Behavioral Ecology Vol. 6 No. 2: 117–123

Regulation of worker activity in a primitively eusocial wasp, *Ropalidia marginata*

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Ropalidia marginata, a tropical, primitively eusocial, polistine wasp, is unusual in that the queen (the sole egg-layer) is neither the most behaviorally dominant nor the most active individual in the colony. The queen by herself rarely ever initiates interactions toward her nest mates or unloads returning foragers. There are always a few workers in the colony who are more dominant and active than the queen. Absence of the queen from her colony does not affect colony maintenance activities such as foraging or brood care, but it always results in one individual becoming very aggressive and dominant. The dominant worker becomes the next queen if the original queen does not return. The queen does not appear to play any significant role in colony activity regulation. Instead, colony activities appear to be regulated by several mechanisms including dominance behavior toward foragers, feeding of larvae, and the unloading of returning foragers, all mediated by workers themselves. Regulation of colony maintenance appears to be based on direct evaluation of the needs of the colony by the workers themselves. The queen however has perfect reproductive control over all workers; workers never lay eggs in the presence of the queen. It appears therefore that the mechanisms involved in regulation of worker activity and worker reproduction are separate in *R. marginata.* These findings contrast with other primitively eusocial species where the queen acts as a "central pacemaker" and controls both worker activity and worker reproduction. *Key words:* colony regulation, dominance behavior, primitively eusocial wasp, queen control, queen signal, *Ropalidia marginata,* worker activity. *[Behav Ecol 6:117–123 (1995)]*

The eusocial insects, including ants, social bees and wasps, and termites can be distinguished by three common traits: cooperative brood care, reproductive division of labor, and overlap of generations (Michener, 1969, 1974; Wilson, 1971). Insect societies, often likened to multicellular organisms to emphasize their high level of social integration, have been called superorganisms (Moritz and Southwick, 1992; Wheeler, 1911; Wilson, 1968; Wilson and Sober, 1989). In all highly eusocial insects with a clear queen–worker dimorphism, the queen maintains her reproductive dominance through pheromonal control, leaving very little option open for workers to reproduce (Bourke, 1988; Ratnieks and Visscher, 1989). The coordination of activities in the honey bee for example does not appear to be under the queen's direct supervision; instead it seems to depend on the ability of the workers to circulate throughout the nest, gather information about the colony's needs, and adjust their activities according to the demands that they perceive (Camazine, 1993; Free, 1965; Huang and Robinson, 1992; Lindauer, 1967; Seeley, 1985, 1986, 1989a,b). It might well be, as Keller and Nonacs (1993) have persuasively argued, that rather than the queen controlling worker reproduction through the production of pheromones, the workers might themselves use the queen pheromone as a signal and be selected to opt out of reproductive competition with her. Nevertheless, the fact remains that the mechanisms bringing about reproductive competition and those bringing about colony activity regulation are quite different.

In the primitively eusocial insects, on the other hand, there are no distinct morphological castes. Workers often retain their capacity for direct reproduction, and thus have the flexibility to adopt different roles. This leads to more strife among nest mates for reproductive dominance. The most dominant individual is usually the principal egg-layer and is called the queen. In these groups, mechanisms underlying queen control of worker oviposition may be the same as, or intimately related to, those regulating worker activity (Reeve and Gamboa, 1983). The queen, the most behaviorally dominant individual, monopolizes egg-laying, and her overt dominance may retard or suppress ovarian development in the subordinates (Pardi, 1948; Pratte, 1989; for a review, see Röseler. 1991). In *Polistes fuscatus, Polistes metricus, Mischocyttarus labiatus,* and the primitively eusocial bee *Lasioglossum zephyrum,* the queen has also been shown to be the most active individual, initiating most of the interactions in her colony and regulating worker activity through her behavioral interactions with them. She has thus been considered to act as a "central pacemaker" (Breed and Gamboa, 1977; Brothers and Michener, 1974; Buckle, 1982; Dew, 1983; Gamboa et al., 1990; Litte, 1981; Reeve, 1991; Reeve and Gamboa, 1983, 1987).

Ropalidia marginata is an old-world tropical, primitively eusocial polistine wasp, widely distributed in peninsular India (Gadagkar, 1991). Earlier studies of this species have shown that the queen rarely takes part in behavioral interactions with workers, and is not the most behaviorally dominant individual, but is nevertheless the sole egg-layer in the colony (Chandrashekara and Gadagkar, 1991). The present study aims to investigate the mechanisms involved in coordinating worker activities such as foraging and brood care, and the role of the queen, if any, in regulating these in *R. marginata.*

METHODS

This study consisted of 13 experiments conducted between February 1991 and March 1992 on 12 post-emergence colo-

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Received 6 December 1993; revised 10 February 1994; accepted 25 February 1994.

nies of *R. marginata* (Lep.) (Hymenoptera: Vespidae) that were maintained in the vespiary at the Indian Institute of Science, Bangalore (13°00′ N, 77°32′ E). One nest alone was used for two experiments, with a gap of six months, by which time there was a complete turnover of all the individuals (including the queen) in the colony. The number of wasps in the colonies at the time of the experiment ranged from 9 to 29 (median = 18). The wasps from these colonies foraged both from natural sources and from feeding stations in the vespiary provided with an ad libitum supply of honey, *Corcyra cephalonica* (Lepidoptera: Galleridae) larvae, and water. Eight of the 12 nests used were naturally initiated in the vespiary, and the four others were transplanted from outside. All individuals in each colony were given unique color codes using quick drying paints, for individual identification.

Data collection

Each experiment consisted of observations over 3 days, 10 h each day, between 0800 h and 1800 h (except on the day of queen removal; see below). Sampling methods included instantaneous scanning and recording of all occurrences of selected behaviors (Altmann, 1974; Martin and Bateson, 1986). Instantaneous scans consisted of recording a "snap shot" of the behavioral state of each individual in the colony at predetermined instants of time. The "all occurrences" sessions consisted of recording all occurrences of dominance–subordinance interactions, nest maintenance activities, bringing food or building material, unloading, and feeding larvae by any wasp during an arbitrarily chosen 5-min period. For more details see Gadagkar and Joshi (1983, 1984). A total of 51 such scans and 51 "all occurrences" sessions were performed alternately in the 10-h period each day. The observations on the first day were on an undisturbed nest.

The queen (the sole egg-layer in the colony) was removed from her colony the next morning between 0500 and 0600 h and placed in a ventilated plastic jar provided with honey, water, and *Corcyra cephalonica* larvae. After the day's observation, she was returned to her nest late in the evening between 2000 h and 2100 h. The observations on the third day were thus again on the nest with the queen. In addition to this, observations were also made immediately after removal of the queen when only "all occurrences" of selected behaviors listed above were recorded continuously during the 2-h period.

Data analysis

In all the experiments, soon after the queen was removed from the nest, one of the workers became very aggressive and initiated a high frequency of interactions in the colony. This wasp will be called the "potential queen." The worker, other than the potential queen, that had the highest value for the activity under consideration will be referred to as the "max worker." Note that the max worker does not refer to the same individual for the same activity on each day or for different activities on the same day. For each activity the mean value for all workers including the max worker, but excluding the potential queen, was computed, and this value will be attributed to the "mean worker." An individual who was seen to bring either food or building material, at least once, was called a forager. The proportions of time spent in all common activities such as being present or absent on the nest were calculated from instantaneous scans. Hourly frequencies of the behaviors listed above were calculated from "all occurrences" sessions. The data from the first 2 h after queen removal were analyzed separately.

Frequencies of initiated interactions. The sum of the frequencies of dominance behaviors, unloading, soliciting, approaching, antennating, and allogrooming another wasp, yielded the frequency of initiated interactions. Frequencies of initiated interactions were computed separately for each individual after correcting for the proportion of time it spent on the nest. This was done separately for each day.

Frequencies of dominance behaviors. Although dominance behaviors were included in computing the frequencies of initiated interactions, because a wasp engaged in dominating another can be considered active, dominance behaviors also have other important connotations in a social insect colony. For this reason, frequencies of dominance behavior were also computed and analyzed separately, after correcting for the time spent by different individuals on the nest.

Measures of foraging. Absence from nest and frequency of leaving the nest could not be considered as measures of foraging, as in some earlier studies (Chandrashekara and Gadagkar, 1991, 1992; Gadagkar and Joshi, 1983, 1984; Reeve and Gamboa, 1983, 1987), because on the second day, after queen removal, many individuals that left the nest returned without food or building material. Therefore, rates of bringing food and building material to the colony were considered as measures of foraging activity. These were calculated for each of the three days separately.

Activity level. The proportion of time an individual remained active during the period she was present on the nest was termed her activity level. A wasp was considered active unless she was merely sitting, grooming herself, laying eggs, or passively receiving interactions from others.

Unloading. The act of receiving food from a forager immediately upon its return, by any individual, was defined as unloading.

Association values. The Yule's association coefficient (DeGhett, 1978) was computed as an index of coordination between the activities of the queen, potential queen, and the workers in an undisturbed colony. Yule's association coefficient between animals i and j is given by the formula $Y_{ij} = (ad - bc)/(ad + bc)$, where a is the probability that both animals i and j are active, b is the probability that animal i is active and j is inactive, c is the probability that animal i is inactive and j is active, and d is the probability that both animals are inactive. The values of this coefficient range from -1 to $+1$. A value of -1 would mean that there is no coordination between the activities of the two individuals while a value of $+1$ would indicate that the two wasps show maximum synchronization of their activities. For each individual in a colony, the mean of its association coefficient with every other individual was computed. The maximum of these means yielded the association value for the max worker, and the mean of all the mean values yielded the association value for the mean worker. The association values of the queens and potential queens thus represent their respective mean association values with all individuals in their colonies.

Activity level, unloading, and association values were calculated only for the first day because the disturbance caused by the aggressive potential queen on the second day resulted in many individuals leaving the nest frequently and staying away from the colony for long durations of time.

All statistical comparisons are by the two-tailed Wilcoxon matched-pairs signed-rank test, and all correlations are Kendall's rank correlations (Sokal and Rohlf, 1981).

RESULTS

Day 1: Undisturbed colony with the queen

Initiated interactions and dominance behavior. On day 1, the queens were neither the most behaviorally dominant nor the

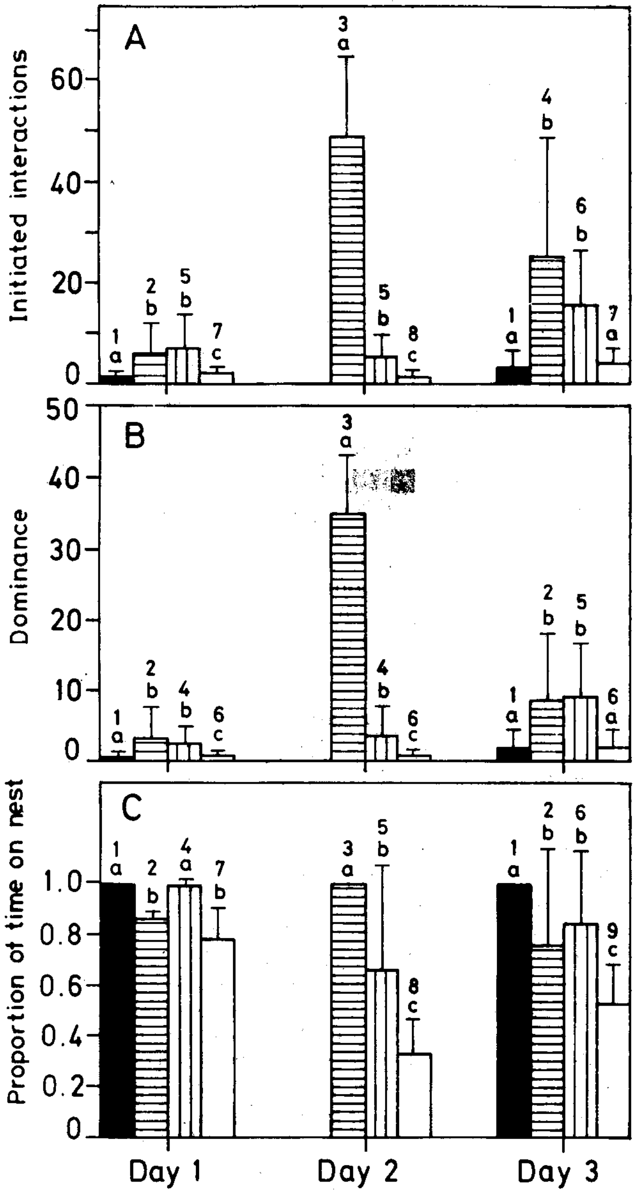

Figure 1
Frequencies per hour of initiated interactions (A), dominance (B), and proportion of time present on nest (C) shown by the queen (black bars), potential queen (horizontally marked bars), max worker (vertically marked bars) and mean worker (open bars) on days 1, 2, and 3. Bars that carry different letters are significantly different from each other ($p < .05$ or less) within each day; bars that carry different numbers are significantly different from each other ($p < .05$ or less) among the three days. Comparisons are by the two-tailed Wilcoxon matched-pairs signed-rank test.

most active individuals in their colonies. At least two individuals (the potential queen and max worker) in each colony showed higher frequencies of initiated interactions and dominance behavior than the queens. The frequencies of initiated interactions by the queen in her colony were significantly lower than the corresponding value for the potential queen ($p < .01$), max worker ($p < .025$), and mean worker ($p < .025$). The potential queen, on the other hand, showed significantly greater frequencies of initiated interactions as compared to the mean worker ($p < .05$), but was not significantly different from the max worker in this regard (Figure 1A). As in the case of initiated interactions, the queen showed a significantly lower frequency of dominance behavior than either the potential queen ($p < .025$), max worker ($p < .025$), or mean worker ($p < .05$). In 10 of the 13 colonies, at least one worker (including in some cases the potential queen) was seen to initiate dominance interactions toward the queen, and in five colonies, the queen initiated no dominance behavior. The frequency of dominance shown by the potential queen was not different from that shown by the max worker, but it was significantly greater than that of the mean worker ($p < .05$) (Figure 1B). The max worker was the same individual in 8 of the 13 colonies for both frequencies of initiated interactions and dominance behavior.

Activity level and association value. The activity level of the queen was significantly lower than that of the potential queen and max worker (both $p < .05$), but not significantly different from that of mean worker (Figure 2A). The mean association value of the queen was not different from that of the mean worker, whereas the potential queen had an association value significantly greater than that of the mean worker ($p < .01$). The association value of the max worker was significantly greater than that of the queen, potential queen, and mean worker ($p < .01$, $p < .025$, $p < .01$, respectively; Figure 2B).

Unloading and feed larva. The max workers and mean workers unloaded food from returning foragers at a higher frequency than the queens ($p < .005$ and $p < .025$, respectively; Figure 2C). But the potential queen did not differ significantly from the queen in this regard. The potential queens, max workers, and mean workers were seen to feed larvae at a significantly higher frequency than the queens ($p < .01$ for all, Figure 2D). In all colonies, the queens spent all their time on the nest. Potential queens spent 86.4% ± 13.3% of their time on the nest, and this was not significantly different from the corresponding value of 78.4% ± 9.5% for a mean worker.

Day 2: Colony without the queen

The transformation that took place in every colony when the queen was removed was striking. In a median time of 22 min (range 2–60 min) after queen removal, one individual—the potential queen—became very aggressive and initiated a series of dominance interactions toward her colony members. She dominated all others and continued to remain as aggressive for the entire period of the queen's absence. In these experiments, the queen was returned to her colony at the end of day 2. If this is not done, the potential queen invariably becomes the next queen (Chandrashekara and Gadagkar, 1992). The mean frequency of dominance shown by the potential queen within the first 2 h after queen removal was 58.1 ± 31.4/h ($n = 11$), as compared to only 7.7 ± 11.9/h shown by the next most dominant individual during the same period.

The potential queen contributed to 88.9% of the initiated interactions and 89.8% of the dominance behavior on day 2 as compared to 35.7% and 48.5% of these behaviors, respectively, on day 1. The frequency of dominance behavior of the potential queen on day 2 (34.9 ± 12.7) was tenfold greater than that shown by her on day 1 (3.35 ± 4.5) ($p < .001$, Figure 1A,B). The frequency of initiated interactions and dominance behavior shown by her was also significantly higher than that shown by either a max worker or a mean worker (both $p < .025$, Figure 1A,B). She never left the nest at all on this day, and this behavior was similar to that of the queen on the first and the third days. The proportion of time spent on the nest by a mean worker, however, decreased significantly on day 2 as compared to day 1 ($p < .005$, Figure 1C). That this decrease could be attributed to the significant increase in the dominance behavior of the potential queen was evident

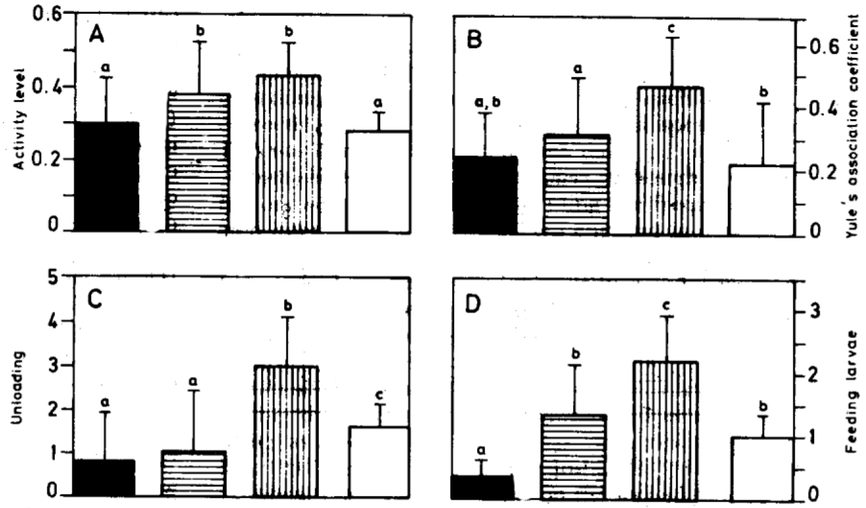

Figure 2
Activity level (A), Yule's association coefficient (B), frequencies per hour of unloading (C), and frequencies of feeding larvae (D) by the queen (black bars), potential queen (horizontally marked bars), max worker (vertically marked bars) and mean worker (open bars) on day 1. For each variable bars that carry different letters are significantly different from each other ($p < .05$ or less). Comparisons are by the two-tailed Wilcoxon matched-pairs signed-rank test.

from the almost invariable departure of individuals following a dominance encounter with the potential queen.

Reintroduction of the queen. As soon as the queen was returned to the nest, at the end of the second day's observation, she was always accepted without any behavioral dominance shown toward her. She too showed no dominance behavior toward her nest mates. The potential queen immediately quieted, walked away to the back of the nest, and approached the queen only from her rear. In eight colonies, the potential queen and a few other workers were observed to lick the queen on her abdomen, a short while after her return to the colony. This licking, best described as a mild mouthing on the queen's abdomen, more toward the posterior segments, was very different from allogrooming, usually shown toward other workers; the latter usually involved the grooming of only the wings and legs. In some colonies, the queen was licked even on the day following reintroduction.

Day 3: Colony after reintroduction of the queen

The behavior of all the colony members on the third day was not very different from what was observed on the first day. There was no significant difference, for example, in the frequency of initiated interactions (Figure 1A) or dominance behavior (Figure 1B) shown on days 1 and 3 by the queen or the mean worker. The frequency of initiated interactions and dominance behavior shown by the potential queen reduced significantly ($p < .01$, Figure 1A,B) from day 2 to day 3, although they were still significantly higher than that shown on day 1 ($p < .05$, Figure 1A,B). The percentage of dominance contributed by her in the colony reduced from 89.8% in the queen's absence to 41.2% when the queen was returned on the third day, and this was also not different from her contribution of 48.2% on the first day. The queen spent all her time on the nest as on day 1, while the potential queen spent a significantly smaller proportion of her time on the nest on day 3 (0.76 ± 0.14) as compared to day 2 (1.00), but not different from that on day 1 (0.86 ± 0.13) (Figure 1C). The proportion of time spent on the nest by the mean worker on the third day (0.53 ± 0.14) was significantly greater than that on the second day (0.33 ± 0.12; $p < .005$), but it was still significantly less than that on day 1 (0.78 ± 0.10; Figure 1C), suggesting that the workers had not completely recovered from the disturbance caused by queen removal.

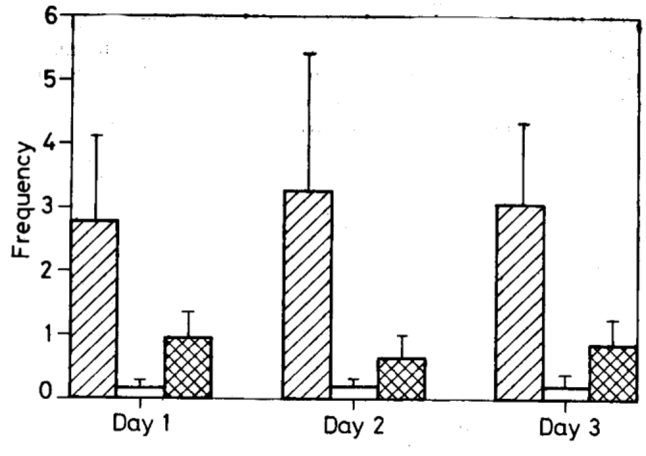

Figure 3
Frequencies per hour of total food brought (hatched bars), food brought per animal per hour (open bars) and feed larvae per animal per hour (cross-hatched bars) are all not significantly different among days 1, 2, and 3. Comparisons are by two-tailed Wilcoxon matched-pairs signed-rank test.

Foraging and brood care in the colony

Because foraging is an important activity in colony maintenance, we compared the rates of foraging over the three days to assess any change due to the queen's absence. The rates at which food was brought to the nests and the frequency of food brought per animal per hour were not significantly different between days 1, 2, and 3 (Figure 3). The total number of foragers on the 3 days (6.25 ± 2.34, 7.1 ± 3.15, and 6.67 ± 3.2) were also not significantly different, though all the foragers were not necessarily active in foraging on all 3 days. There was a significant positive correlation between the rates of foraging by different animals (those that were common to both days) on days 1 and 2 ($\tau = 0.358$, $p = .002$, $n = 38$). The relative contributions of these different individuals to the foraging activity of the nest on the 2 days ($\tau = 0.2645$, $p = .02$, $n = 38$; Figure 4A) were also positively correlated between the 2 days. Frequency of feed larva per animal per hour, a measure of brood care activity, was also not significantly different among the three days (Figure 3). The queen's absence therefore did not seem to affect these activities in the colony.

On the first day, the frequency of dominance received by the foragers (2.06 ± 3.99) was significantly greater than that received by nonforagers (0.85 ± 0.49; $p < .05$). The frequen-

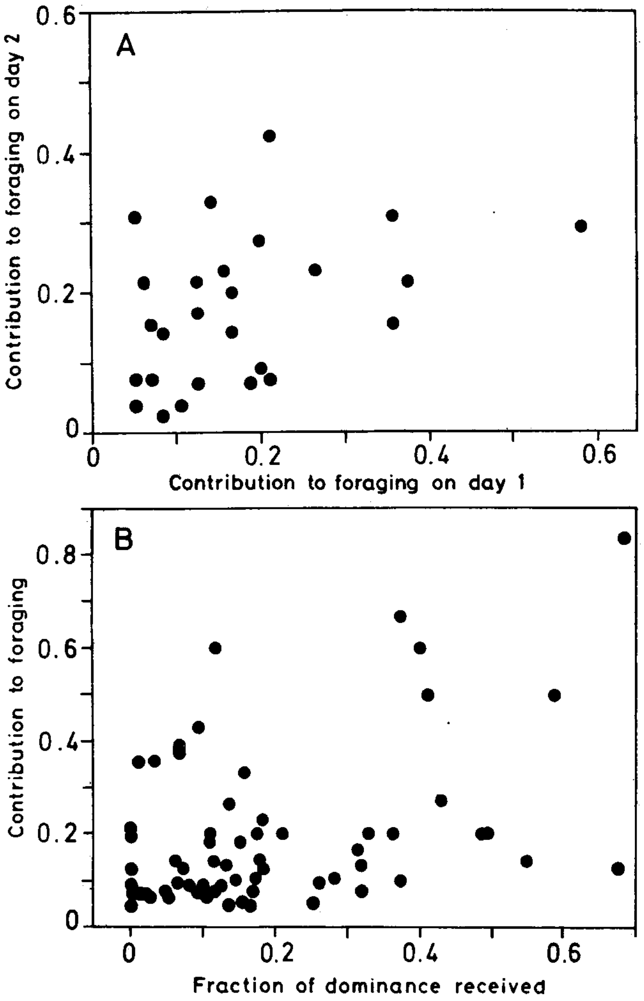

Figure 4
(A) Relative contribution to foraging in the colony by foragers on day 1 and day 2 are positively correlated (Kendall's $\tau = 0.2645$, $p < .02$, $n = 38$) (B) Contribution of food to the colony by a forager is positively correlated with the frequency of dominance she received in the colony on day 1 (Kendall's $\tau = 0.183$, $p = .03$, $n = 67$).

cy of dominance received by a forager was significantly correlated with her foraging rate ($\tau = 0.20$, $p = .02$, $n = 67$). The fraction of total dominance received by a forager in a colony and the proportion of total food contributed by her to the colony were also significantly positively correlated ($\tau = 0.18$, $p = .03$, $n = 67$; Figure 4B). The rate at which foragers were unloaded on day 2 (0.87 ± 0.72) was significantly less as compared to that on days 1 and 3 (3.6 ± 1.70 and 3.18 ± 1.70; $p < .001$, Figure 5A). Interestingly, a corresponding comparison of contribution to feed larva by foragers on the 3 days showed that it was significantly greater on the second day (0.73 ± 0.13) than on first and third days (0.42 ± 0.12 and 0.49 ± 0.23; $p < .001$, Figure 5B).

DISCUSSION

Previous studies on some primitively eusocial insects such as *Lasioglossum zephyrum* (Breed and Gamboa, 1977; Buckle, 1982), *Polistes metricus* (Dew, 1983), and *Polistes fuscatus* (Gamboa et al., 1990; Reeve and Gamboa, 1983, 1987) have shown that the queens in these species are the most active and dominant individuals in the colony, playing a pivotal role in colony activity regulation. Dominance initiated by queens in *P. fuscatus* colonies, for example, stimulates foraging by her nest mates (West-Eberhard, 1969). The aggression of the queen in these primitively eusocial species is therefore believed to play a dual function—prevention of worker reproduction and regulation of worker activity (Dew, 1983; Reeve and Gamboa, 1983, 1987). The results from observations of undisturbed colonies in the present study clearly showed that the queen in *R. marginata* is different from those of the species mentioned above. An earlier study on *R. marginata* (Chandrashekara and Gadagkar, 1991) had shown that the queen was neither the most dominant nor the most active individual in her colony. The present study further reveals that the queen shows lower frequencies of dominance and initiated interactions than many individuals in her colony. The potential queen, the max worker and even a mean worker were more dominant and initiated more interactions than the queen.

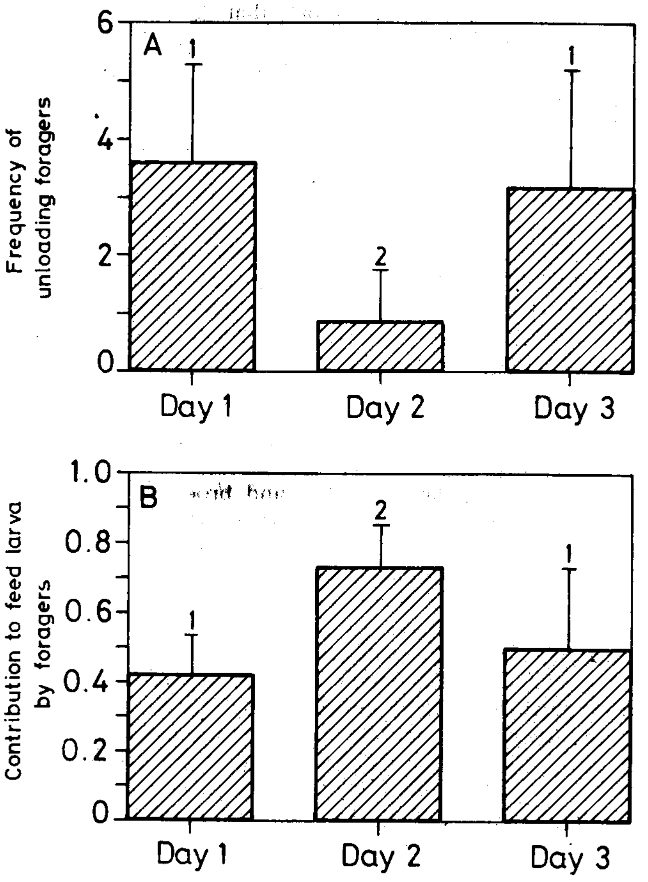

Figure 5
Frequencies at which foragers were unloaded (A) and proportion contributed by foragers to feeding of larvae (B) on days 1, 2, and 3. For each behavior, bars with different numbers are significantly different from each other. Comparisons are by the two-tailed Wilcoxon matched-pairs signed-rank test.

Initial unloading of food and other material brought to the nest has been considered as one form of behavioral control of foragers. In *P. metricus*, the queen has been shown to unload returning forgers significantly more often than her nest mates do (Dew, 1983). In *R. marginata*, on the contrary, the max worker or a mean worker performed this act significantly more often than did the queen. The queen was in fact rarely ever seen to unload returning foragers. These results also show that the potential queen, the max worker, and the mean worker fed larvae at significantly greater rates than the queen did. It seems unlikely, therefore, that the queen regulates worker activity behaviorally.

Removal of the queen from colonies of *P. fuscatus* results in a decrease in the rate of foraging in these colonies (Reeve and Gamboa, 1983, 1987). But in *R. marginata*, foraging and brood-care activities appeared to be unaffected by the queen's absence from her nest. Both the total frequency at which foragers brought food to their nests, and the food brought per animal per hour were not significantly different on the 3 days, and the active foragers in a normal nest continued to forage at nearly the same rate even in the queen's absence. The total number of individuals who foraged was also not different, although they were not always the same individuals on the 3 days. The frequency of feed larva per animal per hour did not differ significantly on the 3 days either. Hence the queen's absence from her colony for even as long as 10 h did not seem to affect the regulation of these essential colony activities.

Who then regulates foraging and brood care and how? They could be regulated through activities that indirectly communicate the colony's needs, its brood content, and larval hunger level to the foragers and other workers, or by activities that involve direct evaluation of the brood's requirements by the foragers themselves. In an undisturbed colony, foragers were seen to receive significantly more dominance than nonforagers, and those that were recipients of greater frequencies of dominance also contributed more food to the colony. Dominance, therefore, could be one of the mechanisms by which foraging is regulated. However, it was not the queen but a group of workers (often including the potential queen) who appeared to perform such regulation, as reflected in their initiation of higher frequencies of interactions and of dominance behavior shown towards the foragers.

Rate of unloading, or the waiting time before a forager is unloaded could be another important cue regulating forager activity, for this could directly depend on the level of satiety of the larvae. In honeybees, the waiting time experienced by a nectar-forager before being unloaded is a sensitive indicator of the colony's needs (Seeley, 1989a,b). In the present study, we observed that a decrease in the frequency of unloading of returning foragers in a disturbed colony, as compared to the normal colony, resulted in a corresponding increase in the contribution to feeding larvae by the foragers themselves. Foragers were thus able to adjust to the changed conditions in the colony. In the queen's absence, with fewer workers at any given time on the nest due to the dominance shown mainly by the potential queen, foragers that came back with food were not unloaded efficiently. This led to the foragers themselves feeding larvae, and thus possibly allowed them to directly evaluate the colony's requirements. Unloading by other individuals and feeding larvae by the foragers themselves thus appear to be coordinated activities that may compensate for each other, depending on the conditions in the colony. This idea is further strengthened by the fact that when the frequency of unloading once again increased on the third day, a corresponding decrease in contribution to feeding larvae by foragers followed. Dominance behavior and unloading could be important in regulating forager activity in an undisturbed colony as a means of communication between workers who feed larvae and foragers who bring food to the colony. On day 2, however, the dominance in the colony was almost completely restricted to the potential queen and worker–worker interactions were negligible. But the foragers fed larvae significantly more on this day than on the first day. This could account for the similar amount of food brought on this day as well. Thus, worker–worker interactions such as dominance and unloading of foragers, or individual activities such as feeding larvae by foragers themselves, could together regulate foraging and other important colony activities.

One important feature that emerges from this study is that workers in *R. marginata* colonies interact with each other and with larvae at a significantly higher rate than a 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. An awareness of the needs of the colony is an important requisite in either recruiting foragers (in species such as honeybees where recruitment occurs) or for a forager to regulate its own activity. Theraulaz et al. (1991) have shown that in colonies of *P. dominulus* the closeness of the relationship with the brood was an important factor for an individual to switch to the task of foraging.

Removal or loss of the queen from colonies of *P. exclamans* (Strassmann and Meyer, 1983), *P. instabilis* (Hughes and Strassmann, 1988), and *P. fuscatus* (Reeve and Gamboa, 1983, 1987) did not seem to result in the immediate increase of dominance behavior of a single individual. In *R. marginata*, however, it resulted in one worker—the potential queen—becoming extremely dominant in a very short period of time. She exercised complete dominance over all other females while dominance interactions among subordinates (other workers) remained rare.

The frequency of dominance behavior of the potential queen during the queen's absence was significantly higher than it was in the queen's presence. Such a marked change in the behavior of the potential queen could be due to the removal of some inhibitory chemical cues associated with the queen (unpublished results from preliminary experiments), but note that the queen did not lose her status despite her absence for more than 14 h from her nest; she was accepted back without any aggression in all the experiments. Licking of queens by workers, often including the potential queen, observed immediately on her reintroduction at the end of the second day, appears to be similar to what has been reported in some highly eusocial Vespinae. In *Vespa orientalis*, workers have been reported to lick the body of the queen especially on the head (Ishay and Schwartz, 1965), whereas *Vespa crabro* workers lick the queen in the abdominal region (Ishay et al., 1970) This behavior may function either in the transfer of some chemical (Ishay, 1981; Ishay and Schwartz, 1965; Matsuura, 1984) or in queen-recognition (West-Eberhard, 1977) in the Vespinae. In *P. fuscatus*, chemical cues originating from both head and ovaries have been shown to communicate status, but not to play a role in control of worker activity (Downing and Jeanne, 1985). Involvement of such direct chemical cues in maintenance of reproductive dominance by the queen cannot be ruled out for *R. marginata*. The rarity of direct behavioral dominance by the queen in an undisturbed colony, the acceptance of the queen almost immediately on her return and without any overt behavior on her part, and the subsequent licking of her abdomen by workers, all suggest a mechanism of reproductive control that is indirect and does not require overt behavioral dominance.

R. marginata colonies are functionally monogynous. Without exception a single individual completely suppresses egg-laying by all her nest mates, although she may be replaced by another individual who then becomes the sole egg-layer until she, in turn, is replaced (Gadagkar et al., 1993). Removal of the queen did not lead to any significant change in colony maintenance activities by the workers. This always resulted in one individual becoming aggressive and eventually taking over as the next queen (Chandrashekara and Gadagkar, 1992). It appears therefore that the mechanisms involved in regulation of worker reproduction and worker activity are separate in *R. marginata*. The mechanism of regulation of colony maintenance activities such as foraging and brood-care appears to involve worker–worker interactions as well as direct evaluation of the colony's needs by the workers themselves. No single individual (including the queen or the potential queen) appears to be responsible for the regulation of these activities. A group of active and dominant workers thus contribute to a greater extent to these regulatory interactions, rather than a single "central pacemaker," as has been described for other primitively eusocial bees and wasps.

This work was supported by grants from the Council for Scientific and Industrial Research and the Ministry of Environment and Forests, Government of India. We thank R.L. Jeanne, N.V. Joshi, W. Fortelius, and an anonymous reviewer for their critical comments.

REFERENCES

Altmann J, 1974. Observational study of behavior: sampling methods. Behavior 49:227–267.

Bourke AFG, 1988. Worker reproduction in the higher eusocial Hymenoptera. Q Rev Biol 63:291–311.

Breed MD, Gamboa GJ, 1977. Behavioral control of workers by queens in primitively eusocial bees. Science 195:694–696.

Brothers DJ, Michener CD, 1974. Interactions in colonies of primitively eusocial bees. III. Ethometry of division of labour in *Lasioglossum zephyrum* (Hymenoptera: Halictidae). J Comp Physiol 90:129–168.

Buckle GR, 1982. Queen-worker behavior and nestmate interactions in young colonies of *Lasioglossum zephyrum*. Insectes Soc 29:125–137.

Camazine S, 1993. The regulation of pollen foraging by honey bees: how foragers assess the colony's need for pollen. Behav Ecol Sociobiol 32:265–272.

Chandrashekara K, Gadagkar R, 1991. Behavioural castes, dominance and division of labour in a primitively eusocial wasp. Ethology 87: 269–283.

Chandrashekara K, Gadagkar R, 1992. Queen succession in the primitively eusocial tropical wasp *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). J Insect Behav 5:193–209.

DeGhett VJ, 1978. Hierarchical cluster analysis. In: Quantitative ethology (Colgan PW, ed). New York: Wiley; 115.

Dew HE, 1983. Division of labour and queen influence in laboratory colonies of *Polistes metricus* (Hymenoptera: Vespidae). Z Tierpsychol 61:127–140.

Downing HA, Jeanne RL, 1985. Communication of status in the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). Z Tierpsychol 67:78–96.

Free JB, 1965. The allocation of duties among worker honey bees. Symp Zool Soc Lond 14:39–59.

Gadagkar R, 1991. *Belonogaster, Mischocyttarus, Parapolybia* and independent founding *Ropalidia*. In: The social biology of wasps (Ross KG, Mathews RW, eds). Ithaca, New York: Cornell University Press; 149–187.

Gadagkar R, Chandrashekara K, Chandran S, Bhagavan S, 1993. Serial polygyny in a primitively eusocial wasp: implications for the evolution of sociality. In: Queen number and sociality in insects (Keller L, ed). Oxford: Oxford University Press; 187–214.

Gadagkar R, Joshi NV, 1983. Quantitative ethology of social wasps: time-activity budgets and caste differentiation in *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). Anim Behav 31:26–31.

Gadagkar R, Joshi NV, 1984. Social organization in the Indian wasp *Ropalidia cyathiformis* (Fab.) (Hymenoptera: Vespidae). Z Tierpsychol 64:15–32.

Gamboa GJ, Wacker TL, Scope JA, Cornell ThJ, Shellman-Reeve J, 1990. The mechanism of queen regulation of foraging by workers in paper wasps (*Polistes fuscatus*, Hymenoptera: Vespidae). Ethology 85:335–343.

Huang Z-Y, Robinson GE, 1992. Honey bee colony integration: worker-worker interactions mediate hormonally regulated plasticity in division of labor. Proc Natl Acad Sci USA 89:11726–11729.

Hughes CR, Strassmann JE, 1988. Age is more important than size in determining dominance among workers in the primitively eusocial wasp, *Polistes instabilis*. Behaviour 107:1–15.

Ishay J, 1981. On the filial attachment phenomenon in colonies of the oriental hornet, *Vespa orientalis* (Hymenoptera: Vespidae). Entomol Gen 7:167–174.

Ishay J, Gitter S, Schaudinischky L, Schwartz A, 1970. Cybernetic processes between adults and larvae of the oriental hornet *Vespa orientalis*. Int Congr Cybern Namur 1–16.

Ishay J, Schwartz J, 1965. On the nature of the sounds produced within the nest of the oriental hornet, *Vespa orientalis* F. Insectes Soc 12: 383–387.

Keller L, Nonacs P, 1993. The role of queen pheromones in social insects: queen control or queen signal? Anim Behav 45:787–794.

Lindauer M, 1967. Communication among social bees. New York: Atheneum.

Litte M, 1981. Social biology of the Polistine wasp *Mischocyttarus labiatus*: survival in a Colombian rain forest. Smithson Contrib Zool 327: 1–27.

Martin P, Bateson P, 1986. Measuring behaviour: an introductory guide. Cambridge: Cambridge University Press.

Matsuura M, 1984. Comparative biology of the five Japanese species of the genus *Vespa* (Hymenoptera, Vespidae). Bull Fac Agric Mie Univ 69:1–131.

Michener CD, 1969. Comparative social behaviour of bees. Annu Rev Entomol 14:299–342.

Michener CD, 1974. The social behavior of bees. Cambridge: Harvard University Press.

Moritz RFA, Southwick EE, 1992. Bees as superorganisms: an evolutionary reality. Berlin: Springer-Verlag.

Pardi L, 1948. Dominance order in *Polistes* wasps. Physiol Zool 21:1–13.

Pratte M, 1989. Foundress association in the paper wasp *Polistes dominulus* Christ. (Hymen. Vesp.): effect of dominance hierarchy on the division of labour. Behaviour 111:208–219.

Ratnieks FLW, Visscher PK, 1989. Worker policing in honeybees. Nature 342:796–797.

Reeve HK, 1991. *Polistes*. In: The social biology of wasps (Ross KG, Matthews RW, eds). Ithaca, New York: Cornell University Press; 99–148.

Reeve HK, Gamboa GJ, 1983. Colony activity integration in primitively eusocial wasps: the role of the queen (*Polistes fuscatus*, Hymenoptera: Vespidae). Behav Ecol Sociobiol 13:63–74.

Reeve HK, Gamboa GJ, 1987. Queen regulation of worker foraging in paper wasps: a social feedback control system (*Polistes fuscatus*, Hymenoptera: Vespidae). Behaviour 102:147–167.

Röseler P-F, 1991. Reproductive competition during colony establishment. In: The social biology of wasps (Ross KG, Matthews RW, eds). Ithaca, New York: Cornell University Press; 309–335.

Seeley TD, 1985. Honeybee ecology. Princeton, New Jersey: Princeton University Press.

Seeley TD, 1986. Social foraging by honey bees: how colonies allocate foragers among patches of flowers. Behav Ecol Sociobiol 19:343–354.

Seeley TD, 1989a. Social foraging in honey bees: how nectar foragers assess their colony's nutritional status. Behav Ecol Sociobiol 24:181–199.

Seeley TD, 1989b. The honey bee colony as a superorganism. Am Sci 77:546–553.

Sokal RR, Rohlf FJ, 1981. Biometry, 2nd ed. New York: Freeman.

Strassmann JE, Meyer DC, 1983. Gerontocracy in the social wasp *Polistes exclamans*. Anim Behav 31:431–438.

Theraulaz G, Gervet J, Tian-Chanski SS, 1991. Social regulation of foraging activities in *Polistes dominulus* Christ: a systematic approach to behavioural organization. Behaviour 116:292–320.

West-Eberhard MJ, 1969. The social biology of Polistine wasps. Misc Publ Mus Zool Univ Mich 140:1–101.

West-Eberhard MJ, 1977. The establishment of reproductive dominance in social wasp colonies. Proceedings of the 8th International Congress of the International Union for the Study of Social Insects; 223–227.

Wheeler WM, 1911. The ant-colony as an organism. J Morphol 22:307–325.

Wilson DS, Sober E, 1989. Reviving the superorganism. J Theor Biol 136:337–356.

Wilson EO, 1968. The superorganism concept and beyond. In: L'effet de groupe chez les animalia (Chauvin L, ed). Paris: NRS; 27–39.

Wilson EO, 1971. The insect societies. Cambridge: Harvard University Press.