



The queen is not a pacemaker in the small-colony wasps *Polistes instabilis* and *P. dominulus*

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(Received 12 April 2005; initial acceptance 19 August 2005;
final acceptance 4 November 2005; published online 20 March 2006; MS. number: A10129)

How work is organized varies in social insect colonies. Some investigators have argued that the queen plays an active role in regulating worker activity in species with small, simple colonies, but that work is self-organized in species with large, complex colonies. Here, we present data that suggest that two species of paper wasps do not fit this pattern. *Polistes* wasps are traditionally classified as primitively eusocial wasps, showing characteristics of simple insect societies, such as small colony sizes, lack of queen–worker dimorphism, and queen control of both reproduction and worker activity. Colony activity in *Polistes* is episodic; quiet periods are followed by periods of intense activity when most wasps in the colony are active. We tested whether queens in *P. instabilis* and *P. dominulus* controlled work by initiating active periods, goading workers into activity. Instead, we found that colony activity was initiated by the behaviours of workers arriving at the colony, walking across the nest face or, less commonly, antennating, leaving or gaster wagging. Queens initiated no more activity periods than the average worker. Furthermore, activity levels in colonies of *P. dominulus* in which the queen was removed did not differ significantly from activity levels in colonies with queens. *Polistes instabilis* and *P. dominulus* colonies showed characteristics of primitively eusocial insect societies, but also showed worker initiation of colony activity, suggesting that these two species represent examples of an intermediate level of colony organization in which queens control reproduction but do not control the organization of work.

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Bourke (1999), building on syntheses by Wilson (1971) and Alexander et al. (1991), argued that colony size is a critical variable for understanding the organization of social insect societies. Broadly speaking, species with small colonies have simpler colony organization. For example, species with smaller colony sizes have shorter colony life spans and less complex communication. They also lack morphological caste differentiation; thus, the queen physically suppresses reproduction of other colony members. As colony size increases, the more numerous workers can win conflicts with the queen, but the queen's reproductive dominance may actually increase because it no longer requires physical superiority, but instead depends on the acquiescence of workers, or even on the active repression of workers by other workers. Although there

may be exceptions to these kinds of trends, they do help to structure our thinking about how social insect colonies evolve.

Part of the reason for these differences in colony organization is that, as colony size increases, workers experience a decrease in opportunity to act as a reproductive replacement, so they evolve reduced competition for direct reproduction and increased commitment to colony function (Alexander et al. 1991; Bourke 1999). These two types of societies differ in how selection acts at group and individual levels. Small colonies are fraught with conflict, which can often be won by the dominant queen, but in large-colony species, the collective interests of the workers are more likely to be met (e.g. Arévalo et al. 1998; Hastings et al. 1998).

Other research (reviewed in Jeanne 2003) suggests that the organization of work in colonies adds another dimension to this picture. In simple societies, the queen may use physical dominance not only to suppress worker reproduction, but also to coordinate work, goading the

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sometimes reluctant workers to forage, build, feed brood and otherwise tend to the colony (Breed & Gamboa 1977; Strassmann 1981; Dew 1983; Reeve & Gamboa 1983, 1987; Bonabeau et al. 1997). Because the colony is small enough for one individual to accurately monitor, and because there are relatively few workers to dominate, the queen may evolve to function as a central pacemaker and coordinator of colony activities (Reeve & Gamboa 1983, 1987).

In larger colonies, the queen becomes less able to monitor all the colony's needs and less able to physically dominate all the workers. Work in large-colony social insect societies is viewed as essentially self-organized; there is little central control and each worker responds to local information from the nest or other workers in a manner that meets the needs of the colony (Herman et al. 2000; Anderson & McShea 2001; Jeanne 2003).

In the polistine wasps, this distinction seems fairly clear (Jeanne 2003). In large complex wasp societies, the queens typically do not physically stimulate worker activity (Jeanne 2003). Colonies of the swarm-founding wasp, *Parachartergus colobopterus*, typically have hundreds of workers, and queens are rarely involved in interactions and do not regulate worker activity (Herman et al. 2000). In another such species, *Polybia occidentalis*, work is highly specialized, with workers focusing on gathering either food or nest material, and patterns appear to emerge via self-organization (O'Donnell & Jeanne 1990; Jeanne 2003).

Reeve & Gamboa (1983, 1987) argued that the queen directs worker activity in the small-colony paper wasp, *Polistes fuscatus*, in part because queens are involved in more interactions than any other wasp in the colony. Reeve & Gamboa also monitored worker foraging rates right after queen removal or cooling, and they found that worker foraging levels decreased after the treatment; however, they also found that worker activity did not covary with queen interaction rate and that queens did not directly induce workers to forage. They suggested that worker activity level is 'temporally coupled' with the level of queen activity, and that in the absence of the queen (or 'pacemaker of the colony'), worker activity diminishes.

We revisited the question of how work is organized in *Polistes* paper wasps. We chose *Polistes* because of past work (Reeve & Gamboa 1983, 1987) and because it is a classic example of a simple society. Colonies are usually begun by one or a few singly mated queens. There is no caste differentiation between workers and queens, and in some species, active foragers even replace lost queens (Strassmann & Meyer 1983). The queen is clearly active in dominance interactions, preserving her role as primary egg layer in the colony by fighting, threatening the other workers and egg eating (Pardi 1948; West-Eberhard 1969; Strassmann 1981). The queen's interests often override worker interests, in contrast to related large-colony swarm-founding species (Arévalo et al. 1998; Hastings et al. 1998; Strassmann et al. 2003).

Activity in *Polistes* colonies is episodic, occurring in bursts (Reeve & Gamboa 1983; personal observations). Wasps in *Polistes* colonies often spend more than half of the daylight hours inactive (Reeve & Gamboa 1983). During periods of colony inactivity, wasps on the nest

remain immobile until something abruptly triggers all or nearly all the wasps on the nest to become active. During the activity periods, workers feed larvae, build on the nest, interact aggressively and leave the nest to forage. Thus, the initiation of such activity bursts must be an important determinant of colony activity. Specifically, one can test whether it is the queen or the workers that are responsible for stimulating such bursts. It is this behaviour that we investigated in *Polistes instabilis* and *P. dominulus*.

METHODS

To investigate whether queens or workers initiate activity, we observed 10 colonies of *P. instabilis* and 16 colonies of *P. dominulus*. We studied *P. instabilis* in subtropical McAllen, Texas, U.S.A. (26°14'N, 98°13'W) and *P. dominulus* in temperate Cavriglia, Italy (43°51'N, 11°48'W). In *P. instabilis*, nests are founded in March and sometimes continue to the next year, although most wasps leave their nests in October (Hughes & Strassmann 1988). *Polistes dominulus* nests are founded in mid-April and end in October, although brood rearing may end much earlier (Pardi 1942, 1946). We located *P. instabilis* nests on house eaves and located *P. dominulus* nests in 12-cm diameter plastic tubes that protected saplings in a reforestation area. We observed *P. instabilis* colonies between 17 and 20 April 1995 and used the 10 colonies for which we had the clearest video of colony interactions. For *P. dominulus*, we observed two colonies during 12–13 June 1997 and 14 colonies during 12–22 June 1999.

Before dawn, we marked all or nearly all of the wasps on both *P. instabilis* and *P. dominulus* nests with a unique colour pattern using Testor's PLA enamel (Rockford, Illinois, U.S.A.). We videotaped each colony between 1000 and 1700 hours using Sony Hi8 camcorders and Hi8 evaporated metal particle videotape. For *P. instabilis*, we analysed 42.2 daytime hours of videotape, during which 366 activity-initiating interactions occurred across all nests. For *P. dominulus*, we analysed 29 h of videotape, during which 220 activity-initiating interactions occurred across all nests. We analysed approximately 4 h per colony of *P. instabilis* and 2 h per colony for *P. dominulus*. After we completed videotaping, we collected the nests and associated wasps.

We videotaped *P. instabilis* colonies of varying ages, including one pre-emergent colony, five young post-emergent colonies, and four older colonies from the previous year that had several generations of adults. The 10 nests had 34–268 cells and 6–27 adult wasps. Seven of the colonies had only one queen, two colonies (Colonies 5 and 14) had two and four queens, respectively, and one colony (Colony 12) had no queen, as determined by ovarian development and insemination status. All *P. dominulus* colonies analysed were at the same stage of the colony cycle, with workers having emerged recently. The 16 nests analysed had 77–237 cells and 8–43 adults. All colonies initially had only one queen; 24 h before videotaping, we removed the queen from five colonies.

We analysed the videotape for each nest by documenting the identity of the wasp and the action that initiated activity after a period of inactivity. To obtain data on the

organization of work and to avoid bias from the inclusion of behaviours specifically associated with reproductive dominance, we recorded all activities that specifically initiated colony activity, regardless of reproductive role. The observers recording colony interactions did not know whether individuals were queens or workers when they analysed the videotapes. We considered pauses in activity of more than 10 s as periods of colony inactivity, although periods of inactivity were often much longer. A colony was considered inactive if no wasps were moving. If a single wasp was moving slightly, we included this as an inactive period. Periods of inactivity continued until a wasp performed an abrupt action that triggered resumption of activity by all wasps on the nest. Five distinct types of actions initiated generalized activity in colonies of *P. instabilis* and *P. dominulus*: antennating, arriving, leaving, walking and gaster wagging. Fanning also initiated activity only on *P. instabilis* nests, and feeding a larva initiated activity only on *P. dominulus* nests.

Antennations occur when one wasp touches her antennae to the body of another wasp, usually around the head. We designated the wasp that moved first as the individual initiating the antennation. ‘Arriving’ describes the return of a wasp to the nest. ‘Leaving’ involves the departure of a wasp from the nest. The wasp always leaves by flight, and a quick walk usually precedes the take-off (Strassmann 1981). ‘Walking’ describes the action of a wasp simply moving across the nest face, often feeding larvae or checking the contents of brood cells in the process. ‘Gaster wagging’ describes the action of a wasp vibrating her gaster from side to side as she walks across the nest. In *P. instabilis* and *P. dominulus*, gaster wagging is associated with dominance (Strassmann 1981; Hughes & Strassmann 1988). However, in *Polistes* species of the subgenus *Fuscopolistes*, this behaviour may be associated with the release of pheromones involved in adult–larvae communication (Gamboa & Dew 1981; Downing & Jeanne 1985). ‘Fanning’ occurs when a wasp vigorously beats her wings while standing still on the nest. This action cools the nest by facilitating evaporation of water that has been deposited on the cell walls (Strassmann 1981). ‘Feeding larvae’ describes the action of a wasp lowering her head into one of the cells and then pulling it back out, and could include larval trophallaxis.

We also evaluated worker departures from three nests of each species to determine whether they were caused by the queen. We evaluated worker departures because we hypothesized that if worker arrivals initiated activity, then queens might be indirectly stimulating colony activity by their prior inducement of workers to leave. Thus, activity initiation could be caused directly by a worker’s return and indirectly by the queen.

After videotaping was completed, we dissected all individuals to determine whether they were workers or queens. We categorized a female as a queen if she had sperm in her spermatheca and she had developed ovaries. Queens had substantial numbers of mature or nearly mature eggs in their ovaries (*P. instabilis*: mean \pm SD = 21 ± 12.6 eggs, $N = 13$; *P. dominulus*: 14 ± 6.6 eggs, $N = 13$), and workers seldom had any eggs in their ovaries (*P. instabilis*: 0.12 ± 0.78 eggs, $N = 101$; *P. dominulus*:

0.7 ± 1.8 eggs, $N = 228$). The dissection data for three of the 16 *P. dominulus* colonies were incomplete and could not be used for this analysis.

We examined the roles of queens and workers in initiating activity after quiescence in five ways. First, for both species, we evaluated whether queens initiated more activity bursts than would be expected if activity initiation was equally distributed among all wasps. This analysis was done by fitting a logistic regression model with a binomial error structure (Hosmer & Lemeshow 1989) to the observed proportion of activity bursts initiated by queens using the proportion of queens as the independent variable. The probability that i activity bursts are initiated by a queen given N bursts of activity are observed can be calculated as follows:

$$P(i|N) = \binom{N}{i} q^i (1-q)^{N-i} \quad (1)$$

where q is the probability that a burst is queen initiated. In this equation we set $q = f^b$, where f is the proportion of queens among all wasps and b is a positive constant. If a queen and a worker have the same likelihood of initiating activity, q will be equal to f , and consequently $b = 1$. Generally, q will be a function of f , which can be modelled by means of the logistic relationship

$$q = \frac{e^{\beta_0 + \beta_1 f}}{1 + e^{\beta_0 + \beta_1 f}} \quad (2)$$

where β_0 and β_1 are the regression line estimates for the intercept and proportion of queens (f), respectively. For each species we fitted the logistic model to the data by applying the PROC GENMOD procedure in SAS version 8.1 (SAS Institute 1994), and the resulting regression line was plotted with the expected line $q = f$ in a figure showing the association of the proportion of queens among all wasps and the proportion of bursts that were initiated by a queen. If the resulting regression line included the expected line $q = f$ within its 95% confidence envelope, we could not reject the null hypothesis that a queen and a worker had equal probabilities of initiating activity on the nest. Alternatively, if the regression line was significantly above or below the expected line, this would indicate that a queen had a higher or lower likelihood, respectively, than a worker of initiating an activity burst.

Second, we estimated the overall proportion of bursts that were initiated by queens and workers, respectively, to see which class initiated more total activity bursts. Third, we examined which specific behaviours initiated activity on the nests, and whether queens and workers differed in the frequency distribution of these behaviours. The number of observations of some trigger actions on specific nests was low, so we applied the exact G test (Goudet et al. 1996) in all comparisons of the frequency of behaviours using 15 000 randomizations of the data. Fourth, we investigated whether workers left the nest following contact with the queen, because worker–queen contact may subsequently induce worker activity upon their return to the nest. Finally, we compared the average pause length and total time paused for *P. dominulus* nests that had queens and for *P. dominulus* nests from which the queen had

been removed experimentally. For statistical analyses, all proportional data were arcsine square-root transformed to normalize their distributions.

RESULTS

Queens Did Not Initiate Activity Bursts

On average, *P. instabilis* colonies were inactive 60% of the time, and had an average of eight periods of inactivity per hour. These periods of inactivity had an average duration of 4.04 min. *Polistes dominulus* colonies were inactive only 15% of the time, with an average of eight pauses per hour and an average pause duration of 1.08 min.

For each species, the association of the proportion of queens in the colony and the proportion of activity bursts initiated by a queen is shown with the logistic regression line that best fit the observations (Fig. 1). Our null hypothesis was that a queen and a worker would have equal probabilities of initiating activity on the nest, implying that the proportion of queen-initiated activity is expected to be equal to the proportion of queens among all wasps.

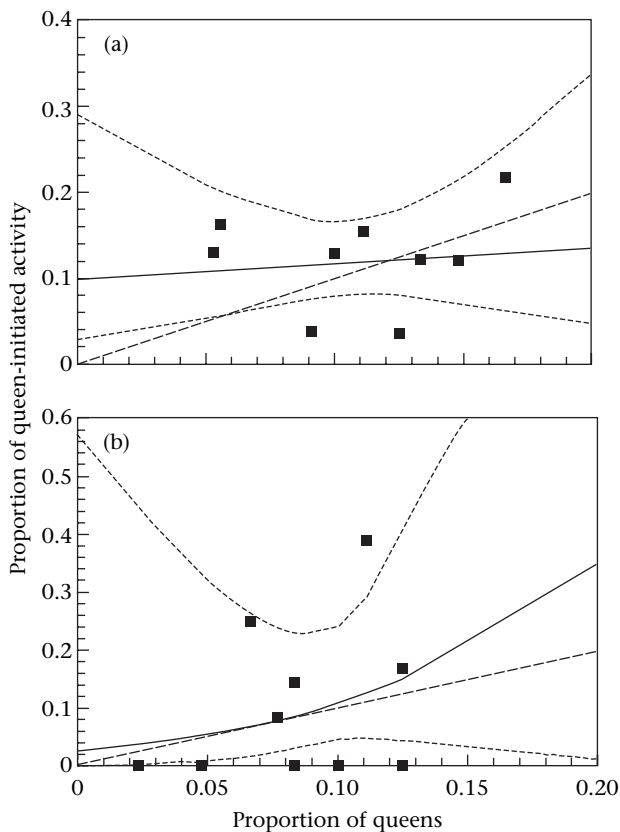


Figure 1. Association between the proportion of queens in the colony and the proportion of activity bursts initiated by a queen (■) for (a) *P. instabilis* and (b) *P. dominulus*. Solid lines: regression lines for the logistic models that best fit the data (*P. instabilis*: intercept $\beta_0 = 1.79$, proportion of queens $\beta_1 = -2.21$; *P. dominulus*: $\beta_0 = 14.9$, $\beta_1 = -3.61$). Dotted lines: 95% confidence limits. Dashed lines: expected association if the proportion of activity initiated by queens and workers, respectively, is equal to their proportions in the colony (slope = 1).

The regression line was not significantly different from that expected (slope = 1) within the range of observed queen proportions for either species, so queens did not initiate significantly more or fewer bursts of activity than expected based on their proportion in the colony.

There was no significant difference in per capita initiation of activity, and there were far more workers than queens, implying that most activity bursts were initiated by workers (Fig. 2). The overall percentage of worker-initiated activity bursts was approximately 88% (95% confidence interval based on binomial probabilities: 84–92%) in *P. instabilis* colonies and 90% (84–94%) in *P. dominulus* colonies, which closely match the workers' representation among all wasps in colonies of each species (89 and 94%, respectively).

Workers Initiated Activity Bursts By Walking or Arriving

The frequency distribution of specific behaviours that initiated activity varied significantly between colonies of the same species (*P. instabilis*: $N = 10$, $P < 0.0001$; *P. dominulus*: $N = 16$, $P = 0.0025$). However, in all but one colony, workers arriving and walking were the most common actions to initiate activity, accounting for, on

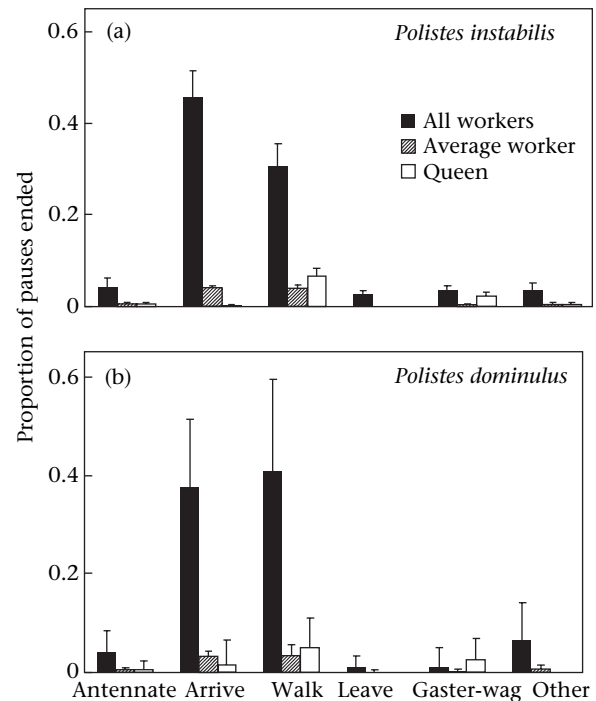


Figure 2. Mean \pm SE proportion of activity bursts initiated by specific behaviours performed by all workers, the average worker and the queen in (a) *P. instabilis* nests ($N = 9$) and (b) *P. dominulus* nests ($N = 11$) where at least one queen was present. For *P. instabilis*, in the two nests with multiple queens, we used the proportion of pauses ended by the most active queen. For nests of both species, we calculated the proportion of activity bursts initiated by the average worker as the proportion initiated by all workers divided by the total number of workers on the nest. The action 'other' denotes fanning in *P. instabilis* and feeding larvae in *P. dominulus*.

average, 83% and 82% of initiated activity following pauses across nests in *P. instabilis* and *P. dominulus*, respectively (Fig. 2). In *P. instabilis*, the relative frequency of trigger actions by the queen(s) was significantly different from that of the average workers of the same colony ($N = 9$, $P = 0.0062$), apparently because queens rarely initiated activity by arriving (data analysed without arrivals: $P = 0.54$; Fig. 2). There was no significant difference in the frequency of trigger actions performed by queens and workers in *P. dominulus* colonies ($N = 5$, $P = 0.20$; Fig. 2).

Queens Did Not Induce Workers To Leave

Of 109 worker departures ($N = 3$ nests each of *P. instabilis* and *P. dominulus*) when the queen was present in the colony, only five departures (4.6%) followed an interaction with the queen. Thus, queens did not directly instigate worker foraging trips at any significant frequency.

Activity Was Not Lower in Experimentally Queenless Colonies

On five of the 16 *P. dominulus* nests that we observed, we removed the queen before videorecording. There was no significant difference between nests that had queens and nests from which the queen had been removed in total time spent inactive (two-tailed t test: $t_{14} = 1.57$, $P = 0.20$) or average pause duration ($t_{14} = 0.92$, $P = 0.457$; Fig. 3). Indeed, the trends were in the opposite direction than that predicted by the hypothesis of queen activation.

DISCUSSION

If the queen is the central pacemaker of the colony, she should be integral to the initiation of the episodic bursts of activity that characterize *Polistes* colonies. We found that, in both *P. instabilis* and *P. dominulus*, queens did not differ from workers in per capita initiation of activity bursts. Because there are fewer queens than workers, this means that significantly fewer total activity bursts are initiated by queens. These findings suggest that the queen is

not acting as a pacemaker in these species. Instead there is a system of colony control closer to self-organization. A system is self-organized when a pattern appears between interacting components of a system rather than from a template or from directions governing the order of the components (Bonabeau et al. 1997; Camazine et al. 2001). In large-colony species, decentralized regulation of colony activity, or worker-regulated colony activity, is considered to be a more effective way of meeting the colony's needs (Jeanne 2003). Our results show that even in small-colony species, at least one pattern, the temporal clumping of activity, appears to emerge from the decentralized activities of workers.

Decentralization of colony activity can allow the colony to continue working and caring for the brood if the queen is lost (Camazine et al. 2001). In contrast, if the queen is the pacemaker, the loss of the queen should significantly reduce colony activity. Activity initiation in our *P. dominulus* colonies 24 h after the queen had been removed did not differ from that of colonies with queens. Strassmann et al. (2004) found a similar effect in *P. dominulus* nests ($N = 9$ queen-removal colonies, $N = 9$ control colonies) 2 days and 11 days after queen removal; there was no significant decrease in any of the behaviours studied, including foraging, although there was a significant increase in chews and lunges. The absence of a queen did not debilitate the colony in a manner that might be expected if the control of colony activity was centralized.

According to Robinson & Page (1989), workers often respond to varying thresholds of task-specific stimuli and may maintain a 'default state' of quiescence until their threshold has been reached. Social insect workers are expected to modify the tasks that they perform in response to changes in colony needs (Oster & Wilson 1978; Calabi 1988), dominance interactions (O'Donnell & Jeanne 1995), environmental cues (O'Donnell 1996) and the activity of nestmates (Dew & Michener 1981). Over 80% of inactive periods were ended by an individual either arriving on or walking across the nest. Unlike behaviours such as antennating or gaster wagging, arriving and walking are not explicitly social. This raises the question of why periods of activity begin with a worker arriving or walking.

Arrivals at the nest provide an obvious cause to stimulate activity because workers arrive with materials for the colony. Although *Polistes* workers are more likely to retain and distribute their own loads than are workers of swarm-founding species, they nevertheless transfer all or parts of many loads to other adults (West-Eberhard 1969). For example, in *P. instabilis*, most nectar, prey and pulp loads are transferred, at least in part, to other adults. Only water loads are usually fully retained by the forager (O'Donnell 1995). Therefore, the arrival of a forager is a sign of work available to do. However, walking by a wasp that is already on the nest provides no such obvious stimulus, but may be the first step in assessing colony needs, which are then communicated to other workers by subsequent behaviours.

Our conclusion that queens do not control worker behaviour is based on the assumption that the control of worker behaviour can be measured by control of activity pulse initiation. Within the activity pulses, the queen may be more active than the workers, and thus it is

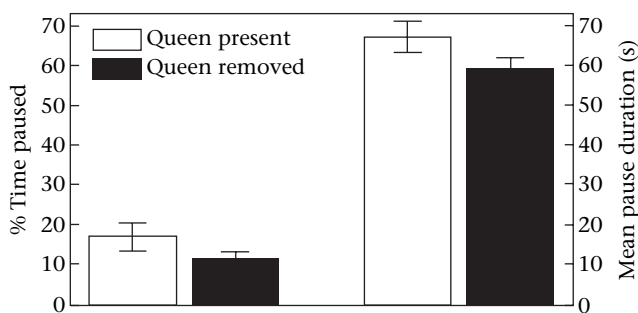


Figure 3. Mean \pm SE frequency of time spent paused and mean pause duration during observations of *P. dominulus* nests when the queen present ($N = 11$ nests) and when the queen had been removed experimentally ($N = 5$ nests).

understandable that in earlier findings, which do not specifically examine activity initiation, that the queen is cited as the most active individual in the colony. This has been found for *P. metricus* (Dew 1983), *P. fuscatus* (Reeve & Gamboa 1983, 1987; Gamboa et al. 1990), *P. annularis* (Strassmann 1981) and *P. instabilis* (Hughes & Strassmann 1988). The key question, however, concerns what the queen's activity accomplishes. There is direct evidence for the hypothesis that much of the queen's aggression is directed towards those highest in a dominance hierarchy, those that become the replacement queen if she is removed (Hughes & Strassmann 1988). Thus, if observers intend to measure colony activity while avoiding bias due to reproductive dominance interactions, a simple method examining the queen's role in initiating colony activity bursts can be used.

Several other studies of primitively eusocial polistines support the idea that the queen does not orchestrate the colony's work. A careful study on a specific foraging behaviour in *P. instabilis* also suggests that it is initiated by workers rather than the queen. Water foraging is done by a few specialists (O'Donnell 1998). If a water forager is removed, she is replaced by a worker that occasionally forages for water. O'Donnell (1998) concluded that nectar and water foraging in *P. instabilis* colonies are not regulated by the queen, but rather by direct assessment of the need and activities of other workers. He suggested that water foraging is regulated in this way to provide a rapid response to changing colony needs.

In another primitively eusocial wasp, *Ropalidia marginata*, no single individual appears to control colony maintenance activities (Premnath et al. 1995). *Ropalidia marginata* queens initiate fewer interactions than the two most behaviourally dominant workers in each colony and they are rarely seen interacting with workers or unloading foragers. Premnath et al. (1995) suggested that because workers and foragers of *R. marginata* are more involved in unloading and feeding larvae themselves, they can more directly evaluate colony needs than the queen. Their results revealed that the average worker of *R. marginata* shows higher activity levels, higher larval feeding rates and higher rates of worker unloading than the average queen. They concluded that the mechanism regulating colony maintenance activity for *R. marginata* involves both worker-worker interactions and direct evaluation of the colony's needs by the workers.

Our study of activity initiation and queen removal as well as other detailed studies of specific foraging behaviours support the view that work in small-colony *Polistes* species is not controlled by the queen. Differences between our results and those of other studies supporting queen pacemaking in *P. fuscatus* (Reeve & Gamboa 1983, 1987) could be partly methodological. It is possible, for example, that queens do not initiate activity bursts but do act to keep them going. However, the contrasting results of queen-removal experiments suggest that there are differences between species in their responses to queen removal. In *P. fuscatus*, removal or cooling of the queen decreased colony activity (Reeve & Gamboa 1983, 1987), but in *P. dominulus*, removal of the queen had no such

effect. Side-by-side comparisons of *P. fuscatus* in its native range with invading *P. dominulus* also revealed differences between species in task allocation. For example, *P. fuscatus* workers appear to be relatively slow to take on tasks, whereas *P. dominulus* workers are more involved in nest activity, especially foraging (Armstrong & Stamp 2003; Gamboa et al. 2002, 2004). We conclude that queen pacemaking is not universal in small-colony species and that studies of additional species are needed to determine which species represent the general rule and which are exceptions to the rule.

Acknowledgments

We thank Jason Longoria for help observing *P. dominulus* colonies. We thank Stefano Turillazzi for facilitating this work and for helpful comments on the manuscript. We thank people of McAllen, Texas, for allowing us to videotape nests on their houses, and we thank ENEL, Italy, for letting us observe wasps in reforestation plots. Carlos Solís and Perttu Seppä kindly helped with videotaping and dissecting the wasps. Gösta Nachman gave valuable advice on the statistical analyses. We thank the social insects journal club in Copenhagen for comments on previous versions of this manuscript. This material is based upon work supported by the National Science Foundation under grant IBN98-8809 and the FW5 EU Research-training network INSECTS (contract HPRN-CT-2000-00052) and the Rice University Century Scholars program.

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