ANIMAL BEHAVIOUR, 2000, **59**, 841–848
doi:10.1006/anbe.1999.1385, available online at http://www.idealibrary.com on IDEAL®

The role of queens in colonies of the swarm-founding wasp *Parachartergus colobopterus*

REBECCA A. HERMAN, DAVID C. QUELLER & JOAN E. STRASSMANN
Department of Ecology and Evolutionary Biology, Rice University

(Received 30 October 1998; initial acceptance 20 May 1999;
final acceptance 2 December 1999; MS. number: A8335)

Social insect queens reproduce while workers generally do not. Queens may also have other behavioural roles in the colony. In small, independent-founding colonies of social wasps, the dominant queen physically enforces her interests over those of the workers and serves as a pacemaker of the colony, stimulating workers to forage and engage in other tasks. By contrast, in large-colony, swarm-founding wasps, the collective interests of the workers are fulfilled in sex allocation and production of males, whether or not they coincide with the interests of the queens. The behavioural role of the queens in such species has not been extensively studied. We investigated the role of the queens both in regulating worker activity and in reducing the numbers of reproductively active queens in the swarm-founding epiponine wasp *Parachartergus colobopterus*. We found no evidence that queens regulate worker activity, as they were rarely involved in any interactions. Worker activity may be self-organized, without centralized active control by anyone. Furthermore, we found no evidence that the reduction in queen number characteristic of this tribe of wasps occurs in response to aggression among queens. The reduction in queen number may be a result of worker treatment of queens, although worker discrimination against some queens was not obvious in our data.

The two main types of females in social insect colonies are workers and queens, and they are mainly distinguished by the degree to which they reproduce: queens do and workers generally do not. Queens may also have other important behavioural roles, particularly in smaller groups where colonies are founded by single queens. Queens may regulate colony activity, or they may regulate reproduction, in particular, suppressing the workers' reproduction.

Among social wasps, both of these roles are well documented in the independent-founding Polistinae, particularly from studies of the genus *Polistes*. Such colonies are begun by one or a few foundresses, which raise one or more generations of workers, followed by male and female reproductives. Colonies usually have fewer than a hundred individuals and there are no morphological castes. In such small colonies, the queen is often the most active individual (Pardi 1942; West-Eberhard 1969; Strassmann 1981; Strassmann & Meyer 1983; Strassmann et al. 1984). Reeve & Gamboa (1983) found that the queen is not only the most active individual, but that she actually stimulates and synchronizes worker activity, acting as a pacemaker; she selectively directs aggressive interactions towards those workers that are least active, and workers temporally couple their activity with each other in the presence of an active queen. Control by a queen that is capable of assessing the status of the entire nest and of dictating behavioural acts to the workers may be common in small groups of social insects and other small groups such as naked mole-rats, *Heterocephalus glaber* (Reeve 1992).

The queen also plays a direct role in the control of reproduction in independent-founding polistines. Typically, dominance hierarchies form, with the queen at the top (e.g. Strassmann 1981). Because the colonies are small, a single queen may be able to dominate physically all other individuals, both foundresses and workers. Despite the general cooperativeness of social insect colonies, kin selection theory predicts that there are a number of areas of potential conflict between queens and workers, including the timing of reproduction, sex ratios and which individuals produce the sexuals (Hamilton 1972; Trivers & Hare 1976; Ratnieks 1988; Boomsma & Grafen 1991; Pamilo 1991; Queller et al. 1993; Crozier & Pamilo 1996). In *Polistes*, there is evidence that the queen may win such conflicts. For example, the queen produces the male eggs in *P. bellicosus* and *P. dorsalis* even though it

Correspondence and present address: J. E. Strassmann, Department of Ecology and Evolutionary Biology, Rice University, PO Box 1892, Houston, TX 77251-1892, U.S.A. (email: strassm@rice.edu). R. A. Herman is now at the Department of Psychology, Emory University, Atlanta, GA 30322, U.S.A.

0003–3472/00/040841+08 $35.00/0

is in the workers' collective interest to produce them (Arévalo et al. 1998). Similarly, when a *P. annularis* queen dies, the new queen is either a subordinate foundress or an old worker, even though workers as a class are most closely related to young workers (Queller et al. 1997).

Jeanne (1991) divided all members of the Polistinae into two groups, the independent founders and the swarm founders. The latter include the numerous genera of the Neotropical tribe Epiponini, *Polybioides* and some *Ropalidia*. The swarm founders differ from the independent founders in that they begin their colonies with swarms of queens and workers, have multiple queens and generally have larger colonies, with hundreds or thousands of adults. Jeanne (1994) also proposed that they differ in the two aspects of queen behaviour discussed above: that queens are rather inactive and do not stimulate worker activity, and that queens control reproduction by pheromones rather than by physical dominance. There are good reasons to expect that queens may be behaviourally less influential in the large colonies of swarm-founding wasps. With respect to regulation of activity, it is more difficult for a single individual to monitor and integrate information in these larger colonies, let alone physically stimulate the larger worker population into activity. Moreover, there is no longer a single obvious candidate for this role in the swarm founders, because there are usually many queens. Instead, control may be decentralized and regulated through self-organization. In this case, individuals conduct themselves according to simple rules of behaviour, resulting in coordinated outcomes that are not actively controlled by the queens or by any individual workers (Bonabeau et al. 1997; Pratt 1998).

With respect to queen control of reproduction, similar issues arise. It may be difficult for a queen to physically dominate numerous other queens (Reeve & Ratnieks 1993), let alone the hundreds or thousands of workers. Yet there is a distinct queen winnowing process; after a large batch of new queens is produced, the numbers of active egg layers declines until, when it approaches one, new queens are produced once again. Thus one queen eventually 'wins', but the outcome of this queen competition might be due either to interactions among the queens themselves, or to their interactions with workers. Queens might deploy pheromones, but neither workers nor other queens should reduce reproduction in response to pheromone signals unless doing so promotes their own interests (Keller & Nonacs 1993). Workers, because they are so numerous, may be in a better position to regulate queen reproduction. There is evidence that the collective interests of epiponine workers are met in other contexts (unlike in *Polistes*). For example, workers are generally more closely related to the sons of queens than to the sons of other workers, and it is the queens that produce most of the males (Hastings et al. 1998; M. Henshaw, J. E. Strassmann, S. Q. Quach & D. C. Queller, unpublished data), perhaps through a system of worker policing (Ratnieks 1988). Workers also benefit from the timing of sexual reproduction. As noted above, new queens are produced only in colonies with one or very few queens (West-Eberhard 1978; Strassmann et al. 1991, 1997, 1998; Queller et al. 1993), maximizing the chance that workers will produce highly related full sisters, while males are produced in colonies with higher queen numbers (Queller et al. 1993).

Our study investigates queen behaviour and queen control in *Parachartergus colobopterus*, a swarm-founding epiponine wasp. Colonies of *P. colobopterus* have variable numbers of queens, large numbers of workers, and little or no morphological caste differentiation between workers and queens (Strassmann et al. 1991, 1997, 1998). We studied the behaviour of *P. colobopterus* queens to determine whether queens play an active role in determining the activity of the colonies, as in *Polistes*, or if the queens are merely bystanders. A minimum condition for a queen (or queens) to be a pacemaker would be frequent behavioural interactions. In the second part of our study, we investigated whether the queens were active in the queen-reduction process, behaving aggressively towards one another and repressing reproductive competitors. Determining both the queens' place in orchestrating nest activity and in asserting reproductive rights in the queen cycle in this species will contribute to our understanding of social control within social insect colonies.

METHODS

To assess worker and queen behaviour, we videotaped seven wild nests of *P. colobopterus* in Maracay, Venezuela (10°16′N, 67°36′W, 450 m elevation; Table 1). Two colonies were taped at Hotel Maracay from 24 July to 6 August 1992 (trip V19) and five at the Universidad Central de Venezuela from 25 July to 8 August 1993 (trip V20). Nests V19-30 and V19-42 were young and had not yet produced any new adults. Nests V20-7 and V20-13 were slightly older and had already had adults emerge from the cells. Nests V20-8, V20-38 and V20-45 were older nests that had had several generations of adults emerge from their cells. These nests had between 164 and 518 cells in four to nine combs, totaling 64–297 wasps and 1–94 queens (see Strassmann et al. 1997 for per colony numbers). Before videotaping, we marked as many wasps as we could either after coaxing them onto the exterior of the nest envelope or on the combs after opening the nest envelope. We could open the envelope because in *P. colobopterus* the envelope is attached directly to the substrate and does not contact the combs which are themselves also attached to the substrate, not to the envelope. Once the wasps were accessible we put dots of paint on the thorax, abdomen or wings of each with Testor's® glossy enamel or paint pens.

The nest envelope remained off the combs during videotaping, and removing it did not obviously affect the activity of the colony except that the number of workers rebuilding the nest envelope increased. Using Sony Hi8 camcorders and Hi8 evaporated metal or metal particle videotape, we set the cameras to record a portion of each nest, usually two to four combs, providing sufficient resolution to permit identification of individual paint marks. We videotaped each nest for 1–3 days for 6–8 h daily. Once videotaping was complete, we collected the nest and associated wasps at dusk by slipping a zip-shut

Table 1. The nest ID, the period of observation, and the number of wasps dissected, the number observed as an actor, the number of acts observed by behaviour category and the number of participants for each behaviour

	Nest ID	Time observed (h)	Marked wasps dissected	Observed in at least one action	Antennations (individuals)	Social groomings (individuals)	Feedings (individuals)	Mandible bites (individuals)	Bites (individuals)
Workers as actors	V19-30	3.0	87	80	436 (69)	16 (13)	473 (76)	25 (14)	32 (12)
	V19-42	7.3	142	85	23 (17)	141 (63)	21 (19)	8 (8)	289 (43)
	V20-07	5.5	78	76	633 (62)	55 (30)	2492 (75)	33 (19)	152 (26)
	V20-08	8.1	57	48	212 (43)	16 (12)	265 (46)	5 (4)	33 (20)
	V20-13	9.0	82	65	87 (45)	25 (16)	141 (48)	117 (48)	6 (4)
	V20-38	2.1	68	51	86 (31)	14 (8)	137 (43)	13 (8)	22 (9)
	V20-45	1.4	197	89	311 (75)	18 (12)	90 (50)	127 (52)	121 (49)
Undeveloped queens as actors	V20-07	5.5	3	3	14 (3)	2 (2)	37 (3)	1 (1)	2 (1)
	V20-13	9.0	20	17	33 (14)	19 (9)	59 (17)	33 (13)	4 (3)
	V20-45	1.4	3	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Developed queens as actors	V19-30	3.0	2	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	V19-42	7.3	4	2	0 (0)	0 (0)	0 (0)	2 (1)	2 (1)
	V20-07	5.5	6	4	6 (3)	1 (1)	6 (4)	26 (3)	15 (3)
	V20-08	8.1	5	3	4 (3)	0 (0)	1 (1)	0 (0)	0 (0)
	V20-13	9.0	1	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	V20-38	2.1	1	1	0 (0)	0 (0)	2 (1)	0 (0)	0 (0)
	V20-45	1.4	91	42	160 (34)	0 (0)	18 (12)	92 (33)	40 (18)

plastic bag over the nest and enclosing all the wasps and the nest material. We returned to the site periodically over the next few days to check for and collect late foragers.

We dissected all wasps to determine whether they were workers or queens, to assess the state of their ovaries and whether they had mated. We classified all females with sperm in their spermathecae as queens, and we classified wasps as ‘developed’ when we found substantial ovarian development and one or more mature or nearly mature eggs in the ovaries. We classified those wasps with slight or no ovarian development as undeveloped; most workers and some of the queens fitted this category. Three inseminated wasps on V20-07, 20 inseminated wasps on V20-13, and three inseminated wasps on V20-45 had undeveloped ovaries.

To record the behaviours of individual wasps, we watched videotapes from each nest and recorded all interactions, identifying individuals by the paint marks on their bodies. To use the paint marks we took still photographs of all the wasps with an identification number so this number could be matched to individuals on the videotapes. Whether they were queens or workers was unknown to the observers at the time of observation. We classified interactions into five types: antennating, social grooming, feeding, mandible biting and biting other parts of the body (Strassmann et al. 1997).

(1) Antennations occurs when one wasp touches another with her antennae or when two wasps antennate each other simultaneously. Antennations were scored only when no other behaviour immediately resulted from this initial interaction.

(2) Social grooming involves an actor that slowly moves her mouthparts and mandibles over a recipient’s body in gentle motions, and it is most often performed to remove rainwater from foragers.

(3) Feeding is initiated by a wasp that has food and then approaches and offers the food to another wasp.

(4) Mandible bites are solicitations for food. The actor directs her bites at the recipient’s mandibles attempting to gain food from the recipient. If a mandible bite and feeding interaction occurred together, we scored the interaction as a mandible bite only.

(5) Biting involves an actor that bites any part of the recipient’s body, excluding the mandibles. This can be rather vicious at times as the biter moves from body part to body part, and the actor may even climb on to the victim. The victim typically lies motionless in a hunched position and may curl over on her side. If a biting interaction included, among others, bites directed to the mandibles, we scored the interaction as a bite only.

We considered both social groomings and feeding to be cooperative acts while we classified both biting and mandible biting as aggressive acts. For aggressive interactions and grooming, we classified each participant as an actor or a recipient. We attempted to do the same for antennation and feeding interactions, but determining which of the pair was actor and which was recipient was more difficult for these interactions.

We used the same database as an earlier study of kin discrimination (Strassmann et al. 1997), but the number of interactions reported differs slightly because the earlier study required that both participants be identifiable, whereas we used interactions with only one marked

Table 2. The nest ID, the period of observation, and the number of wasps dissected, the number observed as recipients, the number of acts observed by behaviour category and the number of participants for each behaviour

	Nest ID	Time observed (h)	Marked wasps dissected	Observed in at least one action	Antennations (individuals)	Social groomings (individuals)	Feedings (individuals)	Mandible bites (individuals)	Bites (individuals)
Workers as recipients	V19-30	3.0	87	78	445 (68)	18 (11)	487 (77)	18 (12)	28 (19)
	V19-42	7.3	142	105	21 (18)	130 (64)	19 (14)	7 (7)	304 (80)
	V20-07	5.5	78	78	591 (62)	40 (19)	2500 (75)	54 (33)	144 (46)
	V20-08	8.1	57	47	219 (42)	6 (6)	267 (47)	6 (5)	24 (18)
	V20-13	9.0	82	67	83 (36)	44 (22)	168 (47)	121 (49)	8 (7)
	V20-38	2.1	68	47	85 (30)	17 (11)	169 (40)	5 (5)	30 (17)
	V20-45	1.4	197	93	445 (86)	13 (11)	108 (47)	208 (73)	112 (48)
Undeveloped queens as recipients	V20-07	5.5	3	3	20 (3)	1 (1)	55 (3)	2 (2)	19 (2)
	V20-13	9.0	20	18	26 (11)	7 (5)	44 (16)	23 (11)	3 (1)
	V20-45	1.4	3	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Developed queens as recipients	V19-30	3.0	2	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	V19-42	7.3	4	2	1 (1)	1 (1)	0 (0)	1 (1)	1 (1)
	V20-07	5.5	6	4	4 (2)	1 (1)	3 (2)	1 (1)	1 (1)
	V20-08	8.1	5	2	2 (1)	0 (0)	1 (1)	0 (0)	0 (0)
	V20-13	9.0	1	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	V20-38	2.1	1	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	V20-45	1.4	91	15	24 (9)	5 (3)	1 (1)	8 (5)	42 (6)
	V20-45*	1.4	89	13	12 (7)	4 (2)	0 (0)	3 (3)	4 (4)
	V20-45†	1.4	2	2	12 (2)	1 (1)	1 (1)	5 (2)	38 (2)

*Two queens that were the recipient of an unusually high number of actions were removed from the totals.
†Totals for the two queens that were removed.

participant. Also, the number of wasps indicated for each nest in Tables 1 and 2 differ from the totals in Strassmann et al. (1997), because we provide the number of marked wasps collected and dissected, while Strassmann et al. (1997) included some unmarked wasps, which were used for genetic studies.

To determine whether queens orchestrated the activity in the colony, we compared the behaviour of queens and workers using two estimates of activity. First, to discover whether queens interact at a level consistent with the pacemaker role, we compared the average number of behavioural acts initiated by each queen on a nest with the average number initiated by a worker on the same nest (N=7, Wilcoxon signed-ranks test). However, this test would not reveal a single dominant queen. Thus, a second test, again using the Wilcoxon signed-ranks test, compared the number of acts initiated by the most active queen to the average number of acts initiated by an active worker. The most active queen was determined separately within each behavioural category by the number of acts initiated, and active workers were those that initiated an act of the same category at least once. Because the most active queen is compared to the average of active workers, not the most active worker, any bias would be in the direction of exaggerating the queen's role.

To investigate the mechanism involved in the reduction of queen number on the nests, we examined all behavioural acts directed towards the queens, focusing particularly on aggressive actions. First, we considered all colonies. Then, we looked at only those nests that included queens with and without ovarian development. Because queens coexisting on a nest in this species come from the same age cohort and are typically full sisters (Strassmann et al. 1991; Queller et al. 1993), queens lacking ovarian development are probably formerly reproductively active queens. Nests with both reproductively active and inactive queens are therefore most likely to be undergoing active queen reduction. On these nests we compared behaviour towards reproductively developed queens, undeveloped and thus, reproductively inactive queens, and workers.

RESULTS

Queens as Regulators of Activity

On average, queens performed no activity more frequently than workers (Fig. 1). Queens groomed others and fed others significantly less often than workers did (Wilcoxon signed-ranks test: T=0, N=7, P=0.018; T=0, N=7, P=0.018; Fig. 1). The most active queen in the colony performed no act significantly more often than active workers did (Fig. 1). The most active queen did not differ from active workers in the frequency of antennating, feeding, mandible biting, or biting, but she groomed others significantly less often than did active workers (T=0, N=7, P=0.018; Fig. 1). Because workers were

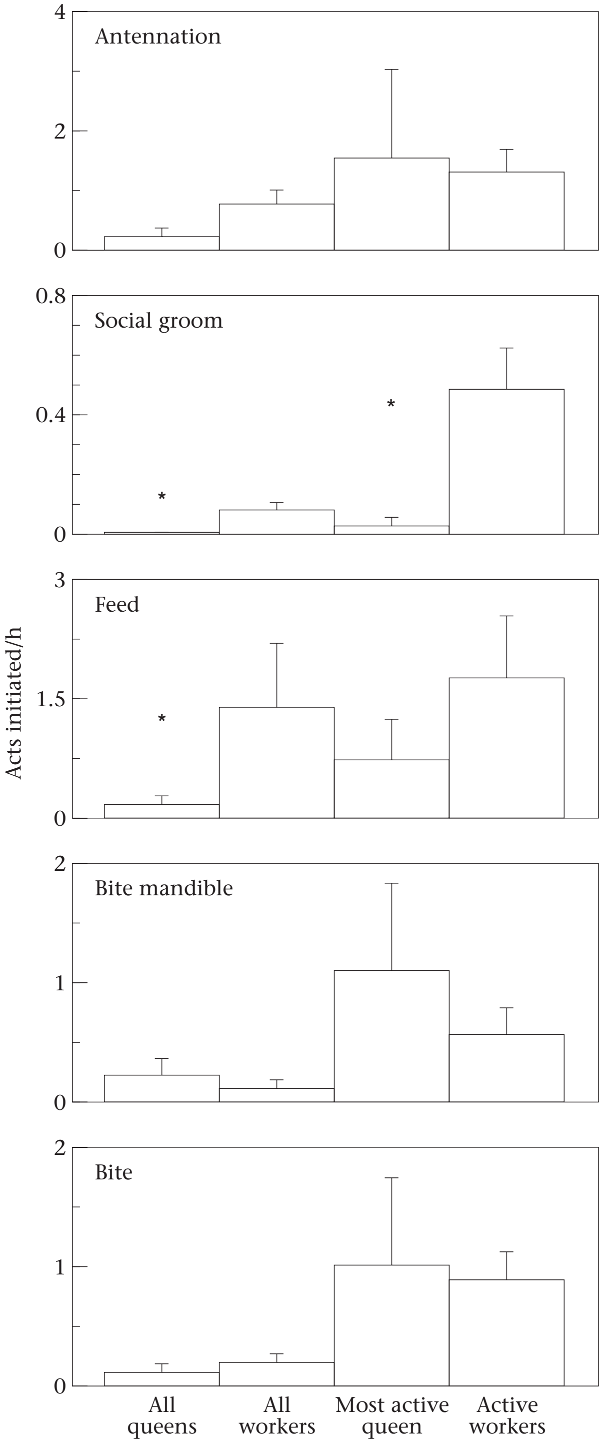

Figure 1. Mean+SE number of acts initiated per h per individual. Wilcoxon signed-ranks test compares average number of acts initiated by all queens on a nest to all workers on a nest and the number of acts initiated by the most active queen on a nest to the active workers on the nest (*$P<0.05$).

much more numerous on the nests than were queens, most interactions of each type were initiated by workers (Fig. 2). Activity on the nests of *P. colobopterus* is not controlled by the queens.

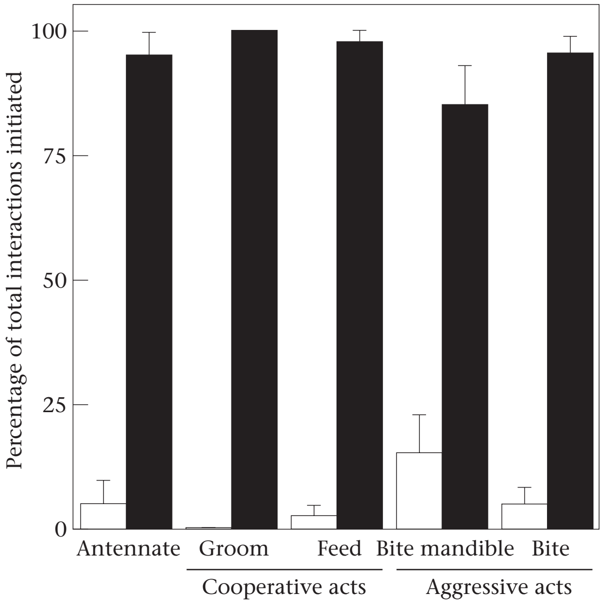

Figure 2. Mean+SE percentage of total interactions on each nest initiated by queens (□) and workers (■).

Suppression of Reproduction and Reduction of Queen Numbers

Queens with developed ovaries were rarely, if ever, the object of interactions (Table 2) with the exception of two queens on nest V20-45, which repeatedly received bites. These two queens may have been just beginning to be excluded from egg-laying status, although they were not yet discernibly different from the other queens. Workers almost always initiated the few acts directed towards queens. Actions in which developed queens were both actor and recipient were never observed on any nest, with the exception of one feeding interaction.

In the three nests that had inseminated wasps with no ovarian development, the undeveloped queens behaved differently from developed queens and were treated differently by other members of the colony. While queens rarely interact with each other, the undeveloped queens often initiated interactions among themselves. They were both actor and recipient in 17 acts on nest V20-13, in three acts on nest V20-07 and none on nest V20-45. On these three nests, the behaviour of developed queens, undeveloped queens and workers varied greatly (Fig. 3). For example, on nest V20-13, the single developed queen was never observed in an interaction, whereas on nest V20-45, the three undeveloped queens were completely inactive. However, a comparison of the number of times the three groups were recipients of each behaviour type indicated differences between groups. Undeveloped queens were significantly more likely than developed queens to be the recipients of all actions except bites (Mann–Whitney *U* comparisons, $P<0.01$). Workers were more likely than developed queens to be the recipients of all actions (Mann–Whitney *U* comparisons, $P<0.01$). Undeveloped queens and workers did not differ in their likelihood of being the recipient of any actions (Mann–Whitney *U* comparisons). On nest V20-07, undeveloped

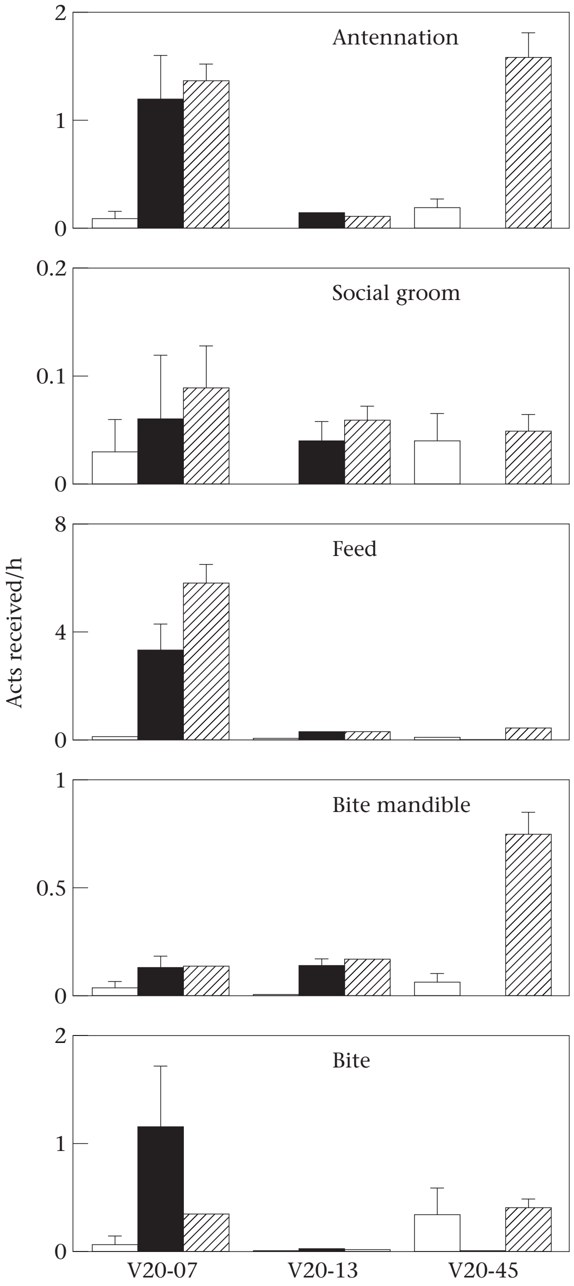

Figure 3. Mean+SE number of acts received per wasp per h on the three nests that included members of all three groups: developed queens (☐), undeveloped queens (■), and workers (▨).

queens were almost 20 times as likely to be bitten as were developed queens and were four times as likely as workers. On nest V20-13, only one undeveloped queen was bitten, and she was bitten repeatedly, whereas the workers were rarely bitten. Workers were overwhelmingly responsible for the acts directed towards undeveloped queens. Those few actions that workers did not initiate were almost all initiated by fellow undeveloped queens; of the acts initiated by known individuals, only one was the action of a developed queen (which bit an undeveloped queen on nest V20-13).

DISCUSSION

Queens of *P. colobopterus* show no evidence of being active pacemakers in their colonies. They are typically inactive and do not direct interactions towards workers. Thus, they are not responsible for control of colony activity or for stimulation of worker behaviour. The only behaviour that queens appear to initiate as often as workers is biting mandibles. Because queens do not forage, they need to solicit workers to obtain food. It is unlikely that this action serves as a cue for continued foraging because it is infrequent and easily explained as serving the simpler purpose of feeding the queen.

The different role of the queens in *Polistes*, which are active pacemakers and assert reproductive dominance, and *P. colobopterus*, which apparently do little more than produce eggs, can be at least partially explained by differences in the features of their colonies, something Jeanne (1994) first pointed out. A *Polistes* queen rules a small nest from which she can easily assess the condition of the entire colony and control nestmates' actions, whereas in the large colonies of *P. colobopterus* and other epiponine species, assessment and control by one or a few individuals is more difficult. In species with large colonies, distributed control and self-organization are probably more effective (Jeanne 1994; Pratt 1998).

Our approach for studying pacemaker behaviour differs from the approach of Reeve & Gamboa (1983), who recorded as many movements as possible on small nests (mean 7.5 wasps). They measured the proportion of time in which each wasp was active, determined whether the activity of the queens was directed towards inactive workers, and calculated covariation of queen and worker activity. Although this provides a thorough test of pacemaker behaviour, we could not recreate the study using the *P. colobopterus* colonies. Large colony size prohibited observing all interactions on a nest simultaneously, and following a single wasp for long was not always possible. Reeve & Gamboa's (1983) study also involved experimental manipulation, in which queens were removed or inactivated. We could not perform such experiments because, without morphological caste differentiation, determining the identity of the queens was not possible before dissection. Because *P. colobopterus* queens perform so few acts, their behavioural presence on the nest may practically go unnoticed compared with, for example, *P. annularis*, where queens initiate 65% of aggressive acts (Strassmann 1981). Therefore, the behavioural pacemaker hypothesis can be excluded outright without assessing behavioural coordination.

In *P. colobopterus*, the individual workers, like the queens, also may be unable to assess the status of the entire colony. Their coordinated efforts may thus be the natural consequence of self-organization. In self-organization, complex outcomes result from the sum of simple individual behaviours. Foraging patterns of ants and honeybees, colony development in *Polistes*, and pattern formation on the combs of honeybee colonies have been explained by self-organization (Bonabeau et al. 1997). In other swarm-founding species, evidence exists for similar self-regulation by workers in situations in which intricate systems of specialization depend upon feedback among the workers, as in nest construction of the epiponine species, *Polybia occidentalis*, with specialists in water foraging, pulp foraging and building (Jeanne 1986, 1994, 1996). This productive activity is accomplished without behavioural dominance by a queen. Similarly, constructing the correct proportion of drone comb and worker comb in honeybee colonies is not dependent upon a queen to gather and disperse information (Pratt 1998). Instead, workers across the nest probably make the necessary assessments.

We found support for the hypothesis that inseminated wasps with undeveloped ovaries are no longer behaving as queens and are in the process of being eliminated from the nest. The reduction in queen number is not directly controlled by the queens as developed queens do not interact with the repressed queens. Instead, workers are responsible for acts directed towards queens with regressing ovaries. We hypothesized that worker behaviour towards some queens causes both regression of the ovaries and the eventual death of these queens. A queen's eventual elimination from the nest could also be the natural consequence of increased mortality risk, when the actions of the workers force the former queen to begin worker-like behaviours, such as foraging.

This study does not show how the surviving queens are chosen. Alhough we found that queens do not participate in the reduction in queen number, other studies with different species have found that queens may be involved. *Metapolybia aztecoides* queens are first tested by workers, and the subordinate queens are then attacked (West-Eberhard 1978). However, fellow queens have been observed to push and chase queens that workers attack, although true fighting has not been observed between queens (West-Eberhard 1978). Queens also directly compete with each other through aggressive bending and eating each other's eggs. Queens that are attacked persistently are eliminated from reproduction. Forsyth (1975) observed aggression among *M. cingulata* queens in small colonies. West-Eberhard (1978) has suggested that some queens may themselves cease laying eggs and perform worker tasks when a colony is in need of workers, especially in newly founded colonies, a speculation we failed to confirm. Although we found that repressed queens acted like workers, a lack of workers did not cause queens to become worker-like. The colonies with the fewest workers did not have suppressed queens acting as workers. Rather, we found suppressed queens on nests with many workers and queens, where their presence is consistent with active queen reduction.

To date, all interactive facets of reproduction and nest activity studied in *P. colobopterus* are consistent with worker control (Queller et al. 1993; Ezenwa et al. 1998; Henshaw et al., unpublished data). This may be the result of the diminished behavioural role for queens in these colonies.

Acknowledgments

We thank Juan Castilloa, Simonetta Holley de Castillo, Maria Antonietta Castillo Holley and Alicia Castillo Holley for facilitating access to our study areas and for hosting us in Venezuela. We thank the Universidad Central de Venezuela in Maracay for allowing us to work on their grounds. We thank Elisabeth Arévalo and Nicole Gerardo for help with dissections and Alice Green, Jessica Williams, Jenny Klingler, Gary Patterson and Kory Marchowski for behavioural observations. We thank Mike Henshaw, Giorgina Bernasconi and Bob Jeanne for helpful comments on the manuscript. Support for this study was provided by NSF Grants IBN 92-10051 and IBN 9507515.

References

Arévalo, E., Strassmann, J. E. & Queller, D. C. 1998. Conflicts of interest in social insects: male production in two species of *Polistes*. *Evolution*, **52**, 797–805.

Bonabeau, E., Theraulaz, G., Deneubourg, J., Aron, S. & Camazine, S. 1997. Self-organization in social insects. *Trends in Ecology and Evolution*, **12**, 188–193.

Boomsma, J. J. & Grafen, A. 1991. Colony-level sex ratio selection in the eusocial Hymenoptera. *Journal of Evolutionary Biology*, **3**, 383–407.

Crozier, R. H. & Pamilo, P. 1996. *Evolution of Social Insect Colonies: Sex Allocation and Kin Selection*. Oxford: Oxford University Press.

Ezenwa, V. O., Henshaw, M., Queller, D. C. & Strassmann, J. E. 1998. Patterns of buzz running, a swarm initiation behaviour, in the neotropical wasp, *Parachartergus colobopterus*. *Insectes Sociaux*, **45**, 445–456.

Forsyth, A. 1975. Usurpation and dominance behaviour in the polygynous social wasp *Metapolybia cingulata* (Hymenoptera: Vespidae: Polybiini). *Psyche*, **82**, 299–303.

Hamilton, W. D. 1972. Altruism and related phenomena, mainly in social insects. *Annual Review of Ecology and Systematics*, **3**, 193–232.

Hastings, M. D., Queller, D. C., Eischen, F. & Strassmann, J. E. 1998. Kin selection, relatedness, and worker control of reproduction in a large-colony epiponine wasp, *Brachygastra mellifica*. *Behavioral Ecology*, **9**, 573–581.

Jeanne, R. L. 1986. The organization of work in *Polybia occidentalis*: costs and benefits of specialization in a social wasp. *Behavioral Ecology and Sociobiology*, **19**, 333–341.

Jeanne, R. L. 1991. The swarm-founding Polistinae. In: *The Social Biology of Wasps* (Ed. by K. G. Ross & R. W. Matthews), pp. 191–231. Ithaca, New York: Comstock.

Jeanne, R. L. 1994. Patterns of colony organisation within the Vespidae. In: *Les Insectes Sociaux* (Ed. by A. Lenoir, G. Arnold & M. LePage), page 231. Paris: Université Paris Nord.

Jeanne, R. L. 1996. Regulation of nest construction behaviour in *Polybia occidentalis*. *Animal Behaviour*, **52**, 473–488.

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

Pamilo, P. 1991. Evolution of colony characteristics in social insects: I. Sex allocation. *American Naturalist*, **137**, 83–107.

Pardi, L. 1942. Ricerche sui Polistini. V. La poliginia iniziale di *Polistes gallicus*. *Bollettino di Entomologia di Bologna*, **14**, 1–104.

Pratt, S. C. 1998. Decentralized control of drone comb construction in honey bee colonies. *Behavioral Ecology and Sociobiology*, **42**, 193–205.

Queller, D. C., Strassmann, J. E., Solis, C. R., Hughes, C. R. & DeLoach, D. M. 1993. A selfish strategy of social insect workers that promotes social cohesion. *Nature*, **365**, 639–641.

Queller, D. C., Peters, J. M., Solís, C. R. & Strassmann, J. E. 1997. Control of reproduction in social insect colonies: individual and collective relatedness preferences in the paper wasp, *Polistes annularis*. *Behavioral Ecology and Sociobiology*, **40,** 3–16.

Ratnieks, F. L. 1988. Reproductive harmony via mutual policing by workers in eusocial hymenoptera. *American Naturalist*, **132,** 217–236.

Reeve, H. K. 1992. Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature*, **358,** 147–149.

Reeve, H. K. & Gamboa, G. J. 1983. Colony activity integration in primitively eusocial wasps: the role of the queen (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behavioral Ecology and Sociobiology*, **13,** 63–74.

Reeve, H. K. & Ratnieks, F. L. W. 1993. Queen–queen conflicts in polygynous societies: mutual tolerance and reproductive skew. In: *Queen Number and Sociality in Insects* (Ed. by L. Keller), pp. 45–85. Oxford: Oxford University Press.

Strassmann, J. E. 1981. Wasp reproduction and kin selection: reproductive competition and dominance hierarchies among *Polistes annularis* foundresses. *Florida Entomologist*, **64,** 74–88.

Strassmann, J. E. & Meyer, D. C. 1983. Gerontocracy in the social wasp, *Polistes exclamans. Animal Behaviour*, **31,** 431–438.

Strassmann, J. E., Meyer, D. C. & Matlock, R. L. 1984. Behavioural castes in the social wasp, *Polistes exclamans* (Hymenoptera: Vespidae). *Sociobiology*, **8,** 211–224.

Strassmann, J. E., Queller, D. C., Solis, C. R. & Hughes, C. R. 1991. Relatedness and queen number in the neotropical social wasp, *Parachartergus colobopterus*. *Animal Behaviour*, **42,** 461–470.

Strassmann, J. E., Klingler, C. J., Arevalo, E., Zacchi, F., Husain, A., Williams, J., Seppa, P. & Queller, D. C. 1997. Absence of within-colony kin discrimination in behavioural interactions of swarm-founding wasps. *Proceedings of the Royal Society of London, Series B*, **264**, 1565–1570.

Strassmann, J. E., Goodnight, K. R., Klingler, C. J. & Queller, D. C. 1998. The uncoupling of queen and new colony production in swarm-founding neotropical wasps. *Molecular Ecology*, **7**, 709–718.

Trivers, R. L. & Hare, H. 1976. Haplodiploidy and the evolution of the social insects. *Science*, **191,** 249–263.

West-Eberhard, M. J. 1969. The social biology of polistine wasps. *Miscellaneous Publications of the University of Michigan Museum of Zoology*, **140**, 1–101.

West-Eberhard, M. J. 1978. Temporary queens in *Metapolybia* wasps: nonreproductive helpers without altruism? *Science*, **200,** 441–443.