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A possible novel function of dominance behaviour in queen-less colonies of the primitively eusocial wasp *Ropalidia marginata*

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Abstract

Unlike the queens of other primitively eusocial species, *Ropalidia marginata* queens are strikingly docile and non-aggressive individuals, never at the top of the behavioural dominance hierarchy of their colonies. Nevertheless, these queens are completely successful at suppressing worker reproduction, suggesting that they do not use aggression but employ some other mechanism (e.g. pheromones) to do so. Upon removal of the queen from a colony, a single worker, the 'potential queen', immediately begins to display highly elevated levels of aggression towards her nest mates. This individual becomes the next docile queen if the original queen is not returned. We attempt to understand the function of the temporary and amplified dominance behaviour displayed by the potential queen. We find that the dominance behaviour shown by the potential queen is unrelated to the number of her nest mates, their dominance ranks or ovarian condition. This suggests that aggression may not be used to actively suppress other workers and counter threat. Instead we find evidence that dominance behaviour is required for the potential queen's rapid ovarian development, facilitating her speedy establishment as the sole reproductive individual in the colony.

Keywords: Aggression; Dominance behaviour; Evolution of eusociality; Primitively eusocial wasp; *Ropalidia marginata*

1. Introduction

In many species of social insects, especially primitively eusocial wasps and queen-less ponerine ants, physical aggression (often referred to as dominance behaviour) is the mechanism by which queens establish and maintain reproductive monopoly in their colonies and the mechanism by which dead or lost queens are replaced by one of their workers (Pardi, 1948; Gamboa et al., 1990; Röseler, 1991; Ito, 1993; Liebig et al., 1999; Monnin and Peeters, 1999; Kardile and Gadagkar, 2002). Some species, however, use aggression to regulate non-reproductive tasks such as foraging and nest building (Premnath et al., 1995; O'Donnell, 1998, 2001, 2003; Kardile and Gadagkar, 2003; Bruyndonckx et al., 2006). Differences in the function of dominance behaviour can therefore yield insights into social organisation.

Ropalidia marginata (Lep.) (Hymenoptera: Vespidae) is an old world, primitively eusocial, polistine wasp, widely distributed in peninsular India. New colonies may be founded either by a single female or by a small group of females. All multi-female colonies consist of a number of non-reproductive females (workers), and a single egg-layer (queen) who monopolises reproduction in the colony. Unlike the queen in other primitively eusocial species, the *R. marginata* queen is a strikingly docile and non-aggressive individual, never at the top of the behavioural dominance hierarchy of her colony (Gadagkar and Joshi, 1983; Chandrashekara and Gadagkar, 1991a). However, the queen's suppression of worker reproduction is complete (Gadagkar, 2001) and it has been suggested that she does not use aggression but employs some other mechanism (e.g. pheromones; Premnath et al., 1996) to regulate worker reproduction.

Most workers appear to retain the capacity to develop their ovaries and lay eggs although they never do so in the presence of the queen (Gadagkar, 2001). If the queen dies or is removed from the colony, one of the workers becomes the next queen (Chandrashekara and Gadagkar, 1992). Workers may be mated or unmated individuals, and when unmated workers replace

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a lost queen, mating may occur subsequent to queen replacement since colonies with replacement queens have been known to produce both male (haploid) and female (diploid) offspring (Chandrashekara and Gadagkar, 1991b). Soon after the removal of the queen from a colony, a single worker, the 'potential queen' (PQ), immediately begins to display highly elevated levels of aggression towards the other members of the colony. It is this individual who establishes herself as the new queen if the original queen is not returned (Chandrashekara and Gadagkar, 1992). It should be noted however that we cannot predict which worker of the colony will become the potential queen, before removing the queen. Potential queens appear to be 'unspecialised intermediates' (Chandrashekara and Gadagkar, 1992; Deshpande et al., 2006). We identify the potential queen only after removing the queen and retrospectively analyse data on this individual, collected prior to queen removal. Unlike the docile queen, a potential queen always occupies rank 1 in the colony's dominance hierarchy during the brief period before she in turn becomes a docile, established queen. On average, there is about an 18-fold increase in her level of dominance behaviour relative to herself in the presence of the queen, and a 269-fold increase relative to the queen when she was still present (Sumana and Gadagkar, 2003). The potential queen accounts for nearly 83% of the total dominance behaviour observed in the queen-less colony (Sumana and Gadagkar, 2003). The behavioural profile of the potential queen changes gradually to conform to that of the docile established queen in about a week, by which time she establishes herself as the sole egg-layer of her colony. There are thus striking and predictable changes in the behavioural profile of a single individual, first from a relatively docile worker to a highly aggressive potential queen, and again from a highly aggressive potential queen to a very docile queen. What is the function of this temporary and amplified dominance behaviour displayed by the potential queen?

We consider two potential hypotheses that may address this question. As we show below, these hypotheses yield mutually exclusive predictions.

Hypothesis 1. The potential queen uses amplified aggression to suppress the other workers in the colony while she establishes and consolidates her position as queen.

Predictions. If the PQ does indeed use aggression as a mechanism to suppress workers posing a threat to her, then the amount of aggression shown by the PQ is expected to correlate with factors that contribute to this threat. The three such factors we consider are (1) number of nest mates, (2) dominance status of the aggressed individuals and (3) ovarian condition of the aggressed individuals. We expect one or more of these three variables to be positively correlated with the amount of aggression displayed by the PQ if the first hypothesis is valid.

Hypothesis 2. The amplified aggressive behaviour shown by the PQ may be necessary for the rapid development of her ovaries.

Prediction. If aggressive behaviour is essential for the potential queen to rapidly develop her ovaries, we predict that a lone PQ, lacking the opportunity to be aggressive, should take significantly longer to lay her first egg in comparison with a PQ who can aggress nest mates.

2. Materials and methods

Forty-five post-emergence nests of *R. marginata*, collected from different localities in Bangalore, India (13°00′N and 77°32′E) were used in this study. Ovarian measurements and egg-laying data was not collected for all colonies on which behavioural observations were made, since this work was part of a larger study. Hence sample sizes differ between results.

2.1. Behavioural observations

Quantitative behavioural observations were made by three observers between December 2004 and November 2005. Several joint observation sessions were conducted prior to the start of experiments, where pairs of observers made independent, concomitant observations on the same nest. These data were compared and experiments commenced only once inter-observer differences were under 5%. Nests were observed in closed cages to ensure that animals could be monitored off the nest and to prevent confounding estimates of colony size due to the departure of animals from the nest.

The size of colonies used for behavioural observations, including the queen and PQ, ranged between 3 and 14. All animals were marked uniquely with spots of quick drying paint to enable individual identification. Colonies were provided with *ad libitum* food consisting of final instar *Corcyra cephalonica* larvae, honey, and water. Each colony was observed for 5 h per day, between 10:30 and 18:00 h, for 2 days. On day 1 the unmanipulated colony was observed and the queen was identified by her egg-laying behaviour, or occasionally by the characteristic way in which they are known to drag their abdomens on the nest. On day 2, the queen was removed from the colony approximately 10 min before the start of the first observation session. Sampling methods consisted of 16 scans and 34 all-occurrence sessions, each lasting 5 min (Gadagkar, 2001), randomly intermingled and spread across the 5 h of observations per day. Since this was part of a larger study, we recorded the behavioural state of every individual at the time she was scanned and every occurrence of every act of behaviours such as dominance behaviour, subordinate behaviour, bring food, feed larva, bring building material, build the nest, snatch and lose food or building material, etc.

The frequency per hour of total aggression displayed by the potential queen was computed from the all-occurrence sessions on day 2 for each colony. Aggression includes the acts of attacking, nibbling, pecking, chasing, holding in mouth, sitting over another wasp or engaging in falling fights with another wasp. For each wasp, the deviation from the amount of aggression she was expected to receive if the PQ directs aggression uniformly to all individuals, was calculated as, the difference between the frequency per hour per individual of dominance behaviour shown by the potential queen and the actual frequency per hour of dominance behaviour received by that individual. To make this comparable across nests, we divided it by the total frequency per hour of dominance behaviour shown by the potential queen. An index of dominance, computed from data from day 1 was used to construct a dominance hierarchy (Premnath et al., 1990; Gadagkar, 2001). This hierarchy represents the relative dominance status of each individual based on levels of aggression in the un-manipulated colony (day 1). Since analyses were conducted with data pooled across colonies, normalised ranks (rank, divided by number of animals in the colony) were used for statistical analyses.

2.2. Data on egg laying

The time taken by the PQ to lay her first egg after queen removal was determined in two types of colonies: (i) those that had more than two adults so that the PQ was accompanied by one or more nest mates even after queen removal and (ii) those with only two adult wasps, such that once the queen was removed there remained a lone PQ with no nest mates. A nest map, recording the content of each cell was maintained from the day before the removal of the queen until the PQ laid her first egg. The PQ was considered to have laid an egg if a new egg was observed in, one of the empty cells, a newly constructed cell, a cell previously containing a larva or pupa or, occasionally, when an egg was observed in a different position in a cell previously containing an egg. This excludes the unlikely event where a PQ replaces an egg of the previous queen with her own egg, in exactly the same position. However, *R. marginata* PQ's rarely cannibalise the brood of the previous queen (unpublished observation by the authors) so that the probability of an egg replacement event is low. Besides, 17 of the 20 nests that we studied contained an empty cell on day 2 so that the PQ could lay an egg without cannibalising an egg of the previous queen. Hence we believe that our estimation of the time taken to lay eggs is reasonably accurate.

2.3. Dissections

All adult wasps (except the lone PQ's) were collected and preserved at −20 °C, on the day of the first recorded egg-laying event by the PQ. Later they were dissected to measure their ovaries. For each wasp, seven ovarian parameters were measured/computed, namely, length and width of the largest proximal oocyte, average length and average width of all six proximal oocytes, total number of oocytes, total number of mature oocytes and total number of oocytes with yolk. These data were pooled across colonies and subjected to a principal components analysis, and the value of the first principal component for each wasp was designated as her ovarian index (see Chandrashekara and Gadagkar, 1991a for details). Within each colony all individuals were ranked, such that the individual with the highest ovarian index was assigned rank 1. To facilitate comparison across colonies, the ranks were normalised (rank, divided by number of animals in the colony). Both absolute ovarian indices as well as normalised ovarian ranks were tested as potential predictors of the amount of aggression individuals received from their respective PQ's. These data were also used to confirm that the individual identified as the PQ by her behaviour, was indeed that with the best developed ovaries.

To obtain a measure of ovarian development of PQ's on the day of queen removal, PQ's from 14 other nests with 2–57 individuals in the queen-right phase were dissected on the day of queen removal. For these individuals, the absolute values of the ovarian index (and not the ranks) were used to compare lone PQ's and PQ's with nest mates.

3. Results

3.1. Is the amount of aggression shown by a PQ a function of the number of her nest mates?

All PQ's showed elevated levels of aggression upon removal of their queens (mean ± S.D. for 24 PQ's = 30.21 ± 17 acts of aggression per hour), which was 25.7 ± 25.8-fold higher compared to their rates before they became PQ's, i.e., when the queen was present (mean ± S.D. for 24 PQ's = 2.86 ± 4.13 acts of aggression per hour). It should be noted that during the period that the PQ's showed these high levels of aggression they themselves did not receive a single act of aggression from their nest mates. However, the total amount of aggression displayed by the PQ's in the absence of their queens did not scale with the number of nest mates present on the nest. Slope of the linear regression is not significantly different from zero ($p = 0.17$; $r^2 = 0.085$, $N = 24$; Fig. 1).

3.2. Is the amount of aggression received by an individual a function of her dominance rank?

The amount of aggression received by wasps (computed as the deviation from expected aggression, see Section 2) was not found to be a function of the normalised dominance rank of the aggressed individual. Note that dominance ranks were calculated using data collected in the presence of the queen. Slope of the linear regression is not significantly different from zero ($p = 0.82$; $r^2 = 0$, $N = 135$; Fig. 2).

3.3. Is the amount of aggression received by an individual a function of her ovarian development?

The amount of aggression received by wasps (computed as the deviation from expected aggression, see Section 2) was not found to be a function of either their absolute ovarian indices

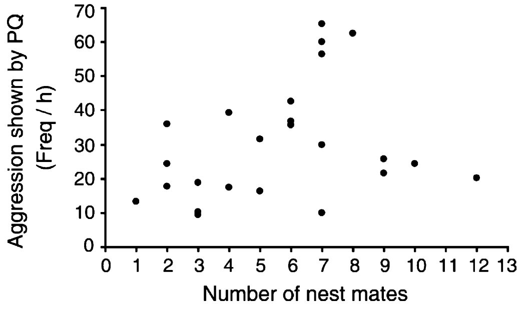

Fig. 1. Aggression (frequency per hour) shown by PQ, plotted against the number of her nest mates. Slope of the linear regression is not significantly different from zero ($p = 0.17$; $r^2 = 0.085$, $N = 24$).

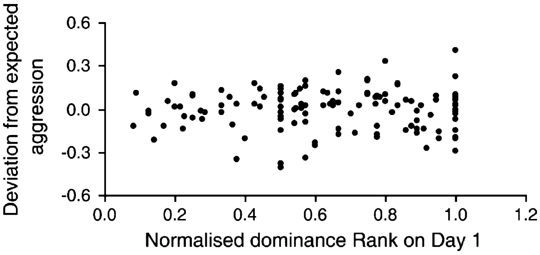

Fig. 2. Deviation from expected aggression (see Section 2) for each wasp plotted against her normalised dominance rank on day 1. Note that a numerically lower rank corresponds to higher dominance status. Slope of the linear regression is not significantly different from zero ($p = 0.82$; $r^2 = 0$, $N = 135$).

(Fig. 3a) or their normalised ovarian ranks (Fig. 3b). Slopes of the linear regressions are not significantly different from zero (ovarian index: $p = 0.62$; $r^2 = 0.007$, $N = 36$; ovarian rank: $p = 0.75$; $r^2 = 0.003$, $N = 36$; Fig. 3a and b).

3.4. *Time taken by PQ's to initiate egg laying*

Lone PQ's (those without any nest mates) took significantly longer to lay their first eggs compared to PQ's with nest mates (Mann–Whitney U = 73, $p = 0.03$; Fig. 4a). A logistic regression treating the presence/absence of nest mates as a binary dependent variable and time taken to initiate egg laying as the independent variable, confirmed this result ($\beta = -3.88$, $p < 0.05$; $\chi^2 = 5.99$, $p < 0.05$).

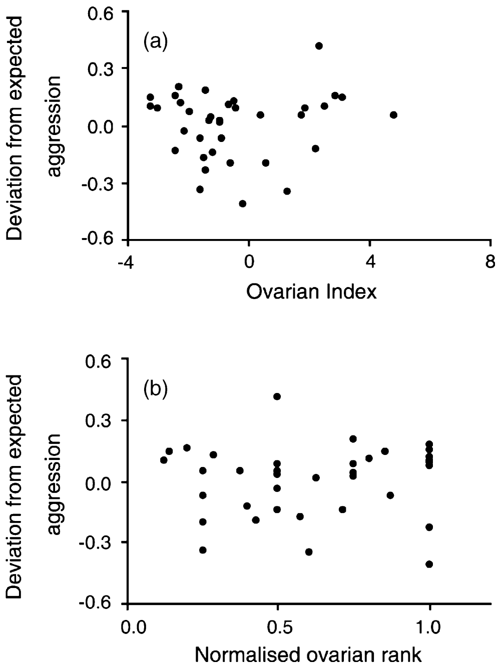

Fig. 3. Deviation from expected aggression (see Section 2) for each wasp plotted against her (a) absolute ovarian index and (b) normalised ovarian rank (where a numerically lower rank corresponds to better developed ovaries). Slopes of the linear regressions are not significantly different from zero (ovarian index: $p = 0.62$; $r^2 = 0.007$, $N = 36$; ovarian rank: $p = 0.75$; $r^2 = 0.003$, $N = 36$).

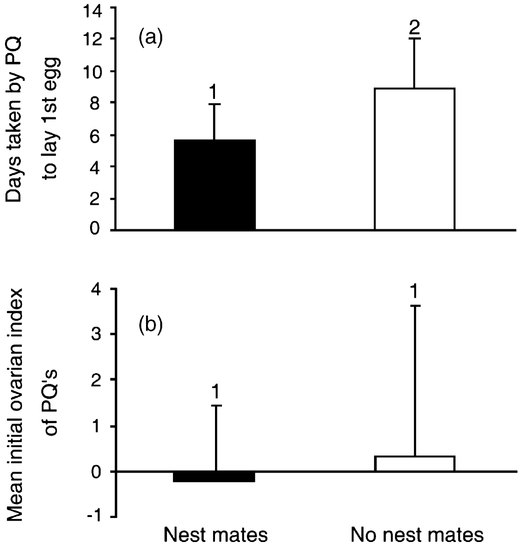

Fig. 4. Means and standard deviations of (a) the time taken to lay their first eggs, by PQ's with nest mates (filled bar: $M = 5.62$, S.D. = 2.29, $N = 13$), and those without nest mates (unfilled bar: $M = 8.85$, S.D. = 3.18, $N = 7$) and (b) ovarian indices of PQ's with nest mates (filled bar: $M = -0.23$, S.D. = 1.69, $N = 8$), and without nest mates (unfilled bar: $M = 0.31$, S.D. = 3.31, $N = 6$), on the day of queen removal. Bars with different numbers are significantly different from each other (a: Mann–Whitney $U = 73$, $p = 0.03$; b: Mann–Whitney $U = 27$, $p = 0.76$). Logistic regression analyses treating the presence/absence of nest mates as a binary dependent variable and the time taken to initiate egg laying ($\beta = -3.88$, $p < 0.05$; $\chi^2 = 5.99$, $p < 0.05$) or ovarian index on the day of queen removal ($\beta = -0.100$, $p > 0.05$; $\chi^2 = 0.186$, $p > 0.05$) as the independent variables, confirmed the above results.

3.5. *Ovarian development of PQ's on the day of queen removal*

On testing for a possible difference in the degree of ovarian development between PQ's with and without nest mates, on the day of queen removal, we found that the ovarian indices of lone PQ's were no different from those of PQ's with nest mates (Mann–Whitney $U = 27$, $p = 0.76$; Fig. 4b). A logistic regression treating the presence/absence of nest mates as a binary dependent variable and the ovarian index of the PQ as the independent variable, confirmed this result ($\beta = -0.100$, $p > 0.05$; $\chi^2 = 0.186$, $p > 0.05$). Thus both types of PQ's started with similar ovaries and yet the lone PQ's took longer to initiate egg laying.

4. Discussion

Our primary aim was to distinguish between two probable functions of the temporarily amplified dominance behaviour exhibited by the potential queen. Previous work has suggested that physical aggression (dominance behaviour) may be used by potential reproductives to establish themselves as the sole reproductive individuals of their colonies, both in the context of queen replacement as well as nest founding (Premnath et al., 1996). In this study we attempted to identify the possible mechanisms by which dominance behaviour might serve this function.

Our first hypothesis was that the potential queen uses amplified aggression to suppress the other workers in the colony while she establishes and strengthens her position as queen. However, the total amount of aggression displayed by the potential queen did not increase with the number of her nest mates and the amount of aggression received by an individual was not a function of either her dominance rank or her ovarian condition. Thus our results do not uphold any of the three predictions of this hypothesis.

Our second hypothesis was that the amplified aggressive behaviour of the potential queen may be necessary for the rapid development of her ovaries. As predicted by this hypothesis, we find that lone potential queens lacking the opportunity to show aggression take significantly longer to lay their first eggs, compared to potential queens with nest mates. It may be argued that the lone potential queens in our experiments may have been at a physiological disadvantage to start with, having borne the brunt of the previous queen's suppressive cues, whatever they may be, as opposed to potential queens with nest mates who may have received only a fraction of the queen's cues. However, this cannot be an alternative explanation for our result since we show that potential queens with and without nest mates did not differ in ovarian development on the day of queen removal.

Although our results show that a lone PQ who lacks the opportunity to show aggression, takes longer to lay her first egg compared to PQ's who do show aggression, at this stage we cannot rule out the possibility that some other component of the social environment is responsible for this effect. For instance, Gadagkar et al. (1991) have suggested that "cooperative thermoregulation" or the sharing of metabolic heat may influence the initiation of egg laying. However, it seems unlikely that PQ's with nest mates in our experiments had the advantage of cooperative thermoregulation because their extreme aggression quickly drove other animals off the nest and prevented them from staying on the nest for extended periods of time. Hence lack of opportunities for cooperative thermoregulation may not be an adequate explanation for the longer time taken by the lone PQ to lay her first egg. Another potential reason for the delayed egg laying by the lone PQ may be inadequate access to food. Although the absence of nest mates could entail lower food supplies for a lone PQ under natural conditions, all our experiments were conducted in closed cages with *ad libitum* supply of food. Thus lack of nutrition/energy may be an inadequate explanation for the longer time taken by lone PQ's to lay their first egg in our experiments.

Thus, since the aggression of the potential queen is unrelated to the number of her nest mates, their dominance ranks or ovarian condition, we suggest that dominance behaviour may not be used to actively suppress other workers and counter threat. Instead we propose and support the novel hypothesis that the ability to show aggression may be required for the PQ's rapid ovarian development, facilitating her speedy establishment as the sole reproductive individual in the colony. Although at this stage we cannot entirely rule out other components of the social environment as possible explanatory variables for the rapid ovarian development observed amongst the PQ's with nest mates in our study, the results from this study suggest new experiments in hitherto unexpected directions. More detailed behavioural and physiological measurements are in progress in order to further clarify the relationship between the PQs' amplified dominance behaviour and their ovarian development proposed here. At the present time we do not know the physiological processes that might link the act of showing aggression with ovarian development but it seems reasonable to imagine that hormonal changes that result from the expression of aggressive behaviour might trigger ovarian development in the aggressor. This is an attractive hypothesis because, given that queens in most primitively eusocial species use aggression to suppress worker reproduction, it is also expected that hormonal changes in the recipients of aggression should lead to converse physiological changes that suppress ovarian development. Juvenile hormone is a promising candidate for mediating such opposing physiological changes in aggressors and their victims since it is known that dominant females in some primitively eusocial species exhibit higher titres of juvenile hormone, accompanied by greater ovarian development than their subordinate counterparts (Barth et al., 1975; Röseler, 1991). Our results and the hypothesis proposed here suggest new avenues for investigating the interaction between aggression and juvenile hormone.

The hypothesis that we propose and support here for the function of elevated levels of aggression shown by the potential queens also has an interesting implication for the evolution of sociality. During nest initiation, the co-foundress who becomes the sole egg-layer in multiply founded nests shows levels of amplified aggression comparable to that of a PQ, until the time of hatching of the first egg (Premnath et al., 1996). Hence a foundress with the opportunity to show aggression may be able to develop her ovaries faster than solitary foundresses. Thus we have here yet another factor that may promote the evolution of sociality.

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