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Docile sitters and active fighters in paper wasps: a tale of two queens

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Abstract *Ropalidia marginata* and *Ropalidia cyathiformis* are sympatric, primitively eusocial paper wasps widely distributed in peninsular India. We compare the two species, especially their queens, in an attempt to begin to understand the role of the power of queens over their workers, in social organisation and evolution. Queens of *R. marginata* have lower levels of activity, rates of interactions and dominance behaviour, compared with queens of *R. cyathiformis*. For the same variables, *R. marginata* queens are either indistinguishable from or have lower values than their workers, while *R. cyathiformis* queens have higher values than their workers. *R. marginata* queens never occupy the top rank while *R. cyathiformis* queens are always at the top of the behavioural dominance hierarchies of their colonies. *R. marginata* queens thus do not appear to use dominance behaviour to suppress reproduction by their workers, while *R. cyathiformis* queens appear to do so. These different mechanisms used by the two queens to regulate worker reproduction give them different powers over their workers, because *R. marginata* queens are completely successful in suppressing reproduction by their nestmates while in *R. cyathiformis* colonies, other individuals also sometimes lay eggs. There is also some evidence that the different powers of the queens result in different mechanisms of regulation of worker foraging in the two species – decentralised, self-regulation in *R. marginata* and relatively more centralised regulation by the queen in *R. cyathiformis*. Thus we show here, perhaps for the first time, that the power of the queens over their workers can have important consequences for social organisation and evolution.

Introduction

Ropalidia marginata is an old-world, tropical, primitively eusocial, polistine wasp, widely distributed in peninsular India. In multiple foundress nests, there is a single egg-layer (queen) while the remaining wasps function as non-egg-laying workers. The latter are responsible for all tasks associated with nest building, brood care and foraging (Gadagkar 2001). Compared with the queens of most other primitively eusocial species (e.g. Gamboa et al. 1990), the *R. marginata* queen is rather unusual. She is a strikingly docile individual, never at the top of the behavioural dominance hierarchy of her colony. It is remarkable that she is, however, completely successful in suppressing reproduction by all her nestmates; in observations of hundreds of nests by many different observers during the last 20 years, we have never seen an unmanipulated nest with more than one egg-layer at a time (Gadagkar 2001). We have therefore postulated that queens of *R. marginata* do not use dominance behaviour to suppress/regulate reproduction by their nestmates and that they perhaps use a pheromonal mechanism to do so (Premnath et al. 1996; Gadagkar 2001). However, behavioural dominance–subordinate interactions are not lacking in this species; they are frequently shown by the workers. Indeed, a dominance hierarchy can be recognised among the workers (Gadagkar 2001; Sumana and Gadagkar 2001). Based on this and other evidence, we have also postulated that the dominance–subordinate interactions among workers may serve as a system of signals for workers to regulate each other's non-reproductive activities, especially foraging (Premnath et al. 1995; Gadagkar 2001).

If these postulates are correct, *R. marginata* may be said to represent a relatively advanced level of sociality among primitively eusocial wasps. Since *R. marginata* appears to be relatively unusual, its utility in studies of social organisation and evolution would be considerably enhanced if it can be compared with a related species that is not so unusual or advanced. We have therefore initiated a comparative study of social organisation in *R.*

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marginata and in the closely related, congeneric, sympatric *Ropalidia cyathiformis*. In both species, multivariate statistical analysis of time-activity budgets of individually identified wasps (workers as well as queens) reveals the existence of three rather distinct behavioural clusters in each colony; these behavioural clusters have been interpreted as behavioural castes. Based on their behavioural profiles, these clusters have been labelled as “sitters”, “fighters” and “foragers”. In such studies, *R. marginata* and *R. cyathiformis* are indistinguishable, except for the position of the queens in the system of behavioural caste differentiation. Queens of *R. marginata* are almost always classified as sitters and queens of *R. cyathiformis* are almost always classified as fighters (Gadagkar and Joshi 1983, 1984; Chandrashekara and Gadagkar 1991; Gadagkar 2001). In the present study, we have therefore carried out a detailed comparison of the behavioural characteristics of *R. marginata* and *R. cyathiformis*, and especially of their queens.

Materials and methods

Behavioural observations were made on eight post-emergence, monogynous, free-foraging nests each of *R. marginata* and *R. cyathiformis* on the campus of the Indian Institute of Science, Bangalore (13°00' N and 77°32' E), India, between February 1999 and June 2000. All wasps on all nests were uniquely marked with small spots of quick-drying paint. Behavioural observations were approximately uniformly distributed between 0630 hours and 1830 hours. Each nest was observed for 4 to 8 h per day for 4–6 days, except in the case of two nests of *R. cyathiformis* and one nest of *R. marginata* where 9 h of observations were made in a single day. Sampling methods for behavioural observations consisted of 45–120 instantaneous scans and 45–120 all-occurrence sessions (Gadagkar 2001), intermingled randomly and spread over 9–24 h of observations, per nest.

The proportions of time spent by individual wasps in different common behaviours were computed from the instantaneous scans. Frequencies per hour of performance of less common behaviours were computed from the all-occurrence sessions. Statistical comparisons were made for the following behaviours:

1. Activity: a wasp was considered active if she was not sitting, grooming or laying eggs.
2. Dominance behaviour: a wasp was considered dominant if she was seen to attack, nibble, peck, chase, hold in mouth, sit over another wasp or engage in falling fights with another wasp. The sum of the frequencies of each of these behaviours yielded the frequency of dominance behaviour.

3. Initiated interactions: these included the dominance behaviours described above as well as the active components of other paired interactions such as antennating, approaching, allogrooming, soliciting, and snatching food, liquid or building material from another wasp.
4. Total interactions: these included the sum of all active and passive components of all paired interactions, including dominance–subordinate interactions.

Dominance hierarchies were constructed for each colony using an index of dominance (see Gadagkar 2001). For each colony the following three variables were computed: (1) the proportion of individuals exhibiting dominance behaviour, (2) an index of dominance skew [by adapting the index of reproductive skew proposed by Reeve and Keller (1995)], and (3) an index of the diversity of dominance behaviour (computed as the number of types of dominance behaviours among those listed above).

Results

The aim of this study was to compare queens and workers of *R. marginata* with those of *R. cyathiformis*. The number of wasps present on the nests chosen for study did not differ between the two species (Table 1). Thus any differences we detected are not attributable to differences in colony size. We compared queens and workers of the two species in the proportion of time spent active, in the rates of total interactions, initiated interactions, dominance behaviour, and in the values of the dominance index. In the case of *R. marginata*, queens had lower values for all variables, compared with the highest scoring (Max) workers of their colonies, and were either indistinguishable from, or had lower values compared with the average (Avg) workers of their colonies; however, they had higher values than the lowest scoring (Min) workers of their colonies. On the other hand, *R. cyathiformis* queens were either indistinguishable from, or had higher values than their Max workers and always had higher values than Avg and Min workers. Interspecies comparisons revealed that *R. marginata* queens had lower values than *R. cyathiformis* queens and that Max, Avg and Min workers of *R. marginata* were indistinguishable from their counterparts in *R. cyathiformis* (see Fig. 1a–e).

With reference to dominance behaviour, the interspecies comparisons are even more striking. The mean frequency of dominance behaviour shown by *R. cyathiformis*

Table 1 Nest code, total number of wasps and dominance rank of queens of the 16 nests used in this study

<i>Ropalidia marginata</i>			<i>Ropalidia cyathiformis</i>		
Nest code	No. of wasps	Rank of queen	Nest code	No. of wasps	Rank of queen
M01	13	9	C01	16	1
M04	8	4.5 ^b	C02	19	1
M06	13	8	C03	30	1
V235	22	6.5 ^b	C07	35	1
V268	17	16	C08	21	1
V269	13	5b	C33	24	1
V270	36	18.5 ^b	C34	22	1
V273	42	27	C38	12	1
Mean ± SD	20.5 ± 12.2 ^a		Mean ± SD	22.4 ± 7.4 ^a	

^a The numbers of wasps on nests of the two species are not significantly different; $t(14)=0.37$, $P=0.72$

^b These queens did not participate in dominance–subordinate interactions

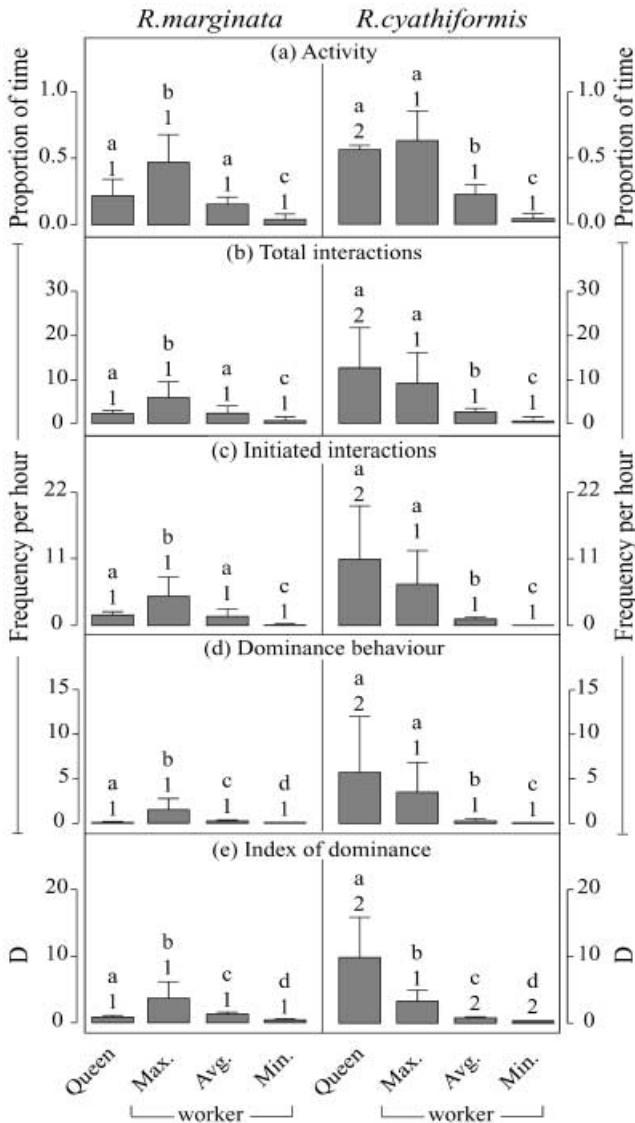


Fig. 1 Means and standard deviations of **a** proportions of time active (frequencies per hour), and of **b** total interactions, **c** initiated interactions, **d** dominance behaviour, and **e** index of dominance (D), for queens, highest scoring (*Max*) workers, average (*Avg*) workers, and lowest scoring (*Min*) workers in *Ropalidia marginata* and *Ropalidia cyathiformis*. Note that the identity of *Max* worker and *Min* worker may vary from variable to variable. For each variable the average value for all the workers is attributed to the *Avg* worker. Bars that carry different letters are significantly different from each other within a species (Wilcoxon signed-rank matched-pair test; $P < 0.05$). Bars that carry different numbers are significantly different from each other across species (Mann-Whitney U test; $P < 0.05$). Note that comparisons across species pertain to similar categories, e.g. queen of *R. marginata* vs queen of *R. cyathiformis*, *Max* worker of *R. marginata* vs *Max* worker of *R. cyathiformis*, etc

mis queens was 95-fold higher than the mean value for *R. marginata* queens; the highest value observed for *R. cyathiformis* queens was 62-fold higher than the highest value seen for *R. marginata* queens and the lowest value seen for *R. cyathiformis* queens was 14-fold higher than the highest value seen for *R. marginata* queens. However, it is worth reiterating that the *Max*, *Avg* and *Min*

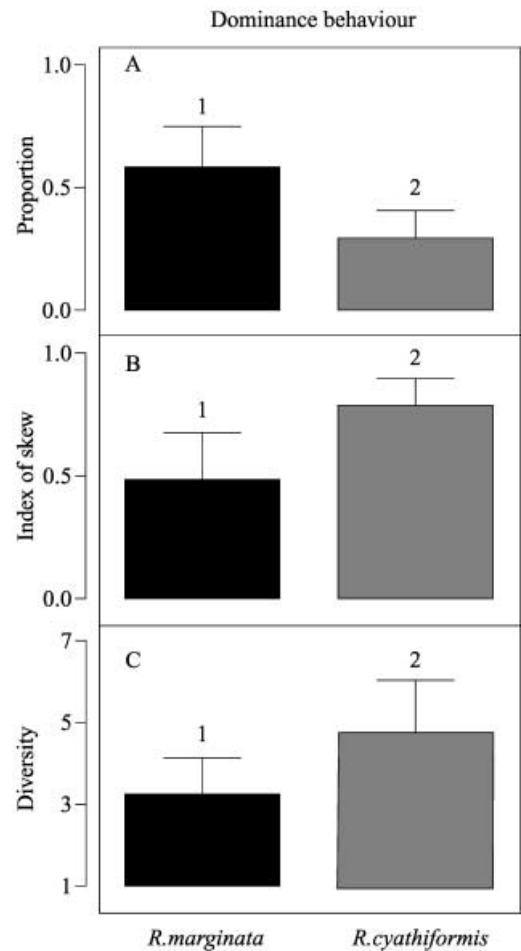


Fig. 2 Means and standard deviations of **A** proportion of wasps showing dominance behaviour, **B** index of dominance skew, and **C** diversity of dominance behaviour, in *R. marginata* and *R. cyathiformis*. Values are calculated considering all the wasps in the colonies. Bars that carry different numbers are significantly different from each other (Mann-Whitney U test; $P < 0.05$)

workers of *R. cyathiformis* were no different from their counterparts in *R. marginata* (Fig. 1d).

Striking as these differences in dominance behaviour are, the difference between the queens of the two species is, in some ways, more clearly brought out by a comparison of their ranks in the dominance hierarchies of their respective colonies. In all the eight colonies studied, *R. cyathiformis* queens always occupied the top rank (rank 1) even though the numbers of wasps in their colonies varied from 12 to 35. In contrast, none of the eight *R. marginata* queens ever occupied the top rank, nor even ranks 2 or 3. Their ranks ranged from 4.5 (tied between ranks 4 and 5) to 27, while the number of individuals from their colonies ranged from eight to 42. Low as they are, the ranks of *R. marginata* queens do not tell the whole story either. In four out of eight colonies, *R. marginata* queens simply did not participate in any dominance-subordinate interactions at all [although they could still be ranked by using the index of dominance; see Gadagkar (2001) (Table 1)].

Considering all the wasps in the colonies, the proportion of individuals who participated in dominance interactions in *R. marginata* was higher than the corresponding proportion for *R. cyathiformis* (Fig. 2A). The distribution of dominance acts among the various wasps that show dominance behaviours in a colony is less skewed in *R. marginata* than in *R. cyathiformis* (Fig. 2B). As listed in the Materials and methods section, up to seven different types of dominance behaviour were observed in these two species. However, this repertoire of dominance behaviour was not equally utilised by the two species. The diversity of the repertoire of dominance behaviour used by *R. marginata* was lower than that used by *R. cyathiformis* (Fig. 2C).

Discussion

Multivariate statistical analysis of time-activity budgets of individually identified wasps reveal that queens of *R. marginata* belong to the sitter behavioural caste and that the queens of *R. cyathiformis* belong to the fighter behavioural caste (Gadagkar and Joshi 1983, 1984; Chandrashekara and Gadagkar 1991; Gadagkar 2001). The explicit comparison of the two species made in this study reveals an even more striking contrast between the two species, and especially between their queens. Queens of *R. marginata* are less active, non-interactive and are never at the top of the dominance hierarchies of their colonies. In contrast, queens of *R. cyathiformis* are active, interactive and always at the top of the dominance hierarchies of their colonies.

What is the possible significance of this striking difference between the docile, sitter queens of *R. marginata* and the active and interactive, fighter queens of *R. cyathiformis*? We have speculated earlier that, except when new queens are establishing themselves, *R. marginata* queens may use a pheromonal mechanism, rather than overt dominance behaviour, to suppress/regulate reproduction by their nestmates (Premnath et al. 1996; Gadagkar 2001). In the same vein, we may also speculate that *R. cyathiformis* queens use overt dominance behaviour to suppress reproduction by their nestmates, as shown in other species (Gamboa et al. 1990).

Although *R. marginata* queens do not use dominance behaviour to suppress worker reproduction (except during the establishment of new queens), workers exhibit dominance–subordinate behaviours; they appear to have co-opted these behaviours to serve as a system of signals to regulate their own foraging rates (Premnath et al. 1995; Gadagkar 2001). We suspect, therefore, that dominance–subordinate behaviours in the two species serve somewhat different functions – decentralised, self-regulation of foraging by the workers in *R. marginata* and relatively more centralised, suppression of worker reproduction as well as regulation of worker foraging, by the queens in *R. cyathiformis*. That a higher proportion of individuals show dominance behaviour, that the distribution of dominance behaviour is less skewed and that

the repertoire of dominance behaviour is less diverse, all seem more consistent with the function of dominance behaviour postulated in *R. marginata*. Similarly, that dominance behaviour is restricted to a few individuals, that its distribution is more skewed and that the repertoire of dominance behaviours is more diverse, all seem to be consistent with its postulated function in *R. cyathiformis*.

Another consequence of the differences between the queens of the two species relates to the power of the queens over their workers; queen power being defined as their ability to suppress worker reproduction. *R. marginata* colonies are always monogynous, thus indicating that their queens have greater power over their workers. On the other hand, although it is quite common to have monogynous nests of *R. cyathiformis*, we have also seen fairly small colonies which are polygynous [with 10–30 individuals and 3–5 egg-layers at a given time (Gadagkar 2001)], thus indicating that their queens have less power over their workers.

We believe that such comparative studies of primitively eusocial species, especially those with contrasting queen powers, permit the integration of proximate and ultimate factors and provide novel insights for the study of social evolution.

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