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Short communication

Dominance behaviour and regulation of foraging in the primitively eusocial wasp *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae)

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Abstract

Ropalidia marginata is a primitively eusocial, polistine wasp widely distributed in peninsular India. In spite of its primitively eusocial status, queens of *R. marginata* are surprisingly docile and behaviourally non-dominant (except during the first week or so of their careers as queens). Yet they successfully maintain reproductive monopoly throughout their careers, probably through the use of pheromones. Workers exhibit dominance–subordinate interactions but these behaviours are not involved in regulating reproductive competition among the workers because workers with high dominance ranks are not necessarily the ones who replace lost queens. We have speculated and provided correlational evidence before that dominance-subordinate interactions among the workers have been co-opted in this species for the workers to regulate each other's foraging. Here, we provide experimental evidence in support of the speculation, by reducing demand for food and showing that this results in a significant decrease in the frequency of dominance-subordinate interactions among the workers.

Keywords: Dominance behaviour; Primitively eusocial wasp; Regulation of foraging; *Ropalidia marginata*

1. Introduction

Queens of primitively eusocial wasps are known to be the most active and behaviourally dominant individuals of their colonies and to use dominance behaviour to suppress worker reproduction and thereby monopolise egg laying (Gamboa and Dropkin, 1979; Itô, 1985; Jeanne, 1972; Pardi, 1948; Reeve, 1991; Röseler, 1991; Strassmann, 1981; West-Eberhard, 1969, 1986; West, 1967; Wilson, 1971). Workers also indulge in dominance-subordinate interactions among themselves so that members of a colony can be ranked in a dominance hierarchy. Workers can usually replace lost queens and their relative positions in the colony's dominance hierarchy generally predicts the sequence in which they can do so (Jeanne, 1972; Kardile and Gadagkar, 2003; Klahn, 1981; Miyano, 1986; Morimoto, 1961a,b; Pardi, 1948; Reeve, 1991; Reeve and Gamboa, 1987; Spradbery, 1991; Strassmann and Meyer, 1983; West-Eberhard, 1969; Yoshikawa, 1956). *Ropalidia marginata* is classified as a primitively eusocial wasp due to the absence of morphological differentiation between queens and workers (Gadagkar, 2001). However, queens of *R. marginata* are unlike what is expected in a primitively eusocial species. They are never at the top of their colony's dominance hierarchy and an analysis of their behavioural profiles has led to their being classified as docile sitters (Chandrashekara and Gadagkar, 1991; Gadagkar, 2001; Gadagkar and Joshi, 1983; Kardile and Gadagkar, 2002). Nevertheless, queens of *R. marginata* are entirely successful in maintaining reproductive monopoly in their colonies. Although it is not clear how they do so, the use of pheromones appears a likely possibility (Gadagkar, 2001; Sumana and Gadagkar, 2003).

Even though the queens of *R. marginata* show hardly any dominance behaviour, the workers exhibit dominance-subordinate interactions among themselves so that a clear dominance hierarchy can be recognised (Gadagkar, 1980; Gadagkar, 2001; Premnath et al., 1990; Sumana and Gadagkar, 2001). Such dominance behaviour among the workers does not appear to mediate reproductive competition because there is no correlation between the dominance rank of an individual and

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probability that she will replace a lost queen (Chandrashekara and Gadagkar, 1992; Gadagkar, 2001; Kardile et al., unpublished). Another unusual feature of *R. marginata* is that the queens are not involved in regulating worker activities such as foraging and feeding the larvae; these behaviours continue unaffected even when the queen is removed. Thus the workers appear to regulate their own foraging and larval feeding behaviour in a decentralised, self-organised manner. We have therefore postulated that dominance-subordinate interactions among the workers, which do not seem to have a role in reproductive competition, may have been co-opted to help workers to self-regulate each other's foraging (Premnath et al., 1995). In other words, we view dominance-subordinate interactions exhibited by workers as a system of signals informing the extranidal workers of the hunger levels of the colony's adult and larvae (Gadagkar, 2001; Premnath et al., 1995). This speculation is supported by the facts that dominance received by foragers is: (i) significantly greater than that received by non-foragers; (ii) the frequency of dominance received by a forager is positively correlated with her foraging rate; (iii) that the fraction of total dominance received by a forager is positively correlated with her fractional contribution to the colony's foraging efforts (Premnath et al., 1995). A similar argument that dominance/biting interactions regulate worker foraging has more recently been made for other polistine wasps (O'Donnell, 1998a,b, 2001, 2003).

If the function of dominance-subordinate behaviour shown by the workers in *R. marginata* is indeed to regulate foraging by the workers, one may predict that when there is reduced demand for food in the colony, rates of dominance behaviour should also be reduced. Here, we test this prediction by reducing demand for food by hand-feeding the wasps.

2. Methods

This study was carried out from June 2001 to January 2003 on 11 postemergence colonies of *R. marginata* in Bangalore, India (13°00 N, 77°32′). All the wasps were marked individually with coloured spots of quick drying, non-toxic paints. Each experiment used a different colony and lasted 3 days. On day 1, the colonies were observed in their natural condition. On day 2, in addition to the food the wasps brought back to the nest on their own, they were offered two final instar *Corcyra cephalonica* larvae for every 10 *R. marginata* larvae present in their colony. This was repeated every hour from 8 to 18 h. The adult wasps took the offered food readily, shared it among themselves and also fed it to the larvae. No behavioural observations were made on this day. On day 3, behavioural observations were performed, similar to day 1, without offering any food. Behavioural observations consisted of recording every occurrence of bring food, feed larva, and dominance-subordinate behaviour by all individuals on the colony in 30–50 five-minute blocks with 1 min breaks. Dominance-subordinate behaviours consist of individuals attacking, chasing, pecking, nibbling, holding in mouth and sitting on each other. For a full definition of dominance-subordinate behaviours, see (Gadagkar, 2001). These observations were made for 5–6 h between 8 and 18 h on days 1 and 3. For each colony and for each behaviour, the total number of acts observed in all the 5 min blocks was divided by the duration of observation for that colony to yield the frequency per hour for that behaviour for that colony. Thus we obtained frequencies per hour of bring food, feed larva, and dominance behaviour for each of the 11 colonies, separately for days 1 and 3. We then computed means and standard deviations across the 11 colonies, and compared these values for days 1 and 3, for each behaviour. From our records of the forging behaviour of marked individuals, we also computed separately for days 1 and 3, the proportion of individuals that participated in foraging and compared these proportions between days 1 and 3. Similarly, the total number of acts of any behaviour performed by an individual was divided by the duration of observation for that individual to yield the frequency per hour of that behaviour for that individual. Thus we obtained frequencies per hour of foraging and dominance received for each of the 49 foragers from the 11 colonies. We then computed means and standard deviations across the 49 individuals and compared these values for days 1 and 3, for each of the two behaviours. All statistical analyses were performed using STATISTICA'99 edition.

3. Results and discussion

Our results are based on comparing the behaviour of the wasps on day 1 of the experiment (without any manipulation) and that on day 3 of the experiment (one day after excess feeding). To confirm that such a comparison is valid, we first show that the number of adult wasps present on days 1 and 3 are not significantly different from each other (Table 1). Next, we show that the excess feeding on day 2 was indeed effective. The frequency per hour with which food was brought to the nest, the frequency per hour at which larvae were fed as well as the proportion of wasps which foraged, all decreased significantly on day 3, as compared to day 1 (Fig. 1A–C). Under these circumstances, the hypothesis that dominance-subordinate interactions serve as a signal to foragers to bring more food (Gadagkar, 2001; Premnath et al., 1995), predicts that there should have been a significant decrease in the frequency per hour of dominance behaviour on day 3 as

Table 1
Number of wasps present on the nests on day 1 (un-manipulated nest) and day 3 (one day after excess feeding) are not significantly different from each other (2 tailed paired-sample *t*-test; $t = -0.69$, $p = 0.51$)

Nest	Number of wasps	
	Day 1	Day 3
V281	19	19
V295	16	16
V299	44	44
V382	7	8
V382A	5	4
V386	11	13
V426	9	9
V428	12	13
V429	9	9
V433	15	14
V435	24	24
Average	15.5	15.7

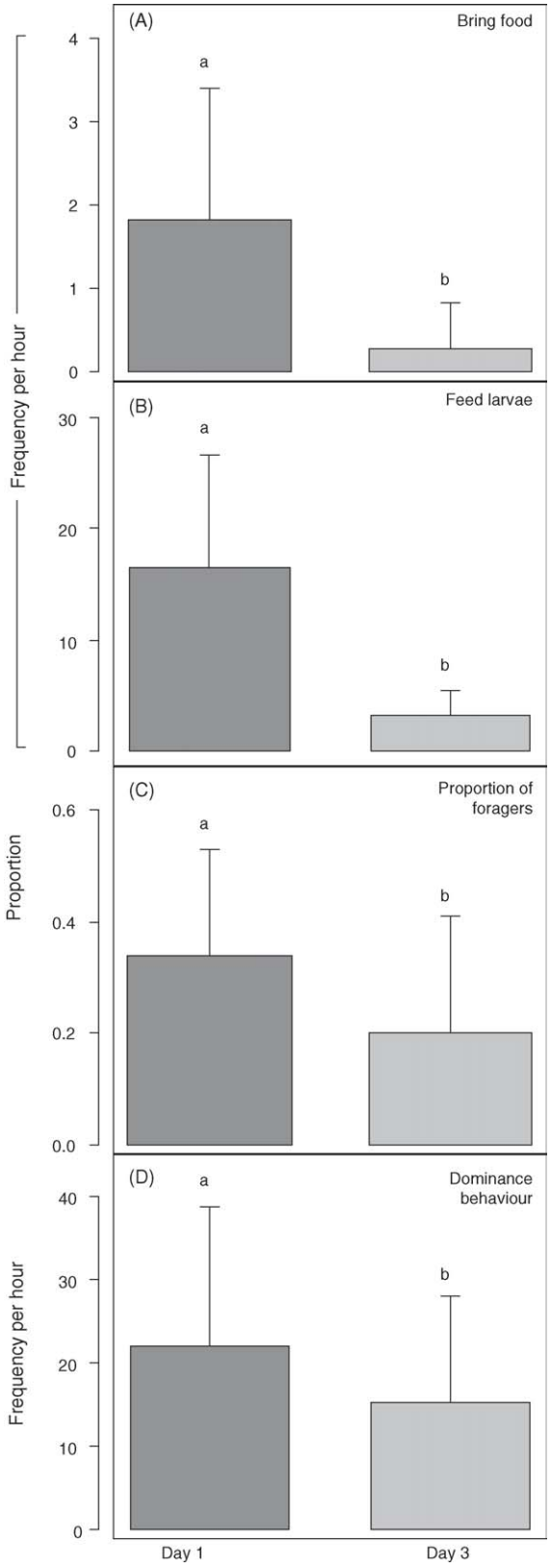

Fig. 1. Comparison of: (A) bring food; (B) feed larvae; (C) proportion of foragers; (D) dominance behaviour on day 1 (un-manipulated nests) and day 3 (one day after excess feeding). Bars shown are the means and S.D.'s across 11 nests. For all variables, values on day 1 are significantly greater than the corresponding values on day 3 (two-tailed Wilcoxon matched-pairs, signed-ranked tests; $p < 0.05$).

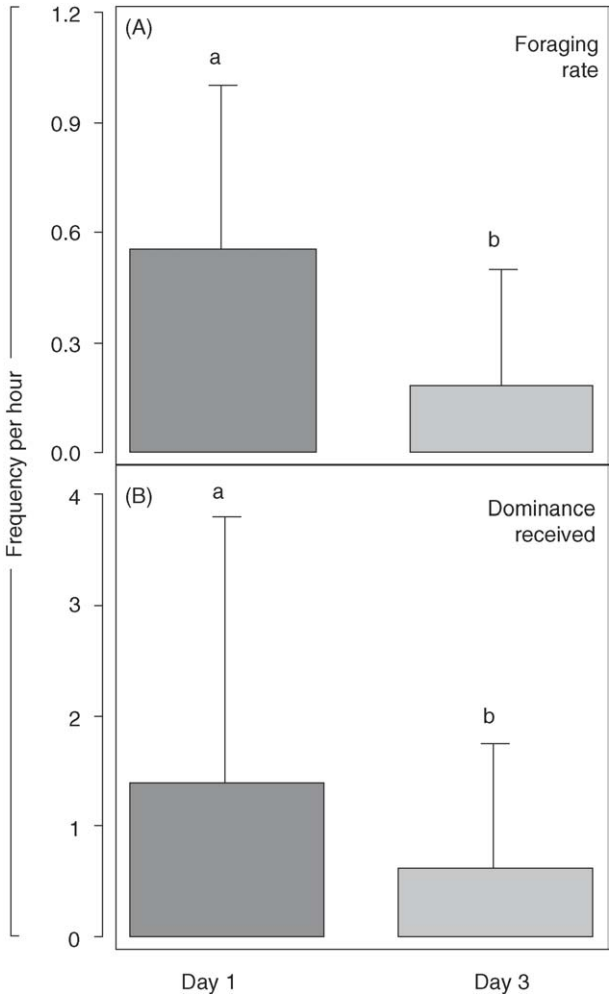

Fig. 2. Comparison of: (A) foraging rate; (B) dominance received by the 49 active foragers on day 1 (un-manipulated nests) and day 3 (one day after excess feeding). Bars shown are the means and S.D.'s for the 49 foragers. Both variables on day 1 are significantly greater than the corresponding variables on day 3 (two-tailed Wilcoxon matched-pairs, signed-ranked tests; $p < 0.05$).

compared to day 1. This was indeed the case (Fig. 1D). Of the 161 individuals present in the eleven nests on day 1 and day 49 were foragers, i.e. they made at least one foraging trip. Considering only these 49 individuals also revealed the same pattern. There was a significant decrease from day 1 to day 3, both in the frequency per hour of foraging as well as in the frequency per hour of dominance received (Fig. 2A and B). These results lend support to our speculation that dominance-subordinate interactions, which no longer serve to express reproductive competition in *R. marginata*, have been co-opted to help workers to self-regulate the colony's foraging efforts.

It is true however that the exact magnitudes of the change in foraging rate and change in dominance received varied considerably and were not significantly correlated with each other. Our hypothesis that dominance-subordinate interactions may have been co-opted to regulate foraging does not automatically predict that the exact magnitudes of dominance received and extent of foraging should be correlated. It may well be that different individuals require different amounts of coercion to forage. Even

more interesting is the possibility that dominance received by one individual influences the probability of foraging by other individuals, which if true, will not necessarily yield a one-to-one correlation between the magnitudes of dominance received and foraging.

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