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Why are there multiple-foundress colonies in *Ropalidia marginata* ?

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ABSTRACT

Female wasps of the primitively eusocial species *Ropalidia marginata* found new colonies either singly or in groups of individuals ranging in number from 2–22, more or less throughout the year. In a twelve-month study in Bangalore, it was found that 35% of newly initiated colonies were single foundress colonies, whereas 65% were multiple foundress colonies. In multiple foundress colonies, only one individual becomes the queen or egg layer, while the remaining perform the role of sterile workers. This is usually thought to be decided by aggressive interactions among foundresses. But, it was found that in 3 out of 5 colonies, the queen was not the behaviourally most dominant individual. Although there is a significant increase in productivity as the number of foundresses increase, the per capita productivity does not increase as a function of group size. The brood reared in multiple foundress colonies is likely to be less related to the workers than their own offspring would have been. The main reason for assuming the role of a sterile worker under such "unfavourable" conditions appears to be the hope that workers will eventually become queens.

INTRODUCTION

Ropalidia marginata is a primitively eusocial polistine wasp where new colonies may be founded either by a single female or by a group of females ranging in number from 2–22. The single foundress builds her nest, lays eggs, forages to feed her growing larvae, guards them from predators and parasites, and brings them to adulthood all by herself. Daughters eclosing on such nests often stay back and assist her in rearing subsequent batches of brood. In multiple foundress colonies on the other hand, only one individual becomes the egg layer or queen while the remaining act as subordinate workers and perform most of the tasks

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of nest building, maintenance and brood care. Why these subordinate workers should not also become solitary foundresses and build their own nests and rear their own offspring instead of working for someone else's brood, is a puzzle.

The answer to this puzzle must lie in the fact that workers get as much or more inclusive fitness compared to solitary foundresses. This is possible if (i) workers rear brood more closely related to themselves than their own offspring would be [1, 2] (ii) workers are sub-fertile and incapable or inefficient of producing their own offspring [3, 4], or (iii) the productivity of multiple foundress nests is disproportionately higher than that of single foundress nests. Previous work has shown that polyandry (multiple mating by queens) and serial polygyny (the sequential turnover of queens) make it very unlikely that workers rear broods more closely related to themselves than their offspring would be [5, 6, 7, 8]. Under laboratory conditions, about 50% of the eclosing individuals seem to be incapable of starting their own nests and ovipositing but the remaining 50% are capable of doing so [9, 10]. Even if this situation holds in nature, this does not explain why so many individuals become workers and so few become solitary foundresses. Sub-fertility is thus unlikely to be the whole explanation. We turn therefore to the third possibility and investigate in this study, the differential productivities of nests with varying number of foundresses.

MATERIALS AND METHODS

Naturally initiated pre-emergence nests of *Ropalidia marginata* were monitored both in the field and in the vespiary. Our field sites included chosen buildings in Indian Institute of Science campus, Univ. Agril. Sciences G.K.V.K. campus and New Public Office, all in Bangalore (13° 00′ N and 77° 32′ E). The vespiary is a room in the Indian Institute of Science measuring 9.3m × 6m × 4.8m, with a wire mesh of 0.75 cm × 0.75cm dimension. The mesh, by virtue of its size, prevents the hornet, *Vespa tropica* from entering and preying on *R. marginata* but permits the latter to fly in and out freely. Intensive searches were carried out once a week both in the field and in the vespiary, to record newly initiated nests. On locating a nest, it was given a unique nest code and all the animals on the nest were individually marked using quick drying paints. Thereafter records were maintained on the number of wasps attending the nest (census) and the brood composition (nest map) at intervals of 1–2 days till the first adult eclosed.

Since these wasps follow a perennial indeterminate nesting cycle, and since the number of individuals per nest changes after the first eclosion, this time duration was chosen as most convenient to terminate monitoring

and compare the productivity of nests with different number of females. The total and per capita productivities measured as total brood was estimated from the nest map records.

In order to ascertain the 'dominance' status of each of the foundresses on a given colony, quantitative data on behaviour was obtained for five colonies by observing each colony for a period of 20h, spread over 4 to 6 days. Two sampling methods namely, "instantaneous scans" and "recording all occurrences of rare behaviours" [11] were used as described by Gadagkar and Joshi [12]. Dominance hierarchies were constructed for each of the five experimental colonies as described by Premnath *et al.* [13].

RESULTS

During the study period a total of 145 colonies were recorded (80 were in the vespiary and 65 were in the field). *Ropalidia marginata* initiated new colonies throughout the year, although large number of nests were found during May to July. The number of animals attending a colony kept fluctuating due to movement of animals. The mean number of foundresses attending the nests and the number of nests in each group size is shown in Fig.1. In the 12-month study we found that 35% of the pre-emergence colonies were founded and attended by a single foundress. This corresponds to 5–12% of the individuals preferring to nest alone while the remaining preferred to nest in groups. The overall success rate was significantly higher in the vespiary than in the field ($G = 5.29$; $p < 0.05$). Multiple foundress colonies survived better than single foundress colonies both in the field and in the vespiary. Total productivity measured as the total brood per colony at the time of the eclosion of the first adult, increased with increasing group size. The per capita productivity, however, did not change with increasing group size (Fig.2). This was the case in spite of taking into consideration the higher success rate of multiple foundress colonies. Behavioural observations carried out during the pre-emergence stage revealed that in 3 out of 5 colonies, the queen was not the behaviourally most dominant individual. There were 1–3 animals behaviorally more dominant than the queen in three colonies (Fig.3).

DISCUSSION

The success rate of multiple foundress colonies was higher than that of single foundress colonies. The major cause for colony failure in the founding phase is the loss of foundresses. Multiple foundress colonies are less likely to fail due to this reason. Similar findings have been reported for *Polistes metricus* [14] and *Polistes fuscatus* [15].

The total colony productivity increased as the number of foundresses increased. This is probably a consequence of efficient division of labour. Similar findings have been reported for social Hymenoptera in general [16], for *Polistes fuscatus* and *P. canadensis* [17], for *Polistes fuscatus* [15] and for *Ropalidia fasciata* [18].

The per capita productivity remained constant with group size. Similar observations were reported for *P. fuscatus* [15]. While Michener reported a decreasing per capita productivity with increasing group size for social Hymenoptera in general [16], West Eberhard reported a similar trend for *P. fuscatus* [17]. The constant per capita productivity in *R. marginata* indicates that each individual, either a solitary foundress or a helper in a multiple-foundress colony, contributes about the same number of individuals to the next generation. But a helper in a multiple foundress colony, contributes about the same number of individuals to the next generation. But a helper in multiple foundress colony contributes nephews and nieces and perhaps more distantly related individuals instead of offspring, thus contributing less than a solitary foundress in terms of genes [7, 8]. Nevertheless about 88–95% of the population in *R. marginata* prefer to nest in groups. The reason for this is perhaps that the workers are waiting for a chance to take over as the next queen. If this explanation is valid, then our results lend greater credence to the theory of mutualism rather than to the haplodiploidy, parental manipulation or sub-fertility hypothesis [19]. Alternatively, or perhaps in addition, the advantage of the worker strategy may lie in other kinds of advantages of group life such as the ability of individuals to serially share the task of brood rearing and thus minimize the ill-effects of early mortality [20, 21].

Reproductive competition during colony establishment is widespread among social wasps and the egg layer is decided by aggressive fights among the foundresses during the early stages of colony founding [22]. The queen is known to be the most aggressive animal throughout the nesting period in several *Polistes* species [23]. In *R. marginata*, however, the queen is not the behaviourally most dominant individual in post-emergence colonies [24]. Here, we show that the queen is not necessarily the behaviourally most dominant individual during the late pre-emergence period either. This suggests that in this species, the queen does not maintain her status by physical aggression, but she maintains it by some other means, perhaps pheromonal.

ACKNOWLEDGMENTS

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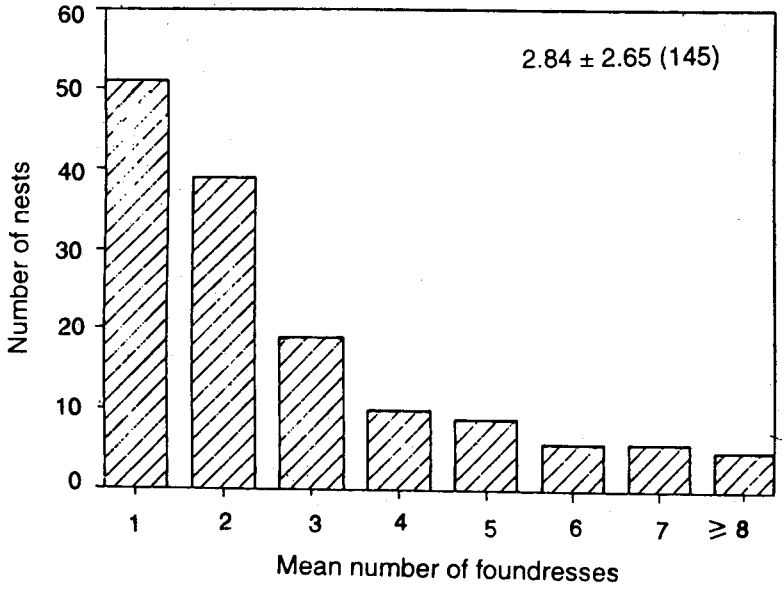

Fig.1 Frequency distribution of nests with different mean number of foundresses.

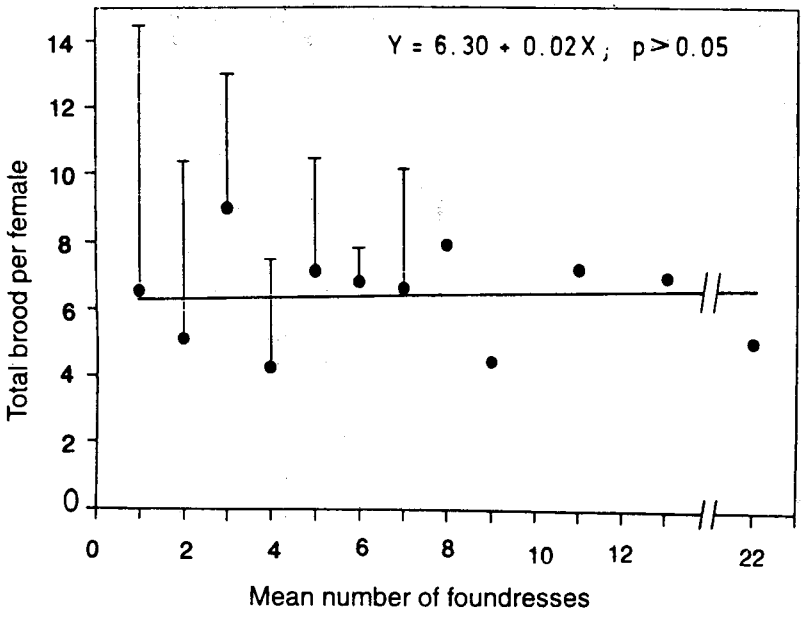

Fig.2 Percapita total brood (eggs + larvae +pupae) counted at the time of the eclosion of the first adult, as a function of mean number of foundresses. The fitted line is given by the equation, Y = 6.30 + 0.02X. The slope is not significantly different from zero, P > 0.05.

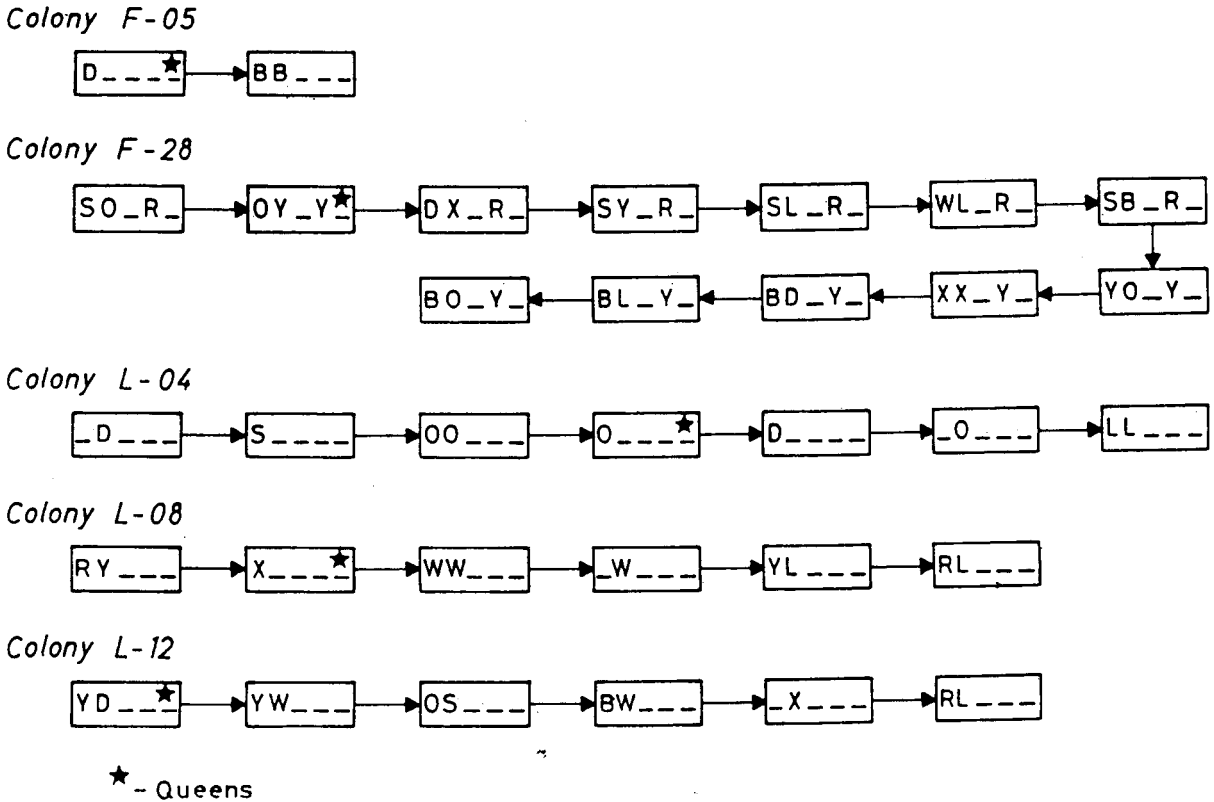

Fig.3 Dominance hierarchies on five colonies of *Ropalidia marginata* based on computation of dominance index as described by Premnath *et al.* (1990). D - - - → BB - - - → means that D - - - → is dominant over BB - - - →.

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