

REGULATION OF WORKER ACTIVITY IN THE PRIMITIVELY EUSOCIAL WASP *ROPALIDIA CYATHIFORMIS*

by

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Summary

Ropalidia marginata, traditionally regarded as a primitively eusocial wasp species appears to have acquired some features reminiscent of highly eusocial species. Queens are behaviorally passive individuals, yet maintain complete reproductive monopoly and probably use pheromones to achieve this. Regulation of worker foraging is achieved by the workers themselves in a decentralized, self-organized manner. If there are other species in the genus *Ropalidia* that do not show such relatively 'advanced' features, this genus can provide an attractive model system to investigate the evolutionary transition from the primitively eusocial to the highly eusocial state. Here, we therefore investigate the congeneric *Ropalidia cyathiformis* and demonstrate that in contrast to *R. marginata*, it appears to be a typical primitively eusocial species. As expected therefore, and in striking contrast with *R. marginata*, *R. cyathiformis* queens are the most, or among the most, dominant, active and interactive individuals and their behavior is consistent with the possibility that they suppress worker reproduction and regulate worker foraging in a relatively centralized manner. Upon removal of the queen, a potential queen with levels of aggression even higher than that of the queen, becomes apparent immediately. Such a potential queen appears to take over inhibition of worker reproduction and regulation of worker foraging by mechanisms similar to that used by the queen so that, there is no disruption in foraging and brood care. We suggest that comparative studies of

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R. marginata and *R. cyathiformis* provide a unique opportunity to investigate the evolutionary transition from the primitively eusocial to the highly eusocial state.

Keywords: dominance behavior, primitively eusocial wasps, regulation of worker activity, *Ropalidia cyathiformis*, *Ropalidia marginata*, social evolution.

Introduction

The contrasts between primitively eusocial insects (*e.g.* polistine wasps and halictine bees) and their highly eusocial counterparts (*e.g.* honeybees and most species of ants) (Wilson, 1971; Hölldobler & Wilson, 1990; Bourke & Franks, 1995; Crozier & Pamilo, 1996; Gadagkar, 2001b) provide rich material for a comparative approach to the study of the evolution of eusociality. Among the many contrasts, those concerning communication between queens and workers are of special interest because they cut across traditional boundaries between studies of reproductive division of labor and division of non-reproductive labor.

In primitively eusocial species, division of both reproductive labor as well as non-reproductive labor is achieved solely and actively (*i.e.* by means of behavior) by the queens who in these species are regarded as ‘central pace-makers’ of their colonies. Queens are generally the most active, aggressive and interactive individuals of their colonies. The aggressive behavior (also referred to as dominance behavior) of the queens and the resulting physical intimidation is thought to be adequate to suppress worker reproduction (West-Eberhard, 1969, 1977; Wilson, 1971; Fletcher & Ross, 1985; Reeve, 1991). Dominance and other behavioral interactions that queens have with their workers also help regulate the levels of foraging and other activities of the workers. Thus the mechanism used by the queens to regulate non-reproductive activities of the workers is thought to be similar or intimately linked to the mechanism by which they regulate worker reproduction (Brothers & Michener, 1974; Breed & Gamboa, 1977; Buckle, 1982; Dew, 1983; Reeve & Gamboa, 1983, 1987; Gamboa *et al.*, 1990; Gadagkar, 1991; Reeve, 1991; Röseler, 1991).

In highly eusocial species by contrast, division of reproductive and non-reproductive labor appears to be achieved rather differently with the queen responsible only for the former, and that too in a behaviorally passive manner. Reproductive division of labor is achieved through a morphological

and physiological caste differentiation initiated and essentially completed, in the early stages of larval development (Wilson, 1971; Winston, 1987; Hölldobler & Wilson, 1990; Bourke & Franks, 1995; Evans & Wheeler, 2000). In species where workers can potentially develop their reduced ovaries and lay small numbers of haploid unfertilized eggs, they usually do not do so in the presence of the queen, a phenomenon attributable to pheromones released by the queen. In large colonies where queens cannot directly interact with any significant proportion of their workers and where they achieve reproductive division of labor by passively releasing pheromones, workers appear to have taken on the task of regulating their own non-reproductive labor in a decentralized, self-organized manner. In honeybee colonies for *e.g.* workers circulate throughout the nest, gather information about the colony's needs and adjust their activities accordingly, often with the aid of direct worker-worker behavioral interactions (Free, 1965; Lindauer, 1967; Winston, 1987; Huang & Robinson, 1992; Camazine, 1993; Seeley, 1995).

Ropalidia marginata is a tropical, polistine wasp widely distributed in peninsular India. By the criteria of absence of morphological caste differentiation between queens and workers, and the potential ability of workers to mate, develop their ovaries and initiate single foundress nests or become queens of their natal nests, *R. marginata* is primitively eusocial. In the matter of division of reproductive and non-reproductive labor however, it is exceptional among all primitively eusocial species studied so far. Established colonies of *R. marginata* are monogynous and their queens are completely successful in maintaining reproductive monopoly (Gadagkar, 2001a, b). However, *R. marginata* queens are strikingly inactive and docile, almost never at the top of the dominance hierarchies of their colonies (Premnath *et al.*, 1996; Gadagkar, 2001b; Kardile & Gadagkar, 2002; Sumana & Gadagkar, 2003). We have speculated, and there is suggestive evidence, that they may use a mildly volatile pheromone to inhibit worker reproduction or, in keeping with the modern terminology, to inform workers of their presence (Premnath *et al.*, 1996; Gadagkar, 2001b; Sumana *et al.*, unpubl. data). Remarkably enough, this situation in a primitively eusocial species, is also accompanied by a decentralized self-regulation of worker activity without the involvement of the queen. There is evidence that *R. marginata* workers have co-opted dominance behaviors to communicate hunger signals and thus regulate rates of each other's foraging, without involving the queen (Premnath *et al.*, 1995; Gadagkar, 2001a, b).

Are these features of *R. marginata* typical of the genus *Ropalidia* or are they related to the fact that this particular species has acquired some highly eusocial qualities? In the latter scenario, the genus *Ropalidia* can potentially provide a unique model system to understand the evolutionary transition between the primitively and the highly eusocial states. Here we study the congeneric *Ropalidia cyathiformis* and show that it is a typical primitively eusocial species with queens behaving as if they use physical dominance to regulate both reproductive and non-reproductive activities of the workers.

Materials and methods

We performed twelve experiments, one after the other, on twelve separate, naturally initiated, post-emergence nests of *Ropalidia cyathiformis* (Fab.) (Hymenoptera: Vespidae), during March 1999 to April 2001, on the campus of the Indian Institute of Science, Bangalore (13°00'N, 77°32'E), India. We marked all wasps on each nest with unique spots of quick drying non-toxic colored paints on their thorax and/or abdomen, for individual identification. Each experiment consisted of behavioral observations for two days, nine hours each day, between 0700-1000 h, 1100-1400 h and 1500-1800 h. Each observation session was of 5-minute duration and was followed by a one-minute break before the beginning of the next session. Observations were of two kinds: instantaneous scans to record the behavioral state of each individual and 'all occurrences' sessions in which we recorded every performance of a selected set of behaviors by every individual. Equal numbers of scans and all occurrences sessions were randomly intermingled to yield 45 scans and 45 all occurrences sessions each day, for each nest (for details, see Gadagkar, 2001b).

On the first day, we observed the nests as described above, without any manipulation. Eleven out of twelve nests were monogynous, *i.e.* had a single egg-layer, designated as the queen. On the only polygynous nest, we observed three egg-layers, laying 5, 2 and 1 egg/s respectively, during the week before the start of the experiment. We designated as queen, that individual who laid five eggs and who cannibalized at least two out of the three eggs laid by the other egg layers. From each colony, we removed the queen on the second day morning, between 0500 h to 0600 h, and observed the queenless nest on that day, as described above. As it has always been successfully accomplished during similar experiments with *R. marginata* (Premnath *et al.*, 1995; Sumana & Gadagkar, 2001), we attempted to return the queens to their nests, after the observations on day 2, but were unsuccessful; the queens often flew away, never to return. Hence we were unable to study the nests with their queens returned on day 3, as has been done in the case of *R. marginata*.

We used data from the instantaneous scans to compute the proportions of time spent by each wasp in various common behaviors, and data from the all occurrences sessions to compute the frequency per hour of performance of the less common behaviors. Here we focus on the following six behaviors:

- (1) Dominance behavior: this includes attack, nibble, peck, chase, hold in mouth, sit on another wasp and falling fight (Gadagkar, 2001b). We computed rates of dominance behavior for each wasp, after correcting for the proportion of time spent by that wasp

on its nest, on that day. Some of these behaviors appear to be overtly aggressive while others appear more ritualized. Therefore we prefer to call these behaviors as dominance behaviors rather than as aggressive behaviors.

- (2) Non-dominance interactions: this includes the active components of paired non-dominant interactions namely, antennate, approach, allogroom, solicit, snatch food, liquid or building material from another wasp. As in the case of dominance behavior, we computed rates of non-dominance interactions for each wasp, after correcting for the proportion of time spent by that wasp on its nest, on that day.
- (3) Activity: this was measured as the proportion of time an individual remained active during the period that the individual was present on the nest. A wasp was considered active unless she was merely sitting, grooming herself or laying eggs.
- (4) Unloading: When one or more wasps on the nest took all or part of the food brought by a forager before the forager fed larvae, the forager was said to have been unloaded and the wasp/s who took food from the forager was/were said to have unloaded the forager. Rates of unloading were measured in two ways, from the point of view of the unloaders (Unloading foragers) and from the point of view of the foragers (Foragers being unloaded).
- (5) Feed larvae, and
- (6) bring food, which are self-explanatory.

In all experiments, within 1-2 hours after the queen was removed from her nest, one of the remaining individuals became very aggressive and initiated high levels of dominance and other interactions. This wasp was labeled as 'potential queen', because we know from previous work (Gadagkar, 2001b) that, if the queen is not returned, this individual will go on to become the next queen of the colony. That worker who, other than potential queen, had the highest value for the variable under consideration, is referred to as the 'max. worker'. Different individuals may have been thus designated as max workers for different variables, even in the same nest. For each variable defined above, the average value for all the workers in a colony, except the queen and potential queen, was labeled as 'avg. worker'. Based on the network of dominance-subordinate interactions observed in each colony, on each day a dominance hierarchy was constructed using an index of dominance (Premnath *et al.*, 1990; Gadagkar, 2001b), which is a modified form of the index of fighting success developed for Red Deer (Clutton-Brock *et al.*, 1979). For each individual wasp, an index of dominance was computed using the expression:

$$D = \frac{\sum_{i=1}^n B_i + \sum_{j=1}^m \sum_{i=1}^n b_{ji} + 1}{\sum_{i=1}^n L_i + \sum_{j=1}^p \sum_{i=1}^n l_{ji} + 1}$$

where n is the number of individuals in the colony, $\sum B_i$ is the sum of the rate at which the subject shows dominance behavior towards colony members and $\sum b_{ji}$ is the sum of the rates at which all individuals dominated by the subject in turn show dominance behavior towards colony members. 1 to m are thus the individuals towards whom the subject shows dominance behavior. Similarly $\sum L_i$ is the sum of the rate at which the subject shows subordinate behavior towards colony members and $\sum l_{ji}$ is the sum of the rates at which those individuals towards whom the subject shows subordinate behavior in turn show subordinate behavior towards the colony members. 1 to p are thus the individuals towards whom the subject shows subordinate behavior. All the wasps in each colony were ranked in descending order of their index of dominance. The individual with the highest value of the dominance index was

assigned rank 1 and individuals with successively lower values were assigned consecutive ranks from 2 to n . It should be noted that individuals who do not participate in dominance-subordinate interactions at all, get a value of 1.0 for the index of dominance and would thus be ranked higher than some individuals who participate in dominance-subordinate interactions but have a value less than 1.0 for their index of dominance.

All statistical comparisons were made using Wilcoxon matched pairs signed rank test with a sample size of 12 as each of the 12 colonies was considered to provide one data point. More details are given in the legends to figures. Kendall's correlation coefficient was used to examine the relationship between the fraction of dominance received by a forager and her contribution to the colony's total foraging efforts.

Results

Day 1: Queenright colonies

On day 1 of the experiment, involving queenright colonies, queens showed behaviors such as, dominance behavior, non-dominance interactions, activity, unloading of foragers and feed larva (see methods for definitions of these behaviors) at levels significantly higher than or equal to the levels at which these behaviors were shown by the max. workers of their colonies. As compared to their avg. workers, queens showed these behaviors at significantly higher levels; the only exception was that the queen fed larvae at rates similar to those of avg. workers (Figs 1A, B, C and 2A, B). The queens always occupied the top rank in the dominance hierarchies of their colonies (Table 1). Potential queens were similar to their queens in the rates with which they showed dominance behavior and non-dominance interactions and were intermediate between queens and avg. workers in activity levels, unloading of foragers and feed larva (Figs 1A, B, C and 2A, B). In 11 out of 12 colonies, potential queens occupied the second highest rank (next to the queen) in the dominance hierarchies of their colonies (Table 1).

Day 2: Queenless colonies

Upon removal of the queen, one of the workers — the potential queen — became very aggressive. Compared to day 1, potential queens showed significantly higher levels of dominance behavior, non-dominance interaction, activity, unloading of foragers and feed larva on day 2. In contrast, max. workers and avg. workers did not change with respect to these behaviors from day 1 to day 2. On day 2, potential queens showed either significantly

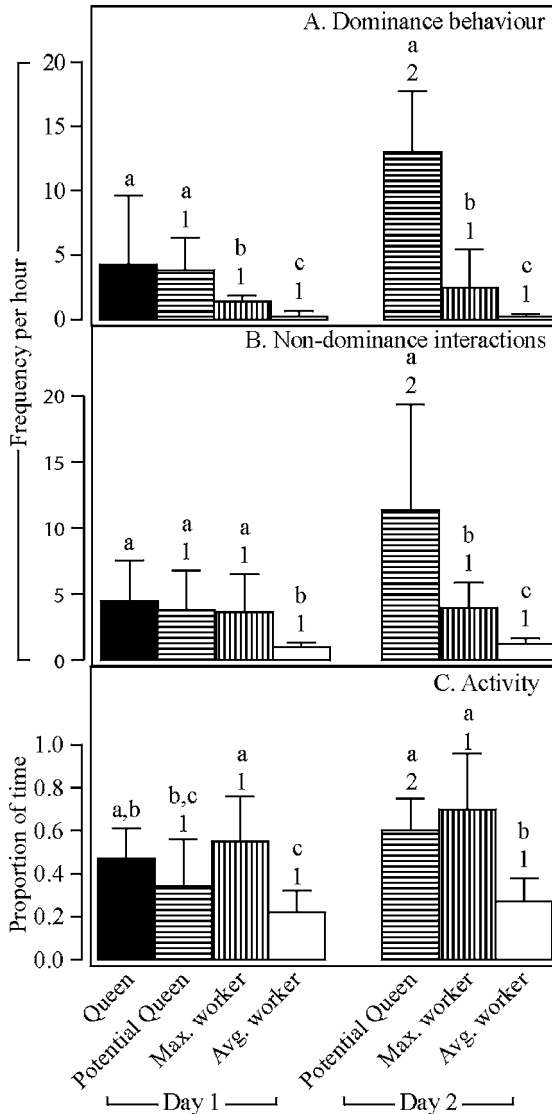


Fig. 1. Means and standard deviations of frequencies per hour of (A) dominance behaviour, (B) non-dominance interactions and (C) proportion of time spent being active on the nest, by queens, potential queens, max. workers and avg. workers on day 1 and day 2. Bars that carry different letters are significantly different from each other within each day ($p < 0.05$). Bars that carry different numbers are significantly different from each other across the two days ($p < 0.05$). Here, comparisons were made between the same category, e.g. potential queen on day 1 and potential queen on day 2, avg. worker on day 1 and avg. worker on day 2. All comparisons across and within days were made by Wilcoxon matched-pair signed rank test.

higher or similar values for all the above mentioned variables, as compared to max. worker and were always significantly higher as compared to the avg. worker (Figs 1A, B, C and 2A, B). On day 2, potential queens dominated all the individuals on their nests and occupied the highest rank in the dominance hierarchies of their colonies (Table 1).

Effect of queen removal on foraging and brood care

It must be emphasized that in spite of the removal of the queen, there was no change in the rates at which food was brought, foragers were unloaded and larvae were fed on the nest on day 2 as compared to day 1 (Figs 3 and 4A). There was no difference between day 1 and day 2 in the contribution of the foragers to the colony's efforts to feed larvae (Fig. 4B). The total number of foragers on day 1 (mean \pm SD, 9.0 ± 3.8) and day 2 (mean \pm SD, 8.4 ± 3.2) were not significantly different ($T = 16.0$, $p = 0.44$). Of all the dominance behavior seen in a colony, we computed the fraction that was received by each forager. We also computed the contribution of each forager to the total foraging effort of her colony. These two variables namely, the fraction of dominance behavior received by each forager and her contribution to the colony's total foraging efforts were negatively correlated, on both days 1 and 2 (Fig. 5A, B). The frequency per hour of dominance received by foragers (day 1 = 1.0 ± 1.2 , day 2 = 1.85 ± 1.99) was not significantly different from that received by non-foragers (day 1 = 1.1 ± 1.2 , day 2 = 1.68 ± 1.21) on both the days ($T = 38$ for the both day 1 and day 2, $p = 0.94$).

Discussion

The results reported here reveal that *R. cyathiformis* behaves approximately as expected of a typical primitively eusocial species. But that is not nearly as interesting as the fact that *R. cyathiformis* is strikingly different from what has been reported previously for the congeneric *R. marginata*. We therefore begin by recapitulating the relevant behavior of *R. marginata*.

Ropalidia marginata

Queens in normal, undisturbed colonies of *R. marginata* are unusual among primitively eusocial species. They show very low levels of dominance behavior, are never at the top of the dominance hierarchies of their colonies and are

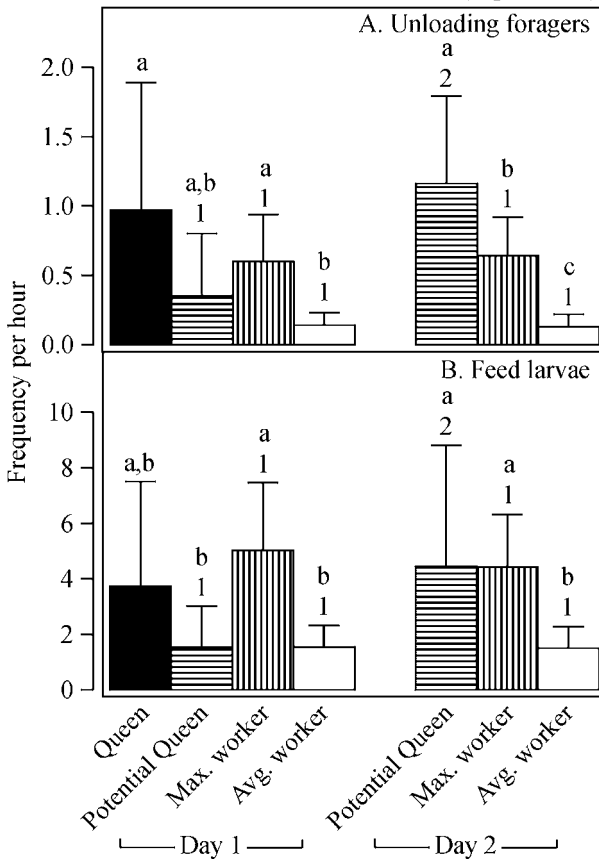


Fig. 2. Means and standard deviations of frequencies per hour of (A) unloading the foragers and (B) feed larvae by queens, potential queens, max. workers and avg. workers on day 1 and day 2. Bars that carry different letters are significantly different from each other within each day ($p < 0.05$). Bars that carry different numbers are significantly different from each other across the two days ($p < 0.05$). Here, comparisons were made between the same category, e.g. potential queen on day 1 and potential queen on day 2, avg. worker on day 1 and avg. worker on day 2. All the comparisons across and within days were made by Wilcoxon matched-pair signed rank test.

strikingly inactive and non-interactive individuals. Based on these and other findings, it has been argued that *R. marginata* queens in established colonies do not use physical dominance to suppress worker reproduction and perhaps use pheromones to do so. These queens also perform tasks such as unloading of foragers and feeding larvae at rates significantly lower than average workers of their colonies. It has also been argued therefore that these queens

TABLE 1. *Nest code, dominance rank of the queen and potential queen in the hierarchies of their colonies and number of wasps on each of the twelve nests studied*

Nest code	Day 1			Day 2	
	Rank of Queen	Rank of potential queen	No. of wasps	Rank of potential queen	No. of wasps
C01	1	2	15	1	14
C02	1	6	14	1	19
C03	1	2	28	1	26
C07	1	2	23	1	23
C08	1	2	21	1	21
C33	1	2	18	1	17
C34	1	2	16	1	15
C38	1	2	11	1	10
C50	1	2	23	1	20
C58	1	2	18	1	19
C59	1	2	19	1	18
C60	1	2	12	1	11

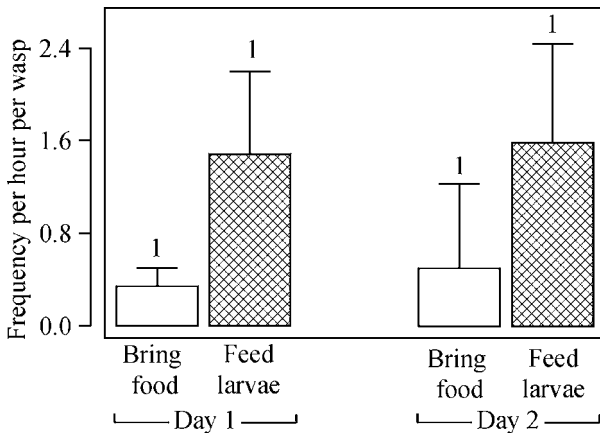


Fig. 3. Frequencies per hour per wasp of bring food and feed larvae, at the colony level, on days 1 and 2. Bars that carry different numbers are significantly different from each other across the two days ($p < 0.05$). Comparisons were made by Wilcoxon matched-pair signed rank test.

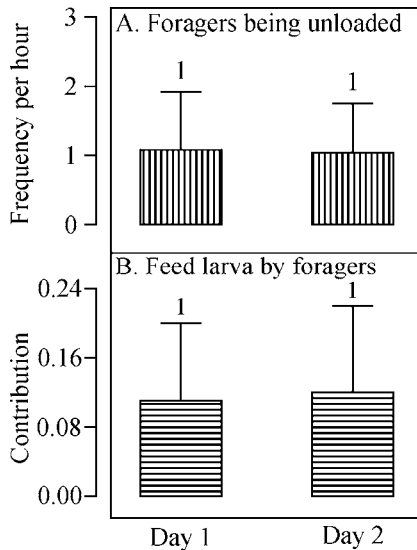


Fig. 4. (A) Frequency per hour of foragers being unloaded and (B) contribution of foragers to feed larvae. The bars that carry different numbers are significantly different from each other across the two days ($p < 0.05$). Comparisons were made by Wilcoxon matched-pair signed rank test.

do not participate in the regulation of such non-reproductive activities of workers as foraging (Premnath *et al.*, 1995; Gadagkar, 2001b). The idea that *R. marginata* queens who show low levels of unloading foragers and feeding larvae may not be involved in regulating worker foraging, is based on the reasonable assumption that feeding larvae provides information on the colony's hunger level and unloading foragers provides an opportunity to communicate this information to foragers. Who then regulates worker foraging and how? Although queens show little or no dominance behavior, many workers show dominance behaviors among themselves. These dominance interactions among workers could well serve to regulate each other's foraging in a decentralized and self-organized manner. Consistent with this idea, there is a positive correlation between the fraction of the colony's dominance behavior received by individual foragers and their contribution to the colony's foraging efforts. This suggests that receiving more dominance behavior increases the forager's efforts to collect food.

In *R. marginata*, removal of the queen results in one of the workers (potential queen) becoming very aggressive relative to her own behavior in the presence of the queen and also relative to the behavior of the queen before

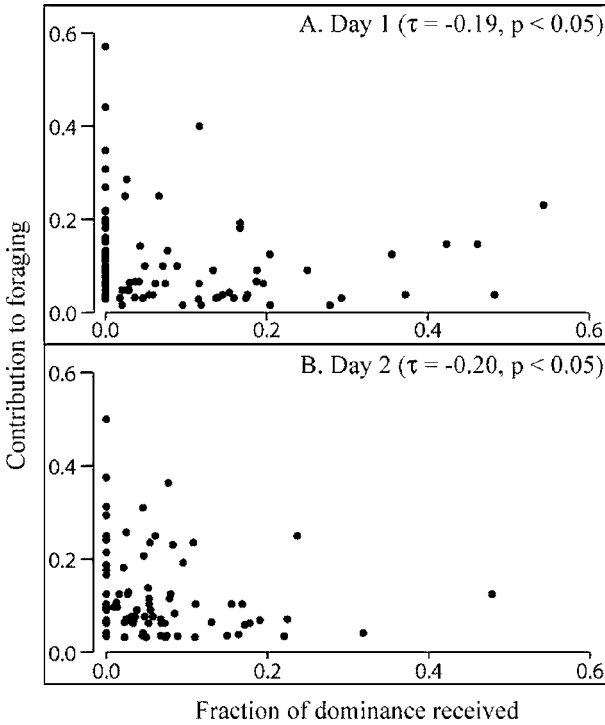


Fig. 5. Contribution of foragers to the total foraging efforts of their colonies and fraction of dominance received by foragers on (A) day 1 and (B) day 2.

she was removed. Because such potential queens are known to go on to become the next queens of their colonies, this has been interpreted to mean that although queens of *R. marginata* in established colonies do not use physical dominance to suppress worker reproduction, potential queens (*i.e.* queens at the time they establish themselves) do use physical aggression to do so (Premnath *et al.*, 1995, 1996; Gadagkar, 2001a, b). Thus potential queens of *R. marginata* take over the role of the queen in suppressing worker reproduction, albeit by a mechanism different from that used by the queens of established colonies. But, what about regulation of worker foraging? Immediately upon removal of queens in *R. marginata*, the potential queen becomes so aggressive that she temporarily drives out most of the wasps performing intranidal activities. This results in disruption of normal activities so that foragers are no longer unloaded efficiently. In response, foragers themselves feed larvae to a much greater extent than they do in the presence of the queen and presumably acquire the required information to regulate their own for-

aging. Thus regulation of foraging, which seems to be done by the intranidal workers in the queen-right condition appears to be taken over by the foragers themselves in the absence of the queen (Premnath *et al.*, 1995, 1996; Gadagkar, 2001a, b; Sumana & Gadagkar, 2001, 2003; Kardile & Gadagkar, 2002; Sumana *et al.*, unpubl. results).

Ropalidia cyathiformis

All that was described above is in striking contrast with the situation in *R. cyathiformis*. As expected for a typical primitively eusocial species, queens of *R. cyathiformis* are the most or, among the most, dominant, active and interactive individuals in normal, undisturbed colonies. Such queens participate in unloading food from foragers and feeding larvae at rates comparable to those workers who show these behaviors at the highest rates in their colonies. Thus, like in other primitively eusocial species, queens of *R. cyathiformis* appear to use physical dominance to suppress worker reproduction and also to participate, along with a small number of workers, in regulating worker foraging, in a relatively centralized manner.

Upon removal of the queen in *R. cyathiformis* colonies, a potential queen becomes evident by her increased levels of dominance behavior, interactions and activity, compared to her own behavior in presence of the queen. Thus potential queens in *R. cyathiformis* appear to fulfill the role of the queens in the absence of the latter. The appearance of a potential queen upon removal of the original queen is reminiscent of what happens in *R. marginata*. It should be noted however that both queens and potential queens are aggressive in *R. cyathiformis* while only potential queens and not queens are aggressive in *R. marginata*. Even more strikingly different from *R. marginata* is the effect of queen removal on the regulation of worker foraging. This difference is two-fold. First, potential queens in *R. cyathiformis* are not only more dominant, active and interactive but they also significantly step up their participation in unloading of foragers and feeding of larvae, relative to their own behavior in the presence of the queen. Thus potential queens of *R. cyathiformis* seem to take on the role of the queen both in suppressing worker reproduction as well as in regulating worker foraging. Secondly the level of aggression shown by potential queens of *R. cyathiformis* is not so high as to drive intranidal workers off the nest. Foragers continue to be unloaded as in the presence of the queen and foragers do not feed larvae at any higher rates

than they do in the presence of the queen. In both *R. marginata* and *R. cyathiformis*, foraging and brood care remain unaffected upon removal of the queen but for different reasons. Thus in *R. marginata*, regulation of foraging that is done by intranidal workers in queenright colonies is taken over by the foragers in the absence of the queen while in *R. cyathiformis*, regulation of foraging done by the queen in queenright colonies is taken over by the potential queen when the queen is removed.

From the results reported here on *R. cyathiformis* and especially in comparison with results of similar experiments with *R. marginata*, it appears that these two congeneric species provide an attractive model system to study the evolutionary transition from the primitively eusocial to the highly eusocial state in general and from physical control to chemical regulation of worker reproduction and from relatively centralized to relatively decentralized control of worker foraging, in particular. It is not surprising that highly eusocial species, with their large colony sizes, employ chemical (pheromonal) regulation of worker reproduction while primitively eusocial species, with their small colony sizes, exhibit physical (by means of dominance behavior) inhibition of worker reproduction. It is also not surprising that highly eusocial species, with their large colony sizes, employ more decentralized regulation of worker foraging, while primitively eusocial species, with their small colony sizes, exhibit centralized control by the queen. It is not however, clear which of these two evolutionary transitions namely, physical inhibition of worker reproduction to pheromonal regulation of worker reproduction and centralized control of worker foraging by the queen to decentralized self organization of worker foraging, evolved first and which followed. Our results suggest a possible causal link between the switch to pheromonal regulation of worker reproduction and decentralized regulation of worker foraging. With the evolution of pheromones that regulates worker reproduction, queens no longer need to exhibit high levels of dominance behavior to achieve reproductive monopoly. If the same dominance behavior by queens is also responsible for regulating worker foraging in primitively eusocial species, the reduction of dominance behavior by queens must result in the concomitant weakening of regulation of foraging. On the other hand, pheromonal regulation of worker reproduction is expected to be more effective as compared to physical control. This should reduce the options for direct reproduction and hence increase selection pressure on the workers to obtain indirect fitness. And one way to do so would be for the workers to efficiently self-organize their own foraging. These arguments suggest that the transition to

pheromonal regulation of worker reproduction may precede the evolution of self-organization of worker foraging. Clearly, many more such comparative studies will be needed to clarify these issues.

References

- Bourke, A.F.G. & Franks, N.R. (1995). Social evolution in ants. — Princeton University Press, Princeton.
- Breed, M.D. & Gamboa, G.J. (1977). Behavioral control of workers by queens in primitively eusocial bees. — *Science* 195, p. 694-696.
- Brothers, D.J. & Michener, C.D. (1974). Interactions in colonies of primitively social bees. III. Ethometry of division of labor in *Lasioglossum zephyrum* (Hymenoptera: Halictidae). — *J. Comp. Physiol.* 90, p. 129-168.
- Buckle, G. (1982). Queen-worker behavior and nestmate interactions in young colonies of *Lasioglossum zephyrum*. — *Insectes Soc.* 29, p. 125-137.
- Camazine, S. (1993). The regulation of pollen foraging by honey bees: how foragers assess the colony's need for pollen. — *Behav. Ecol. Sociobiol.* 32, p. 265-272.
- Clutton-Brock, T.H., Albon, S.D., Gibson, R.M. & Guinness, F.E. (1979). The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). — *Anim. Behav.* 27, p. 211-225.
- Crozier, R.H. & Pamilo, P. (1996). Evolution of social insect colonies: Sex allocation and kin selection. — Oxford University Press, Oxford.
- Dew, H.E. (1983). Division of labor and queen influence in laboratory colonies of *Polistes metricus* (Hymenoptera; Vespidae). — *Z. Tierpsychol.* 61, p. 127-140.
- Evans, J.D. & Wheeler, D.E. (2000). Expression profiles during honeybee caste determination. — *Genome Biology* 2(1), research0001.1-0001.6.
- Fletcher, D.J.C. & Ross, K.G. (1985). Regulation of reproduction in eusocial Hymenoptera. — *Ann. Rev. Entomol.* 30, p. 319-343.
- Free, J.B. (1965). The allocation of duties among worker honey bees. — *Symp. Zool. Soc. Lond.* 14, p. 39-59.
- Gadagkar, R. (1991). *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and independent founding *Ropalidia*. — In: The social biology of wasps (K.G. Ross & R.W. Matthews, eds). Cornell University Press, Ithaca, p. 149-190.
- (2001a). Division of labour and organization of work in the primitively eusocial wasp *Ropalidia marginata*. — *Proc. Indian natn. Sci. Acad.* B67, p. 397-422.
- (2001b). The social biology of *Ropalidia marginata*: Toward understanding the evolution of eusociality. — Harvard University Press, Cambridge, Mass.
- Gamboa, G.J., Wacker, T.L., Scope, J.A., Cornell, T.J. & Shellman-Reeve, J. (1990). The mechanism of queen regulation of foraging by workers in paper wasps (*Polistes fuscatus*, Hymenoptera, Vespidae). — *Ethology* 85, p. 335-343.
- Huang, Z.-Y. & Robinson, G.E. (1992). Honeybee colony integration: worker-worker interactions mediate hormonally regulated plasticity in division of labor. — *Proc. Natl. Acad. Sci. USA* 89, p. 11726-11729.
- Hölldobler, B. & Wilson, E.O. (1990). The ants. — Harvard University Press, Cambridge, Mass.

- Kardile, S.P. & Gadagkar, R. (2002). Docile sitters and active fighters in paper wasps — a tale of two queens. — *Naturwissenschaften* 89, p. 176-179.
- Lindauer, M. (1967). *Communication among social bees*. — Atheneum, New York.
- Premnath, S., Chandrashekara, K., Chandran, S. & Gadagkar, R. (1990). Constructing dominance hierarchies in a primitively eusocial wasp. — In: *Social insects and the environment: Proceedings of the 11th International Congress of IUSSI* (G.K. Veeresh, B. Mallik & C.A. Viraktamath, eds). Oxford & IBH Publishing Co., New Delhi, p. 80.
- —, Sinha, A. & Gadagkar, R. (1995). Regulation of worker activity in a primitively eusocial wasp, *Ropalidia marginata*. — *Behav. Ecol.* 6, p. 117-123.
- —, — — & — — (1996). Dominance relationships in the establishment of reproductive division of labour in a primitively eusocial wasp (*Ropalidia marginata*). — *Behav. Ecol. Sociobiol.* 39, p. 125-132.
- Reeve, H.K. (1991). *Polistes*. — In: *The social biology of wasps* (K.G. Ross & R.W. Matthews, eds). Cornell University Press, Ithaca, p. 99-148.
- — & Gamboa, G.J. (1983). Colony activity integration in primitively eusocial wasps: the role of the queen (*Polistes fuscatus*, Hymenoptera: Vespidae). — *Behav. Ecol. Sociobiol.* 13, p. 63-74.
- — & — — (1987). Queen regulation of worker foraging in paper wasps: a social feedback control system (*Polistes fuscatus*, Hymenoptera: Vespidae). — *Behaviour* 102, p. 147-167.
- Röseler, P.-F. (1991). Reproductive competition during colony establishment. — In: *The social biology of wasps* (K.G. Ross & R.W. Matthews, eds). Cornell University Press, Ithaca, p. 309-335.
- Seeley, T.D. (1995). *The wisdom of the hive — The social physiology of honey bee colonies*. — Harvard University Press, Cambridge, Mass.
- Sumana, A. & Gadagkar, R. (2001). The structure of dominance hierarchies in the primitively eusocial wasp *Ropalidia marginata*. — *Ethol. Ecol. Evol.* 13, p. 273-281.
- — & — — (2003). *Ropalidia marginata* — a primitively eusocial wasp society headed by behaviourally non-dominant queens. — *Current Science* 84, p. 1464-1468.
- West-Eberhard, M.J. (1969). The social biology of polistine wasps. — *Misc. Publ. Mus. Zool. Univ. Mich.* 140, p. 1-101.
- — (1977). The establishment of reproductive dominance in social wasp colonies. — In: *Proceedings of the 8th International Congress of the International Union for the Study of Social Insects*, Wageningen, The Netherlands, p. 223-227.
- Wilson, E.O. (1971). *The insect societies*. — The Belknap Press of Harvard University Press, Cambridge, Mass.
- Winston, M.L. (1987). *The biology of the honey bee*. — Harvard University Press, Cambridge, Mass.
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