoundresses laid their own eggs after the previous queen was removed. For the four successful cofoundress nests, the proportion of their own brood out of the total reared by them ranged from 0.071 to 0.667 (mean ± SD = 0.374 ± 0.338). Secondly, we have reason to believe that cofoundresses may not be unwilling to rear brood which did not belong to them. This reasoning is based on our previous finding that the foundresses move extensively from nest to nest during the preemergence stage in *R. marginata.* In a field study we found that 217 out of 676 marked wasps (32.1%) were seen to join previously established nests and 69 out of 145 nests (47.6%) received at least one joiner each. Although the source of all the joiners was not known, we have definite evidence that at least 16 nests consisted of foundresses coming from two or more source nests, at least 3 nests consisted of foundresses coming from three or more source nests, and at least 1 nest consisted of foundresses coming from four or more source nests [6]. It seems unlikely that wasps would voluntarily make such movements if they were unwilling to rear brood of different levels of relatedness. Using allozyme electrophorosis and pedigree analysis, it has been shown that in *R. marginata* nests, brood may be brothers and sisters, nieces and nephews, cousins, cousins offspring, mother's cousins, mother's cousins' offspring, or mother's cousins' grand-offspring of the workers [13, 14]. This hardly suggests that the wasps will be unwilling to rear brood of different levels of relatedness. The most likely explanation for our results is therefore that cofoundresses forced to nest alone are incapable of rearing as much brood as queens forced to nest alone or a solitary foundress, and hence we suggestion that wasps may choose their nesting strategies based on their brood-rearing abilities.

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