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SHORT COMMUNICATION

Signaling hunger through aggression—the regulation of foraging in a primitively eusocial wasp

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Abstract Primitively eusocial wasps are generally headed by behaviorally dominant queens who use their aggression to suppress worker reproduction. In contrast, queens in the primitively eusocial wasp *Ropalidia marginata* are strikingly docile and non-aggressive. However, workers exhibit dominance–subordinate interactions among themselves. These interactions do not appear to reflect reproductive competition because there is no correlation between the relative position of an individual in the dominance hierarchy of the colony and the likelihood that she will succeed a lost/removed queen. Based on the observation that foraging continues unaltered in the absence of the queen and the correlation between dominance behavior and foraging, we have previously suggested that dominance-subordinate interactions among workers in *R. marginata* have been co-opted to serve the function of decentralized, self-organized regulation of foraging. This idea has been supported by an earlier experimental study where it was found that a reduced demand for food led to a significant decrease in dominance behavior. In this study, we perform the converse experiment, demonstrate that dominance behavior increases under conditions of starvation, and thus provide further evidence in support of the hypothesis that intranidal workers signal hunger through aggression.

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Introduction

In many primitively eusocial species of insects, queens use physical aggression (usually referred to as dominance behavior) to establish and maintain reproductive monopoly in their colonies (Pardi 1948; West-Eberhard 1969; Jeanne 1972; Gamboa et al. 1990; Reeve 1991; Röseler 1991; Kardile and Gadagkar 2002). Although classified as a primitively eusocial species by virtue of the absence of morphological caste differentiation, *Ropalidia marginata* (Lep.; Hymenoptera: Vespidae) appears to be an exception (Gadagkar 2001). Unlike queens of other primitively eusocial species, the *R. marginata* queen is a strikingly docile and non-aggressive individual, never at the top of the behavioral dominance hierarchy of her colony (Gadagkar and Joshi 1983; Chandrashekara and Gadagkar 1991). Despite the queen's docile nature, workers exhibit dominance–subordinate interactions among themselves (Gadagkar 1980; Chandrashekara and Gadagkar 1991; Gadagkar 2001). These interactions do not appear to reflect reproductive competition, as colonies of *R. marginata* have never been seen to have multiple egg layers (Gadagkar 2001), and there is no correlation between the relative position of an individual in the dominance hierarchy of the colony and the likelihood that she will succeed a lost/removed queen (Chandrashekara and Gadagkar 1992; Deshpande et al. 2006; Gadagkar 2001).

We have previously suggested that dominance–subordinate interactions among workers in *R. marginata* have been co-opted to serve the function of decentralized, self-organized regulation of foraging. This suggestion was prompted by the observations that (1) foraging and feeding activities continue unaffected upon removal of the queen, and (2) returning foragers are often the recipients of dominance behavior from intranidal workers. Intranidal workers who unload the foragers and show dominance behavior to them are also the ones who feed larvae and thus have information about colony hunger levels. It therefore seems reasonable to interpret their dominance behavior as a signal to the foragers to continue to bring food (Premnath et al. 1995).

In support of this idea, Premnath et al. (1995) found that (1) the amount of aggression received by foragers was significantly greater than that received by non-foragers, (2) the rates at which workers foraged was positively correlated with the levels of aggression they received, and (3) a forager's fractional contribution to the colonies foraging efforts was positively correlated with the fraction of the colony's total dominance behavior received by her. Studies of the swarm founding polistine wasps *Polybia occidentalis* and *P. aequatorialis* have also provided similar evidence in support of the idea that dominance behavior may be involved in regulating worker foraging (O'Donnell 2001, 2003). However, such correlational evidence does not imply any cause–effect relationship between dominance behavior received and foraging efforts. Cause–effect relationships can be clarified by experimentally manipulating either rates of dominance behavior or rates of foraging. Dominance behavior is not easy to manipulate, but rates of foraging can be more easily manipulated by increasing or decreasing the demand for food.

If the hypothesis that dominance behavior is used to signal hunger levels and stimulate foraging is valid, a decreased demand for food should result in a decrease in dominance behavior. In support of this prediction, Bruyndonckx et al. (2006) reduced demand for food by hand feeding the wasps (in addition to the food they themselves brought to the nest) and reported a significant decrease in dominance behavior. Conversely an increased demand for food should result in an increase in dominance behavior. In this study, we provide evidence in support of this prediction by observing colonies of *R. marginata* on three consecutive days such that, on day 1, they were not manipulated; on day 2, they were starved by preventing foraging, and on day 3, they were once again permitted to forage freely. In such an experiment, we predict that (1) dominance behavior on day 2 should be significantly greater than that on day 1 and (2) dominance behavior on day 3 should return to levels comparable to those on day 1, provided foraging rates on day 3 have also returned to the levels on day 1.

Materials and methods

Eight post-emergence colonies of *R. marginata* were studied between March and May 2006 in the vespiary (Gadagkar 2001) at the Indian Institute of Science, Bangalore (13°00 N, 77°32′ E). Colonies were transplanted to and maintained in open cages (Gadagkar 2001), which allowed the wasps to freely forage outside the vespiary until the experiment was begun.

All individuals on each nest were marked uniquely with spots of quick-drying, non-toxic paint to enable individual identification. Each colony was studied for 2 consecutive days. On each day, quantitative behavioral observations were made for 10 h between 0800 and 1800 hours. On day 1, the nest was not manipulated, and the wasps were allowed to forage freely by keeping the cage open. The cage was closed at the end of day 1 and remained closed throughout day 2 to prevent the wasps from foraging. Only water but no food was placed in the cage on this day so that the wasps had no access to food. On day 3, the cage was opened in the morning just before the first observation session so that the wasps could forage freely again.

Two observers made observations in alternate sessions for each day (a total of four sessions per day, where the duration of each session was 2.5 h). Sampling methods consisted of 32 scans and 68 all-occurrence sessions (Gadagkar 2001), randomly intermingled and spread across the 10 h of observation per day.

The number of wasps present on the nest on each day was estimated by including all individuals whose presence was recorded on the nest, either in an interaction or just the appearance on the nest, during the period of observation on that day. The frequency per hour of dominance behavior was computed from the all-occurrence sessions for each colony on each day. Dominance behavior includes the acts of attacking, nibbling, pecking, chasing, holding in mouth, sitting over another wasp, or engaging in falling fights with another wasp. The frequency per hour of dominance behavior received by every individual in each colony was computed separately for each day. The frequencies per hour at which individuals left the nest were also similarly

Table 1 Colony sizes used in the experiment

Nest	Number of wasps		
	Day 1	Day 2	Day 3
V735	8	8	8
V758	13	12	11
V782	15	15	12
V786	11	12	11
V718	10	10	10
V738	13	12	12
V764	14	11	9
V748	4	4	4
Average	11	10.5	9.6

Number of wasps present on the nest on days 1, 2 and 3 are not significantly different from each other (see text).

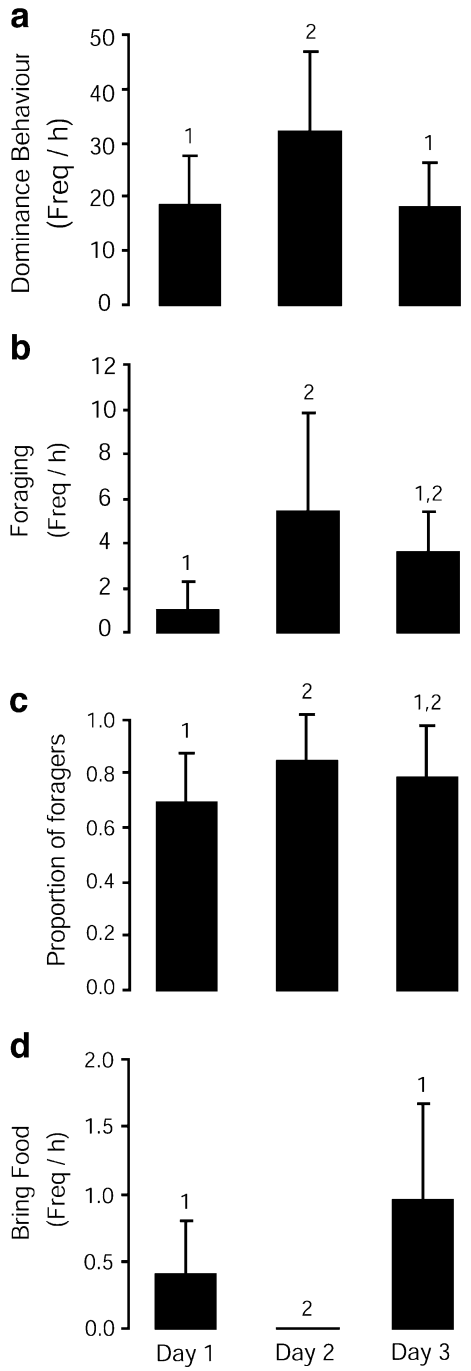

Fig. 1 Mean and SD of **a** frequency per hour of dominance behavior, **b** frequency per hour of foraging, **c** proportion of foragers, and **d** frequency per hour foragers bring food on days 1–3. *Different numbers* indicate a significant difference between the *bars* (see text)

computed for each day. These frequencies are treated as the rates of foraging because a foraging trip need not necessarily result in food being brought back to the nest. Hence, on day 2, a foraging trip was scored every time an individual left the nest for another part of the cage, although no foraging trips involved bringing food back to the nest, as the wasps were in closed cages with no access to food. An individual that had left the nest for at least one foraging trip during the period of observation on a particular day was classified a forager for that day. This classification was used to compute the proportion of foragers in the colony on each day.

Results

There was no significant difference between days 1–3 with respect to the number of adult wasps present on the nest (Table 1; ANOVA, $F_2=0.373$, $p=0.693$), validating our comparison of the frequencies per hour of behaviors between days.

Dominance behavior increases under starvation

The total frequency per hour of dominance behavior observed in the colony on day 2 was significantly greater than that on day 1 (Fig. 1a; Wilcoxon matched-pairs test; $T=1$, $N=8$, $p=0.016$). However, on day 3, the levels of colony aggression reduced significantly with respect to day 2 and became comparable to those on day 1 (Fig. 1a; Wilcoxon matched-pairs test; day 3 vs day 2, $\mathrm{T}=3$, $\mathrm{N}=8$, $\mathrm{p}=0.039$; day 3 vs day 1, $T=18$, $N=8$, $p=1.0$).

Foraging attempts increase under starvation

The rates of foraging, as well as the proportion of foragers, increased significantly on day 2 compared to day 1 (Fig. 1b,c; Wilcoxon matched-pairs test; foraging, $T=1$, $N=8$, $p=0.016$; proportion of foragers, $T=2$, $N=8$, $p=0.047$). The values of both these variables decreased on day 3 and became comparable to those on day 1 (Fig. 1b,c; Wilcoxon matched-pairs test; foraging, $T=8$, $N=8$, $p=0.195$; proportion of foragers, $T=7$, $N=8$, $p=0.563$). In addition, the rates at which food was brought back to the nest on day 3 were not significantly different from those on day 1 (Fig. 1d; Wilcoxon matched-pairs test, $T=5$, $N=8$, $p=0.078$).

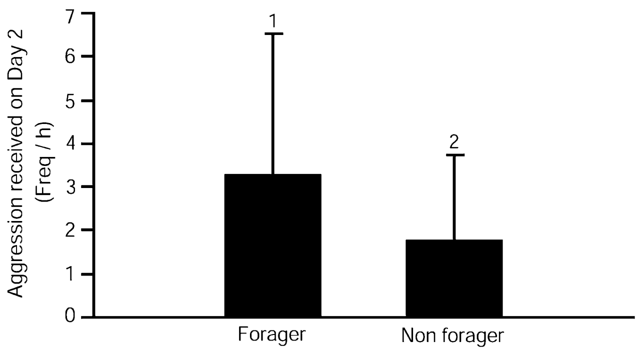

Fig. 2 Mean and SD of frequencies per hour of aggression received on day 2 by foragers and non-foragers of day 1. *Different numbers* indicate a significant difference between the *bars* (see text)

Aggression is directed toward foragers

Although the overall rate of dominance behavior increased on day 2 relative to day 1 (see above), individuals identified as foragers on day 1 received even more aggression on day2 than those identified as non-foragers on day 1 (Fig. 2; Mann–Whitney $U=1{,}110.50$, $N=91$, $p=0.049$). This implies that, although additional individuals attempted to forage on day 2 (Fig. 1c), intranidal workers responded to starvation by especially targeting “known” foragers, i.e., foragers of day 1. This suggests that the increase in dominance behavior on day 2 was a response to the absence of incoming food rather than a randomly directed stress response to closed cage conditions and/or starvation.

Discussion

By experimentally demonstrating that dominance behavior increases under starvation and that it returns to normal levels when foraging rates do so, we provide further support for the hypothesis that hunger is signaled through aggression. This reinforces the idea that dominance behavior in *R. marginata* has been co-opted for the decentralized, self-organized regulation of worker foraging. At this stage, we cannot distinguish between the use of aggression to get idle foragers to start foraging or to get individuals who are already foraging to continue to do so; we suspect that aggression is used for both purposes, and note that both would be consistent with the use of dominance behavior to signal hunger and regulate the supply of food to the nest. There is evidence that aggression may be used by *Polistes* queens, and in some cases workers, to regulate worker foraging and other colony activities (Gamboa et al. 1990; O’Donnell 1995, 1998, 2006; Sumana and Starks 2004). However, as far as we can tell, in these species, dominance behavior continues to serve the function of suppression of worker reproduction. In *R. marginata*, aggression appears to no longer serve the latter function after about a week of the queen establishing herself. Hence, we postulate that a shift has occurred in the primary function of dominance behavior in *R. marginata*, from being the mechanism of reproductive control to being co-opted for the decentralized, self-organized regulation of worker foraging.

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