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## Dominance relationship in the establishment of reproductive division of labour in a primitively eusocial wasp (*Ropalidia marginata*)

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**Abstract** In mature post-emergence colonies of the tropical primitively eusocial polistine wasp *Ropalidia marginata*, the queen is not a behaviourally dominant individual. Nevertheless, she completely suppresses reproduction by the workers and becomes the sole egg-layer in the colony. Mechanisms by which a female is able to establish her exclusive reproductive status in the colony can be investigated by examining dominance-submission relationships and hierarchy formation at particular stages of the colony cycle when reproductive competition is behaviourally manifest. Observations on the behaviour of *R. marginata* females (1) during early stages of colony-founding, (2) when potential queens challenge the existing queen, and (3) immediately after queen replacement show that these wasps use highly aggressive dominance interactions to establish their reproductive status. Both the frequency and the intensity of dominance behaviours are significantly higher at these stages than those observed at phases of the colony when there is no apparent reproductive strife. Once her position as the only egg-layer of the colony has been established, the levels of dominance interactions initiated by the queen decrease and the nature of these interactions also becomes comparatively milder. Thus, the mechanisms by which a queen establishes her social status in her colony and those by which she continues to suppress reproduction of her

nestmates in the absence of overt physical dominance may be quite different.

**Key words** Primitively eusocial wasp · *Ropalidia marginata* · Dominance · Foundress associations · Queen replacements

### Introduction

Dominance-submission relationships are an important component of social organisations and often appear to play a central role in the establishment and maintenance of many such groups, possibly communicating the individual status of the members of these associations (Wilson 1975; West-Eberhard 1977).

Primitively eusocial insect societies are characterised by a lack of morphological differentiation between the one or a few individuals who mate and lay fertilised eggs and the majority of the others who perform tasks such as foraging, nest construction and brood care (Wilson 1971). In such associations, comprising many potentially fertile females, social behaviours such as dominance-submission interactions determine social relationships and mediate the observed reproductive division of labour.

*Ropalidia marginata* is a tropical, primitively eusocial polistine wasp, widespread in peninsular India, that maintains small colonies of usually less than 100 adults, but invariably with a single egg-layer (Gadagkar et al. 1982; Chandrashekara and Gadagkar 1991). Colonies are usually initiated by either a single or a few potentially reproductive females (Shakarad and Gadagkar 1995). Unlike their more familiar temperate counterparts (e.g. *Polistes* spp.), these wasps establish colonies that are typically aseasonal, perennial and do not display well-defined nesting cycles (Chandrashekara et al. 1990; Gadagkar 1991). Moreover, there is no clear distinction between reproductives and workers

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in this species in the sense that many individuals in a colony are potentially capable of reproduction (Chandrashekara and Gadagkar 1992; Premnath et al. 1995). Opportunities for direct reproduction are thus available to females in a perennial colony which, during its lifetime, can have a series of queens who succeed one another (Gadagkar et al. 1993).

How is an individual female able to establish her reproductive monopoly in such a colony? In the genus *Polistes*, a clear dominance hierarchy is established amongst the foundresses during colony initiation, with the individual at the top of the hierarchy becoming the queen (Pardi 1948; West-Eberhard 1969; Dropkin and Gamboa 1981; Strassmann 1981; Reeve 1991). As the colony grows, the queen continues to be the most behaviourally active and dominant individual amongst her nestmates. The queen, in fact, has been described as a central "pace-maker" in *P. fuscatus* (Reeve and Gamboa 1983, 1987).

In mature colonies of *R. marginata*, on the other hand, following the emergence of offspring (post-emergence colonies), the queen is not the most behaviourally dominant individual in spite of being the only egg-layer in her colony (Chandrashekara and Gadagkar 1991). An important question that now arises concerns the manner in which a *R. marginata* female is able to establish her exclusive reproductive status at colony foundation or during queen replacement. Does she exhibit the high levels of behavioural dominance and patterns of activity reminiscent of *Polistes* queens, and only later become behaviourally inactive and resort to controlling worker reproduction by some indirect means? A study of dominance interactions and hierarchy formation at particular stages of the colony cycle when reproductive dominance is established could throw light on this question.

Since colonies of tropical polistine wasps are aseasonal, early foundress-associations of these species are usually difficult to locate. Hence, most studies on colony founding in these wasps have been conducted at least a few weeks after nest-initiation (Kojima 1984; Yamane 1986; Itô 1993), by when dominance hierarchies would most likely have already become established (Yamane 1986; Röseler 1991). In *R. marginata*, however, nests are often destroyed by predators such as hornets and rats, or by natural calamities such as strong winds and rain (Gadagkar 1991; S. Premnath, personal observations). On such occasions, one or more new nests are constructed by subsets of wasps from the disturbed colonies. This is probably a common mode of colony-founding in other aseasonal species as well (e.g. *P. canadensis* on Barro Colorado island; Itô 1993). This phenomenon was exploited in the present study to obtain newly formed foundress associations in order to understand the establishment of reproductive division of labour. Since queen succession in post-emergence colonies is also fairly common in this species, the behaviour of a new queen just before and

immediately after a natural queen replacement were also studied.

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## Methods

The study of foundress-associations consisted of 12 nest-removal experiments performed on 12 separate post-emergence colonies between October 1990 and October 1991. All nests were maintained in the vespiary (Sinha et al. 1993; Premnath et al. 1995) at the Indian Institute of Science, Bangalore (13°00'N, 77°32'E). Eight nests were naturally initiated in the vespiary while four were transplanted from outside. All adult wasps in these colonies were marked with unique colour codes using quick-drying paints on the day of their eclosion for identification.

Observations just prior to a natural queen replacement were performed on six nests. These were chance observations recorded during the course of other studies on natural colonies. Nine other nests were used opportunistically to record observations immediately after a natural queen replacement.

### Definitions

Queen: the sole egg-layer in an established colony

Founding queen: the individual who becomes the egg-layer in foundress associations

Potential queen: a wasp that challenges the existing queen with an apparent bid to take over as a replacement queen

Replacement queen: a wasp that replaces the existing queen on a nest to take over as the sole egg-layer

### Data collection

#### *Nest-removal experiments*

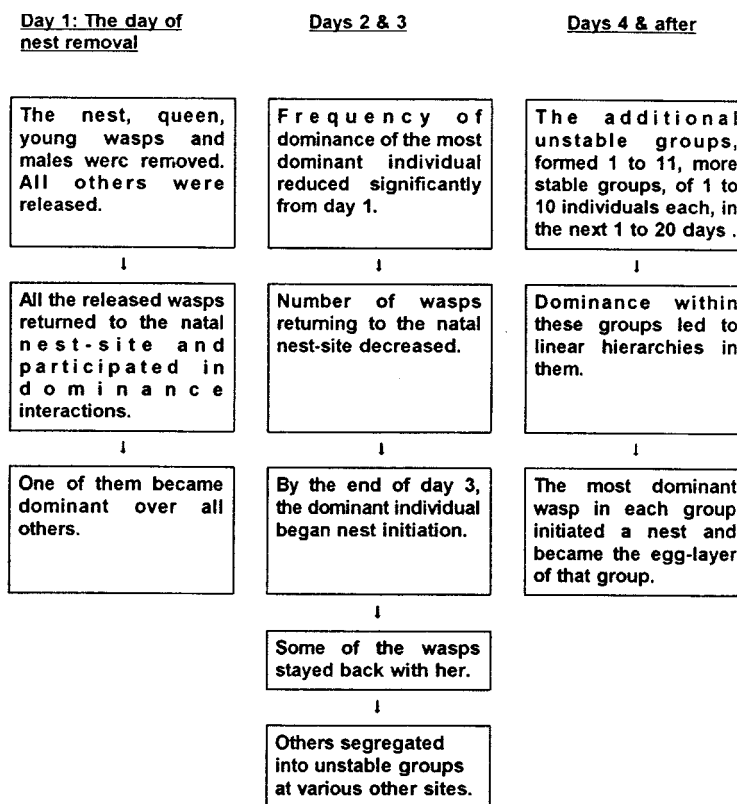
The first part of each experiment, referred to as the pre-removal phase, consisted of observations on the dominance behaviour of individuals in an undisturbed colony. This phase consisted of 20 h of observation on each nest, 10 h each day, on 2 consecutive days, between 0800 and 1800 hours. The sampling method consisted of recording all occurrences (Altmann 1974; Martin and Bateson 1986) of dominance-submission interactions in 51 randomly-chosen sessions of 5 min duration within the 10-h period (Gadagkar and Joshi 1983, 1984). On the morning of the 3rd day, the nest with the queen, black-eyed callow wasps and males were collected before 0600 hours and confined to a separate enclosure. The other adults in the colony were released near their natal nest site and were free to move anywhere within or outside the vespiary.

Post-removal observations commenced from the time the first-released individual returned to the original nesting site. Observations on this phase consisted of recording all occurrences of behavioural interactions, continuously for a minimum period of 5 h on the 1st day. Later, the wasps were opportunistically monitored until they initiated nests either singly or in groups. Founding queens in these newly initiated colonies were then identified by behavioural observations. All female wasps forming a group are referred to as foundresses, while all individuals within such a group other than the founding queens are termed co-foundresses.

#### *Long-term monitoring of the behaviour of founding queens from nest-initiation onwards*

Two additional experiments were performed for the purpose of long-term monitoring of the behaviour of the founding queens. These nests were initiated by the same method as described above

**Fig. 1** Description of the series of events following nest removal



(by removing their original nests). Observations were conducted on the day of nest removal for 5 h, then for an hour a day for 7 days after nest initiation, and later opportunistically once every 2–4 days up to 24 days after nest-removal.

#### *Observations on potential queens challenging queens*

Six instances where the queen was being challenged by a potential queen were encountered. Observations were performed opportunistically whenever a queen was challenged and were terminated when the conflict was resolved by the departure of one of the females.

#### *Natural queen replacements*

Nine instances of natural queen replacements were observed. Observations were performed opportunistically for at least 3 h after the queen of a colony was replaced by a replacement queen, and for 2 h each day during the next 10 days.

#### Data analysis

The frequencies of dominance-submission interactions, corrected for the time spent by the participants on the nest, were calculated from all-occurrence observation sessions during both pre- and post-removal phases of the nest-removal experiments and during the observations following queen replacements. Frequencies have been expressed in terms of the number of dominance interactions initiated per hour, corrected for the total number of potential recipients of such acts present on the nest (i. e. acts per animal per h). All statistical tests were non-parametric and were performed according to Sokal and Rohlf (1981).

## Results

### Nest-removal experiments

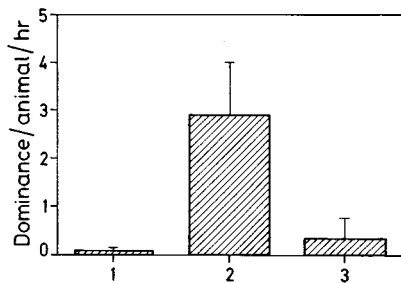
#### *Events following nest removal and the formation of new colonies*

Nest removal was always followed by the formation of foundress-associations, resulting in nest-initiation. In describing these events, days are counted from the day of nest removal which is referred to as day 1. On day 1 (Fig. 1), all wasps that were released from their natal nest returned to their original nest site on their own, and participated in dominance interactions. In all the experiments, one individual became completely dominant over all others, i.e. this wasp dominated all the other individuals from her natal nest at least once, but never received any dominance behaviour from them. On days 2 and 3, fewer of the subordinate wasps were seen to return to this site at any given time. The dominant individual invariably became the queen of the association formed at or very near the original nesting site.

The other subordinate wasps segregated into several groups of unstable composition, at different sites. From day 4 onwards, these individuals remained solitary, or formed stable groups of one to ten individuals at these additional locations. Dominance hierarchies were also established amongst the members of these additional groups and the most dominant individual in each of

**Table 1** Salient features of the original nests used and foundress associations obtained

| Expt. No. | No. of wasps on the natal nest | No. of wasps released | Total no. of wasps that formed groups | No. of nests initiated | Foundress group size (range) | Time taken for first egg laying (days) |
|-----------|--------------------------------|-----------------------|---------------------------------------|------------------------|------------------------------|--|
| 1         | 21                             | 20                    | 8                                     | 3                      | 1-4                          | 5-10                                   |
| 2         | 54                             | 53                    | 31                                    | 7                      | 2-10                         | 6-20                                   |
| 3         | 53                             | 50                    | 24                                    | 11                     | 1-5                          | 4-9                                    |
| 4         | 20                             | 18                    | 13                                    | 3                      | 3-7                          | 5-6                                    |
| 5         | 25                             | 23                    | 11                                    | 5                      | 2-3                          | 6-10                                   |
| 6         | 21                             | 17                    | 10                                    | 3                      | 3-5                          | 6-11                                   |
| 7         | 28                             | 23                    | 7                                     | 2                      | 1-6                          | 7                                      |
| 8         | 16                             | 13                    | 4                                     | 1                      | 4                            | 5                                      |
| 9         | 27                             | 19                    | 12                                    | 4                      | 1-6                          | 5-9                                    |
| 10        | 10                             | 9                     | 4                                     | 2                      | 2                            | 7-11                                   |
| 11        | 13                             | 10                    | 8                                     | 3                      | 2-3                          | 6-15                                   |
| 12        | 21                             | 20                    | 7                                     | 4                      | 1-3                          | 11-14                                  |



**Fig. 2** Frequency of dominance behaviour of the founding queen, the individual next in the hierarchy on the day groups were formed and of the founding queen on the natal nest. Dominance acts per animal per h of a founding queen on the day groups were formed (2) is significantly greater than that of the wasp next in the hierarchy on this day (3) and than that exhibited by the founding queen earlier on the natal nest prior to nest-removal (1) (Wilcoxon matched-pairs signed-ranks test,  $P < 0.001$  for 1 & 2 and 2 & 3)

these foundress associations initiated a nest and became the founding queen of her respective group.

Nests were initiated at the original and additional sites by the most dominant individual in each group within a period of 3–20 days after nest-removal. Although all the released wasps returned on day 1, only about half of them initiated nests or joined groups (mean  $\pm$  SD:  $51 \pm 0.16\%$ , range: 30–80%,  $n = 12$ , Table 1). (It is possible of course that the remaining half initiated nests at sites that were not discovered by us). Of those that returned and stayed on, 34.5% became egg-layers. A total of 48 nests were initiated from the 12 natal nests in this study; 11 of these were founded by solitary individuals, while 37 were by more than one foundress, with group sizes ranging from 2 to 10 (median = 3).

For the analyses that follow, all the foundress-associations (those that initiated nests at the original site as well as those initiated at other sites) have been considered together. This is because the frequency and the nature of dominance interactions and nest-initia-

tion activities at the original and at other sites were similar.

#### *Levels of dominance interactions on the day groups were formed*

Dominance interactions amongst foundresses on the day they first came together were very severe and always resulted in one individual becoming unambiguously dominant over all others. The hierarchy at this time was clearly despotic. The most dominant individual in these associations showed a frequency of  $2.7 \pm 1.1$  dominance acts per animal per h on this day as compared to  $0.1 \pm 0.07$  acts per animal per h shown by her on her natal nest before its removal. This is a highly significant, 30-fold increase in her frequency of dominance acts across these phases (Fig. 2; Wilcoxon's matched-pairs signed-ranks test,  $P < 0.001$ ). In fact, she contributed  $75.7 \pm 16.3\%$  of the total dominance interactions seen on this day. In contrast, the individual next in the hierarchy participated in only  $0.32 \pm 0.43$  acts per animal per h which contributed to only  $9.3 \pm 9.4\%$  of the total dominance in the group; both these values are significantly less than the corresponding values for the most dominant individual (Wilcoxon's matched-pairs signed-ranks test,  $P < 0.001$ ). It is interesting to note that, in contrast to a founding queen, the queen in the pre-removal nest initiated very low levels of dominance interactions ( $0.04 \pm 0.05$  acts per animal per h).

#### *The nature of dominance interactions on the day groups were formed*

Dominance behaviours have been classified into two broad groups depending on their intensity:

1. Chase, peck, nibble and attack are the four commonly-observed dominance interactions that involve

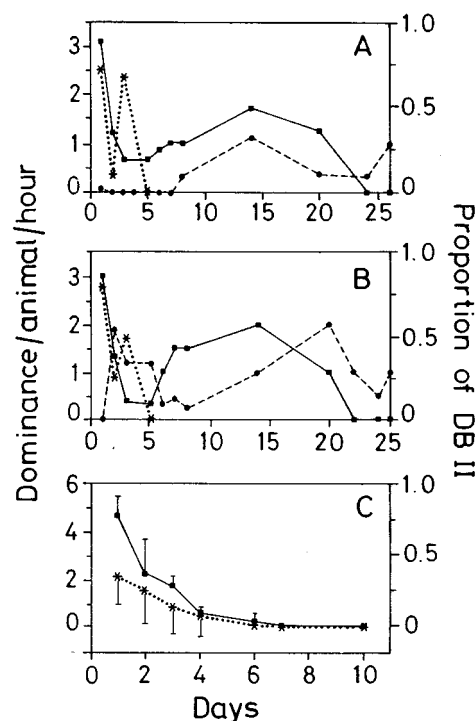
relatively simple actions over short durations of time (Gadagkar and Joshi 1983, 1984; Chandrashekara 1991). These, collectively termed as DB I behaviours, were seen both during the pre- and the post-removal phases of this experiment.

- Falling fight, aggressive biting, aggressive soliciting and sitting on are more intense interactions consisting of a sequence of actions that last relatively longer (even up to 5 min) and occasionally terminate with injury to one of the participants (Chandrashekara 1991). These are collectively referred to as DB II behaviours and were found to be restricted almost entirely to the post-removal phase of the experiment.

The nature of dominance behaviour exhibited by the wasps that returned to the original nest-site after its removal, especially the founding queens, was also different from that on the original colony. In the colony as a whole, the frequency of DB I changed from 0.1 acts per animal per h during the pre-removal phase to 2.65 acts per animal per h on the day the groups first came together. DB II showed an even more dramatic change from 0.008 acts per animal per h to 0.95 acts per animal per h during the corresponding period – a 112-fold increase! Thus, the ratio of the frequency of DB I to DB II decreased significantly from 12.5 during the pre-removal phase to 2.9 on the day a foundress group first associated. This suggests that the behaviours making up DB II may play a more important role when dominance hierarchies are being established, as compared to those behaviours constituting DB I. This is again supported by the fact that the queen in a pre-removal nest never demonstrated any of the DB II behaviours.

#### *Dominance interactions on the two days following group formation*

The frequency of dominance behaviour (DB I and DB II together) of the founding queens decreased significantly from  $2.7 \pm 1.1$  acts per animal per h on the day groups were formed to  $1.3 \pm 0.5$  acts per animal per h on the following day (a decrease of 55%) and to  $0.9 \pm 0.5$  acts per animal per h a day later (a further decrease of 31%) ( $n = 10$ , Wilcoxon's matched-pairs signed-ranks test for all pairwise comparisons,  $P < 0.01$ ). The behaviours classified as DB II continued to be important during this period also; their contribution to the total dominance on these 2 days ( $0.52 \pm 0.25$ ,  $n = 14$  and  $0.5 \pm 0.2$ ,  $n = 11$ ) was not significantly different from that on the 1st day that the groups were formed ( $0.3 \pm 0.19$ ,  $n = 14$ ). This shows that although there was a significant decrease in the levels of aggressive behaviour shown by these dominant individuals during the 2nd and 3rd day of group formation, the nature of these behaviours remained essentially similar across this period.



**Fig. 3** Change in levels of dominance and proportion of DB II behaviours at colony-founding in two nests **A**, **B** and **C** during queen replacement. **A**, **B** Dominance acts per animal per h of the queen (solid line) and that of the mean co-foundress (broken line) from the day that groups first formed till the day of hatching of the first egg. Proportion of DB II behaviours (dotted line) in the total dominance interactions of the queen during this period is represented along the secondary Y-axis. **C** Dominance acts per animal per h of the replacement queen (solid line) and the proportion of DB II (dotted line) from the day of take-over to 10 days after queen replacement. Means and 1 SD are shown for 9 nests for days 1–7 and for 6 nests on day 10

Towards the end of this period, the dominant wasp in every group began to initiate a nest and there was a reduction in the levels of dominance exhibited by these individuals. By then a linear dominance hierarchy among the foundresses was clear (data not shown) with the top-ranking individual in the hierarchy becoming the founding queen of that group.

#### *Change in dominance behaviour of foundresses over time*

In the two separate nests monitored from the time of initiation till the hatching of the first egg (see Methods), the queen was very aggressive and exhibited high levels of DB II behaviours on the day of formation of the foundress groups. Although her total level of dominance subsequently decreased, the proportion of DB II behaviours continued to remain high. However, DB II behaviours were never seen to be exhibited after 4 days (Fig. 3A,B).

The queen's frequency of dominance was higher than that of the mean value for her co-foundresses only until about the time of the hatching of the first egg (Fig. 3A,B), after which she rarely ever took part in dominance interactions. A temporary decline in her dominance level was noticed during the 3rd–5th day after group formation and coincided with a sharp increase in her nest construction activity.

In one of the nests (Fig. 3B), there was a higher level of dominance shown by the co-foundresses from the 2nd to the 5th day of nest-initiation, which possibly reflects a high level of reproductive competition in this group. This is supported by the fact that three of the four co-foundresses in this nest were seen to lay an egg each during this period, which however were soon eaten by the queen. These co-foundresses later remained as workers on the nest.

### Natural queen replacements

Dominance interactions, observed in nests soon after a natural queen replacement, or when a potential queen attempted to replace the queen, were very similar to interactions among foundress groups described earlier, both in their nature and levels of occurrence.

### Levels of dominance interactions.

There was an increase in the level of dominance exhibited by the potential queen or the replacement queen (as the case may be) when she attempted to establish herself as the sole reproductive in the colony. In every case, this individual dominated each one of her nest-mates and the level of aggression was such that it gave almost no opportunity for the others to interact amongst themselves. The rate of dominance shown by these individuals (potential queen:  $3.37 \pm 1.63$  acts per animal per h,  $n = 6$ ; replacement queen:  $4.67 \pm 0.81$  acts per animal per h,  $n = 9$ ) were not significantly different from each other (Mann-Whitney  $U$ -test,  $P > 0.05$ ) or from that shown by the founding queens ( $2.7 \pm 1.1$  acts per animal per h,  $P > 0.05$  for all pairwise comparisons).

### Nature of dominance behaviour

The frequencies of both DB I and DB II behaviours increased whenever an individual attempted to establish herself as a queen in a colony. The DB II behaviours were almost always initiated by the potential queens/replacement queens. Note that the queen in a normal nest never exhibits DB II unless she is challenged (S. Premnath, unpublished work). The frequency of DB II behaviours of the potential queens ( $1.11 \pm 0.6$  acts per animal per h), replacement queens ( $1.5 \pm 0.9$ ) and queens at colony founding ( $0.93 \pm 0.38$ )

were not significantly different from each other (Mann-Whitney  $U$ -test for all pairwise comparisons,  $P > 0.05$ ). The proportion of DB II in the total dominance shown was also not significantly different.

### Change in the level and nature of dominance of the replacement queen with time

The high frequency of dominance interactions ( $4.67 \pm 0.81$  acts per animal per h,  $n = 9$ ) with a high proportion of DB II behaviours ( $0.33 \pm 0.18$ ), observed on the day of queen replacement, gradually decreased with time and the DB II behaviours were hardly seen beyond 4 days of the event (Fig. 3C). The frequency of DB II behaviours seen within the first 4 days was 2.33 acts per animal per h. The frequency of dominance of the replacement queen decreased about 20-fold to a value of  $0.113 \pm 0.13$  acts per animal per h by 10 days ( $n = 6$ ) and to a value of  $0.03 \pm 0.07$  acts per animal per h ( $n = 3$ ) after 20 days. Thus, a comparison of the change in dominance behaviour of queens at nest initiation with that at queen replacements shows a near-identical pattern.

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## Discussion

The most striking finding of this study is that, in *Ropalidia marginata*, aggressive interactions at the time of establishment of reproductive dominance during colony-founding (and also during queen replacements in established colonies) can be very intense. These interactions lead to the formation of initially despotic and later, linear dominance hierarchies with the most dominant individual becoming the founding queen and subsequently, the sole egg-layer in every foundress-association.

Dominance interactions, leading to the establishment of a hierarchy among foundresses, have been widely documented in many *Polistes* species (*P. dominulus*: Pardi 1948; *P. fuscatus*, *P. canadensis*, *P. annularis* and *P. flavus*: West-Eberhard 1967, 1969, 1982a,b, 1986; *P. metricus*: Gamboa and Dropkin 1979; *P. annularis*: Strassmann 1981; *P. canadensis*: Ito 1985, 1993; see also Röseler 1991). Although the severity of such interactions in *Polistes* appear to be quite similar to those observed in *R. marginata* in this study, the time for which these last, during colony-founding, may be much less in *R. marginata* than in many species of *Polistes*. Dominance interactions amongst foundresses of a few species of *Ropalidia* and *Mischocyttarus* have been thought to be of a much milder nature (*R. fasciata*: Ito 1983, 1985; Kojima 1984; Turillazzi and Turillazzi, 1985; *R. variegata jacobsoni*: Yamane 1986; *M. drewseni*: Jeanne 1972; *M. angulatus* and *M. basimaculata*: Ito 1984). This could possibly be due to the fact that most of these studies were also conducted on nests during

later stages of colony initiation (Kojima 1984; Yamane 1986). Interactions at earlier stages in these species too may not, in fact, be very different from those of *R. marginata* foundresses as reported here. Hence, the belief that *Ropalidia* seems to be generally less violent than *Polistes* (see Röseler 1991) may simply reflect the fact that most studies on these genera have focused on different stages of colony-founding.

After colony-establishment, however, the level of dominance behaviour and other behavioural interactions exhibited by the founding queen dropped below that of an average co-foundress (who was by then working for the colony) at about the time of hatching of the first egg. Such low levels of aggression displayed by the queen towards the later part of the pre-emergence period are typical of queens in mature, post-emergence colonies (this study: pre-nest-removal phase observations; Chandrashekara and Gadagkar 1991; Premnath et al. 1995). A decrease in dominance interactions with time has also been reported for *Polistes* foundresses (reviewed in Röseler 1991). But the difference lies in the fact that in many species of *Polistes*, in spite of the reduction in levels of dominance of the queen, she continues to be more behaviourally dominant and active than workers in her colony (West-Eberhard 1969, 1982a,b, 1986; Strassmann 1981; Dew 1983; Reeve and Gamboa, 1983, 1987; Itô 1985, 1993; Hughes and Strassmann 1988; Reeve 1991; Röseler 1991).

The repertoire of dominance interactions used by the founding queens, replacement queens and potential queens during the early stages of colony initiation and queen replacements were also quite different from those of queens in normal established colonies. The type of aggressive interactions observed in the natal nests, for example, constituted only a subset of the kinds of dominance behaviours observed amongst the foundresses at the time of establishment of hierarchies. The more severe forms of dominance interactions – DB II behaviours – were exhibited in high frequencies by the founding queens during early stages of colony-founding, by potential queens while challenging their predecessor and replacement queens immediately after take over, but rarely ever in established colonies. With the onset of nest construction during colony-founding, these behaviours reduced significantly and only the milder DB I behaviours were exhibited. In fact, severe dominance behaviours were never seen after the first 3 days in the two newly-established nests monitored over 3 weeks, and after the first 4 days by a replacement queen following queen turnover. DB II behaviours may thus be of particular significance in establishing reproductive division of labour in these wasp societies.

In the two nests that were monitored till the hatching of the first egg, the dominance hierarchy established at the very beginning persisted for the entire observation period. It is particularly interesting to note that the first foragers in both these colonies were those which had the lowest ranks in the dominance hierar-

chies in their respective colonies. The development of such a hierarchy, in addition to its role in reflecting the reproductive status of foundresses, may also perhaps determine the patterns of social organization and division of labour in mature colonies. The nature of dominance interactions which maintain the now-established social dynamics, however, may be of an entirely different nature. DB I behaviours which were exhibited at all times in the colony, for example, may not only play a role in the establishment and/or maintenance of reproductive dominance, but may also function in regulating forager activity in established colonies (Premnath et al. 1995).

If the queen in an established colony is not behaviourally dominant, then how does she maintain her reproductive status? The gradual decrease in the behavioural dominance of the *R. marginata* queen may be associated with the onset of some other form of reproductive control which does not require overt physical interactions – perhaps through more subtle (chemical?) cues. Such a speculation is not entirely unreasonable. In the eusocial bee *Bombus*, the social dominance of a queen is first established through physical aggression towards workers; direct interactions then become increasingly rare due to a chemical signal from the queen (West-Eberhard 1977; Hölldobler 1984; Free 1987). Besides, *R. marginata* workers have been observed to lick the abdomens of their queens (Premnath et al. 1995) in a manner reminiscent of the behaviour of workers of *Vespa orientalis* and *V. crabro* (Ishay and Schwarz 1965; Ishay, 1981; Matsuura 1984) where chemical control of workers by the queens is known. The possible role of chemical cues in recognition of status has also been shown in *P. fuscatus* (Downing and Jeanne 1985; Keller and Nonacs 1993). Thus the mechanism by which an *R. marginata* queen establishes her exclusive egg-laying status when a new colony is formed appears to be quite different from the mechanism by which she continues to suppress egg-laying by her nestmates in mature colonies.

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