Readings in BEHAVIOUR

R. Ramamurthi
Geethabali

How is colony activity regulated in *Ropalidia marginata* ?

Sudha Premnath, Anindya Sinha and Raghavendra Gadagkar* [1]

PUBLISHING FOR ONE WORLD
NEW AGE INTERNATIONAL LIMITED, PUBLISHERS
New Delhi • Bangalore • Bombay • Calcutta • Guwahati • Hyderabad
Lucknow • Madras • Pune • London • Bangkok

How is colony activity regulated in *Ropalidia marginata* ?

Sudha Premnath, Anindya Sinha and Raghavendra Gadagkar* [1]

Centre for Ecological Sciences
Indian Institute of Science
Bangalore 560012, India

ABSTRACT

Primitively eusocial insects often live in colonies consisting of several female adults. Of these, only one is usually the queen or egg layer, and the rest function as sterile, subordinate workers. In some well-studied species, the queen is known to be the most active individual, and is thus thought to regulate colony activity by acting as a central pacemaker. However, studies of the primitively eusocial wasp *Ropalidia marginata* reveal a rather different picture. The queen, inspite of being the sole egg layer, shows significantly fewer dominance behaviours, and unloads food from returning foragers significantly less often as compared to an average worker. Removal of the queen does not lead to any significant difference in the levels of foraging and brood care. Indeed, within minutes of removal of the queen, one of the workers becomes highly aggressive for sometime and then takes over as the next queen. This individual is referred to as a "potential queen". The activity of workers, especially foraging, appears to be regulated by dominance shown to them, not so much by the queen, but by a group of workers, usually including the 'potential queen'.

INTRODUCTION

The "truly" social insects, or eusocial insects as they are called, include the ants, all termites and the more highly organised bees and wasps. They can be distinguished by three traits that they have in common: cooperative brood care, reproductive division of labour and overlap of generations [1, 2]. Eusocial insect societies, often likened to multicellular organisms to emphasize their high level of social integration, have been called "superorganisms" [1].

In all highly eusocial insects, such as termites, ants, some bees and wasps, where there is a clear queen–worker dimorphism, the queen maintains her reproductive dominance through pheromonal control, leaving

[1*] To whom reprint requests should be addressed.

very little option for workers to reproduce. The coordination of activities in such colonies is usually not under the queen's direct supervision. In the best studied species, *Apis mellifera*, it seems to depend upon the ability of the workers to circulate through out the nest, gather information about the colony's needs and adjust their activities according to the demands that they sense [3, 4, 5, 6, 7, 8].

In the primitively eusocial insects on the other hand, there are no distinct morphological castes. All or most individuals in a colony retain their capacity for reproduction and have the flexibility to adopt different roles. This leads to relatively more strife and competition amongst nestmates resulting in 'physical dominance interactions' so that the most dominant individual becomes the queen. In these groups, mechanisms underlying queen control of worker oviposition may be the same or intimately related to those serving regulation of worker activity. The queen being the most dominant individual in social relationships, monopolizes egg-laying, and her overt dominance may retard ovarian development in subordinates [9, 10, 11]. (For a review and further references see [12]). She has also been shown to regulate intra-colony activities through her behavioural interactions with the workers [13, 14, 15, 16, 17, 18].

An earlier study on the primitively eusocial wasp *Ropalidia marginata* had shown that the queen in this species was not the most behaviourally dominant individual [19]. The present study on *R. marginata* was conducted to understand the mechanisms that may be important in coordinating intra-colony activities, and the role of the queen in regulating such activities within her colony. Our results show that the queen, inspite of being the sole egg-layer is not a particularly active individual. She shows significantly less dominance and unloads foods from returning foragers significantly less often when compared to an average worker. Thus the mechanisms underlying colony regulation in this species may be quite different from those of other primitively eusocial insects.

MATERIALS AND METHODS

This study consisted of 13 experiments conducted between February 1991 and March 1992 on twelve post-emergence colonies of *Ropalidia marginata* that were being maintained in a vespiary at the Centre for Ecological Sciences, Indian Institute of Science, Bangalore (13°00′ N and 77°32′ E). One nest alone was used for two experiments, with a gap of six months between the experiments by which time there was a complete turnover of all the individuals in the colony, including the queen. The wasps from these colonies were foraging both from natural sources and from feeding stations in the vespiary with an *ad libitum*

supply of honey, *Corcyra cephalonica* larvae, and water. Eight of the twelve nests used were naturally initiated in the vespiary, while the remaining four were transplanted by us from elsewhere. All individuals in a colony were given unique colour codes using quick drying paints, for individual identification.

Data collection

Each experiment consisted of behavioural observations made for three consecutive days, ten hours each day, between 0800 h and 1800 h. On the first day an undisturbed colony was observed. On the next day, between 0500 h and 0600 h, the queen was removed and observations were made on the colony without the queen. The queen was returned back to her nest at the end of the second day and the observations were repeated on the third day. In this paper we will discuss the results mostly from day one. Sampling methods included instantaneous scanning and recording of all occurrences of selected rare behaviours as described by Gadagkar and Joshi [20]. The two methods were used alternately during the 10 h period each day.

Data analysis

The proportion of time spent on all common behaviours were calculated from instantaneous scans and the hourly frequencies of the certain selected behaviours were calculated from all occurrence sessions, as described earlier [21].

The individual who unloads a forager, immediately on her return with solid or liquid food was recorded and used to calculate the frequencies of unloading. One worker always became extremely aggressive soon after the removal of the queen and this individual is called the "Potential Queen". The worker other than the Potential queen, who had the highest value for the variables under consideration is referred to as the "Maximum Worker". For each variable, the mean value for all workers including the maximum worker, but excluding the potential queen is computed. This value is attributed to the "mean worker". An individual who was observed to bring either food (solid or liquid) or building material, at least once, is called a Forager. All comparisons are by the two-tailed wilcoxon matched-pairs signed ranks test while all correlations are Kendall's rank correlations, unless otherwise mentioned [22].

RESULTS

Queens show a significantly lower frequency of 'dominance behaviour' compared to 'potential queens' ($p < 0.025$), maximum workers ($p<0.025$),

and mean workers ($p < 0.05$). The potential queen's frequency of dominance is not different from that of maximum worker, but significantly greater than that of mean worker ($p < 0.05$; Fig.1). Maximum workers and mean workers unload food at a higher frequency from returning foragers than queens ($p < 0.005$ and $p < 0.025$ respectively) although the 'potential queens' were not significantly different from queens in this regard (Fig.2).

The frequency of dominance shown towards foragers by the individuals in a colony was significantly greater than that shown towards non-foragers ($p < 0.05$). The frequency of dominance received by a forager was significantly correlated with its rate of foraging ($\tau = 0.1995$, $p = 0.02$, $n = 67$). The fraction of dominance received by foragers was also significantly correlated with their contribution to foraging in their colony ($\tau = 0.1825$, $p = 0.03$, $n = 67$). Dominance thus appears to be one of the mechanisms by which foraging in the colony was regulated. Since queens accounted for only 6.2% of the dominance in the colony, and, potential queens and maximum workers accounted for 48% and 35.8% respectively and a mean worker accounts for 9.8%, it is likely that a subset of the workers regulate foraging activities in a colony. It is interesting to note that the potential queen most often belongs to this group.

DISCUSSION

Earlier studies on some primitively eusocial species like *Lassiglossum zephyrum* [13, 14, 23], *Polistes metricus* [15] and *Polistes fuscatus* [16, 17, 18] have shown that the queens are the most active and behaviourally dominant individuals of their colonies and have been considered to be central regulators of intra-colony activity. Our results from observation on undisturbed colonies on the first day of the experiment, clearly showed that the queen in *R. marginata* was different from those of the species mentioned above. The queen in *R. marginata* is not the most dominant individual in her colony. The potential queen, the maximum worker and even an average worker were more dominant. It seems very unlikely therefore that the queen plays a vital role in behaviourally regulating worker activity.

Removal of the queen from colonies of *Polistes fuscatus* resulted in a decrease in the rate of foraging in these colonies [16, 17]. But in *R. marginata*, foraging and brood care activities appeared to be unaffected by the queen's absence from her nest even for more than 10 h. Both the total frequency at which foragers brought food to their nests, and the food brought/animal/hr, were not significantly different. The active foragers in a normal nest continued to forage at more

or less the same frequency even in the queen's absence (unpublished observations).

Who then regulates foraging and how? Foragers seem to receive significantly more dominance than non-foragers, and those that contribute more food to the colony were recipients of a greater fraction of the dominance. Dominance therefore could be a means by which foraging was regulated. The potential queen and the maximum worker together contribute to 83.8% of all the dominance shown in the colony, as compared to only 6% by the queen. It is therefore more likely that a group of workers in the colony who contribute to most of the dominance, regulate foragers. If we consider initial unloading of food as another form of regulating foraging activity, it was again a maximum worker or a mean worker who performed this act significantly more often than a queen. The queen was rarely ever seen to take part in unloading returning foragers. This again was different from what had been reported for *Polistes metricus* [15]. The rate at which foragers would be unloaded would directly depend on the level of satiety of the larvae, and the frequency of unloading or the waiting time before a forager is unloaded could be the cue for foragers to regulate their frequency of bringing food to the colony. In honey bees the waiting time experienced by a nectar forager before unloading to food storer bees has been shown to be a sensitive indicator of a colony's needs [6, 7].

One common feature that emerges out of these results is that workers in *R. marginata* colonies interact with foragers and other colony members at a significantly higher frequency than the queen does. The workers are therefore in a much better position to be aware of the needs of the colony, its brood content and their hunger level, which are important requisites in either recruiting foragers, or for a forager to regulate its own activity. Theraulaz *et. al.* (1991) have shown that in colonies of *Polistes dominulus*, the closeness of the relationship with the brood was an important factor for an individual to switch over to the task of foraging [24]. The mechanism of regulation of foraging in *R. marginata* appears to be more intricate, involving worker–worker interactions, and a group of active and dominant workers contribute to a greater extent to these interactions and hence to regulation of colony activity, rather than a single "central pace maker".

AKNOWLEDGMENTS

We thank Dr. K. Chandrashekara for his very useful comments during the preparation of this paper and Harry William for his help in collecting and maintaining nests. We also thank the Council of Scientific and Industrial Research for financial support.

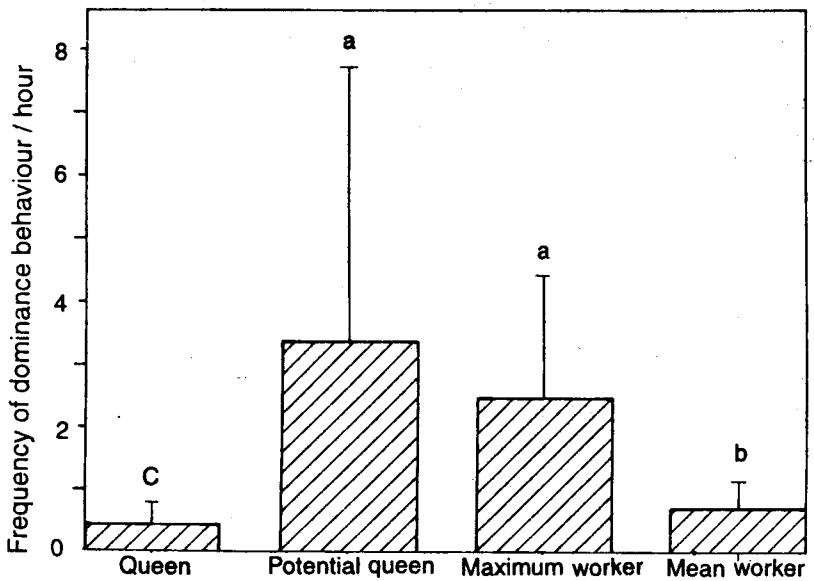

Fig.1 Frequencies of dominance shown by a queen, potential queen, maximum worker and mean worker. Bars that carry different alphabets are significantly different from each other, $p < 0.05$.

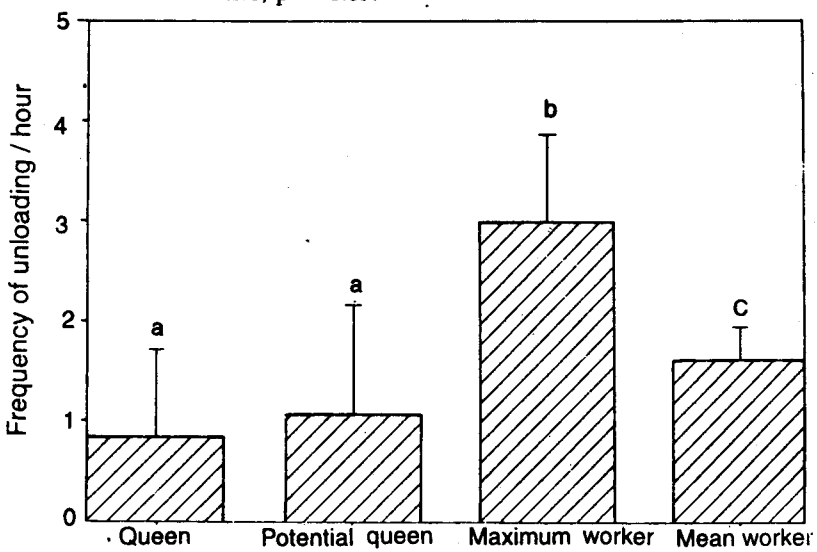

Fig.2 Frequencies of unloading shown by a queen, potential queen, maximum worker and a mean worker. Bars that carry different alphabets are significantly different from each other, $p < 0.05$.

REFERENCES

1. Wilson, E. O., "The Insect Societies", Cambridge: Harvard Univ. Press, 1971.
2. Michener, C. D., "The Social behaviour of bees" , Belknap Press of Harvard Univ., Cambridge, 1974.
3. Lindauer, M., "Communication among social bees", New York: Atheneum, 1967.
4. Free, J. B., "The allocation of duties among worker honey bees", Symp. Zool. Soc. London, **32**, (1965), pp.39–59.
5. Seeley, T. D., "Social foraging by honey bees: how colonies allocate foragers among patches of flowers", Behav. Ecol. Sociobiol., **19**, (1986), pp.343–354.
6. Seeley, T. D., "Social foraging in honey bees: how nectar foragers assess their colony's nutritional status" , Behav. Ecol. Sociobiol., **24**, (1989a), pp.181–199.
7. Seeley, T. D., "The honey bee colony as a superorganism", Amer. Sci., **77**, (1989b), pp.546–553.
8. Huang, Z–Y and G. E. Robinson, "Honey bee colony integration: worker–worker interactions mediate hormonally regulated plasticity in division of labour" , Proc. Natl. Acad. Sci., USA., **89**, (1992), pp.11726–11729.
9. Pardi, L., "Dominance order in *Polistes wasps*", Physiol. zool., **21**, (1948), pp.1–13.
10. West–Eberhard, M. J., "Dominance hierarchies and the evolution of social behaviour", Science, **157**, (1967), pp.1585–1595.
11. Pratte, M., "Foundress associations in the paper wasp *Polistes dominulus* Christ. (Hym., Vesp.), Effect of dominance hierarchy on the division of labour", Behaviour, **111**, (1989), pp.208–219.
12. Roseler, P.F., "Reproductive competition during colony establishment", in Social Biology of Wasps, (ed.) K. G. Ross, and R.W. Matthews, Ithaca: Cornell Univ. Press, 1991, pp.309–335.
13. Breed, M. D. and G. J. Gamboa, "Behavioural control of workers by queens in primitively eusocial bees", Science, **195**, (1977), pp.694–696.
14. Buckle, G. R., "Queen worker behaviour and nestmate interactions in young colonies of *Lassioglossum zephyrum*", Insectes Soc., **29**, (1982), pp.125–137.
15. Dew, H. E., "Division of labour and queen influence in laboratory colonies of *Polistes metricus* (Hymenoptera: Vespidae)", Z. Tierpsychol, **61**, (1983), pp.127–140.
16. Reeve, H. K. and G. J. Gamboa, "Colony activity integration in primitively eusocial wasps: the role of the queen (*Polistes fuscates*, Hymenoptera: Vespidae)" , Behav. Ecol. Sociobiol., **13**, (1983), pp.63–74.
17. Reeve, H. K. and G. J. Gamboa, "Queen regulation of worker foraging in paper wasps: A social feedback control system (*Polistes fuscatus*, Hymenoptera: Vespidae)", Behaviour, **102**, (1987), pp.147–167.
18. Gamboa, G. J., T. L. Wacker, J. A. Scope, T. J. Cornell and J. S. Reeve, "The mechanism of queen regulation of foraging by workers in paper wasps *Polistes fuscatus* (Hymenoptera: Vespidae)", Ethology, **85**, (1990), pp.335–343.

19. Chandrashekara, K. and R. Gadagkar, "Behavioural castes, dominance and division of labour in a primitively eusocial wasp", Ethology, **87**, (1991), pp.269–283.
20. Gadagkar, R. and N. V. Joshi, "Quantitative ethology of social wasps: time-activity budgets and caste differentiation in *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae)", Anim, Behav., **31**, (1983), pp.26–31.
21. Gadagkar, R. and N. V. Joshi, "Social organisation in the Indian wasp *Ropalidia cyathiformis* (Fab.) (Hymenoptera: Vespidae)", Z. Tierpsychol, **64**, (1984), pp.15–32.
22. Sokal, R. R. and F. J. Rohlf, "Biometry", W. H. Freeman and Company, New York, 1981, p.859.
23. Brothers, D. J. and C. D. Michener, "Interactions in colonies of primitively social bees. III. Ethometry of division of labour in *Lassioglossum zephyrum* (Hymenoptera: Halictidae)" , J. Comp. Physiol., **90**, (1974), pp.129–168.
24. Theraulaz, G., J. Gervet and S. S. Tian–Chanski, "Social regulation of foraging activities in *Polistes dominulus* Christ: A systematic approach to behavioural organization", Behaviour. **116**, (1991), pp.292–320.

★ ★ ★