

Research article

Worker reproductive competition affects division of labor in a primitively social paperwasp (*Polistes instabilis*)

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Abstract. Social insects are premier models for studying the evolution of self-organization in animal societies. Primitively social species may be informative about the early stages of social evolution and transitions in self-organization. Previous worker removal studies in *Polistes instabilis* paper wasps suggested that dominant but non-egg-laying workers play an important role in regulating rates of task performance by inducing foraging in subordinates. We extend previous worker removal studies by quantifying changes in individuals' behavior following removals, and by measuring associations between behavioral change and individuals' reproductive capacity (ovary development). Workers changed their rates of aggressive behaviors more than queens following the dominant worker removals. Increases in worker's rates of aggressive behaviors were correlated with decreases in their foraging rates. Changes in individual rates of social aggression were associated with their reproductive capacity: worker females with well-developed ovaries increased their rates of aggression. Further changes in rates of aggression after the dominant workers were returned also depended on ovary development. These patterns suggest that task performance and potential fecundity are linked in workers, and that worker interactions play a strong role in regulating task performance. We conclude that worker reproductive competition may have influenced the evolution of colony organization in social insects.

Keywords: *Polistes instabilis*, dominance, foraging, polyethism, social organization, social evolution.

Introduction

The shift from centralized to distributed social organization is one of the major transitions in the evolution of social behavior (Bourke, 1999; Jeanne, 2003). Social organization in primitively eusocial species, such as independent founding (IF) paper wasps, often depends on physical aggression from queens (Reeve, 1991; Gadagkar, 2001). Queen aggression suppresses direct reproduction in workers, and also promotes helping behavior (Gamboa et al., 1990; Premnath et al., 1996; O'Donnell, 1998b; Bruyndonckx et al., 2006). Inducing helping behavior may further reduce reproductive competition for the queens. For example, foraging precludes subordinates from egg-laying (Keeping, 1992; Powell and Tschinkel, 1999). In some species, queens are the most active individuals in colonies (Reeve, 1991; O'Donnell, 1998b). Queen control of workers' task performance appears to be an effective mode of social organization in small colonies. Reproductive competition may have been the primary mechanism to establish and regulate division of labor in the early stages of social evolution.

In contrast, reproductive competition does not appear to influence task performance in more derived, larger societies, such as swarm-founding paper wasps, honey bees, and ants (Cole, 1981; Robinson, 1987; Bourke, 1988; Robinson et al., 1989; O'Donnell, 2001). Social interactions regulate task performance and even worker reproduction (e.g., worker policing), but do not necessarily reflect reproductive dominance (Wenseleers et al., 2004a; Wenseleers and Ratnieks, 2006). This suggests that a transition from centralized to distributed control of task performance has accompanied the evolution of larger insect colonies (Gordon, 1996; Bourke, 1999; Fewell, 2003; Ratnieks et al., 2006).

Although IF wasps have served as models for the study of queen control, non-egg-laying workers in some primitively eusocial species affect each other's task performance (Chandrashekara and Gadagkar, 1992; O'Donnell, 1998a,b; Jha et al., 2006). For example, workers initiate most of the aggressive interactions and influence foraging activity in *Ropalidia marginata* (Chandrashekara and Gadagkar, 1992; Premnath et al., 1996) and worker-worker interactions appear to regulate foraging rates in *Polistes instabilis* (O'Donnell, 1998a). The relationship between task decisions and reproductive competition in workers from primitively eusocial species may provide important information about evolutionary transitions in social organization.

There is often a dominance hierarchy among IF paperwasp non-reproductive workers (*Mischocyttarus*: Markiewicz and O'Donnell, 2001; *Polistes*: Pardi, 1948; Reeve, 1991; Strassmann et al., 2004; *Ropalidia*: Premnath et al., 1996), which correlates positively with ovarian development and negatively with foraging rates (Gamba et al., 1990; Röseler, 1991; Markiewicz and O'Donnell, 2001). Worker competition can persist in more advanced insect societies: worker dominance hierarchies form following queen loss in many advanced eusocial species (Wenseleers et al., 2004b). Dominant female workers compete among each other to replace lost or missing reproductives (Strassmann and Meyer, 1983; Hughes and Strassmann, 1988; Kardile and Gadagkar, 2003; Strassmann et al., 2004), and reproductive competition may influence many worker-worker interactions. In some species such as *P. instabilis*, the worker hierarchy predicts which female will become a replacement queen (Hughes and Strassmann, 1988). Non-reproductive workers may increase their chances for direct reproduction by inducing others to forage. Social aggression by workers, even before they can reproduce, could suppress the ovarian development of potential competitors and help secure future direct fitness (Jeanne, 1991).

Despite extensive research on queen removal and replacement (*Polistes*: Hughes and Strassmann, 1988; Strassmann et al., 2004; *Ropalidia*: Kardile and Gadagkar, 2003), few manipulative studies have examined the effects of dominant workers on nest mate task performance. Understanding the role of worker dominance in IF paper wasps may be especially useful in understanding the shift in social organization from central control to distributed management of task performance (Schneider et al., 1998; Schneider and Lewis, 2004; O'Donnell, 2001, 2006). One possible evolutionary pathway from centralized (queen) to distributed (worker) control is the changing role of worker reproductive competition in affecting task performance. Interactions among non-ovipositing but reproductively capable workers may have first paralleled those of queen-worker interactions, and may have been later modified as workers lost the ability to replace queens and reproduce directly (e.g., worker policing, Cole, 1986; Bourke, 1988). If this is correct, then some species might occupy an intermediate

stage where worker aggression, rather than queen aggression, is important in task allocation among workers.

Our present study tests the hypothesis that worker reproductive competition regulates task performance in some primitively social species. Previous studies on the paperwasp *Polistes instabilis* suggested that workers, rather than queens, were regulating colony-wide foraging rates (O'Donnell, 1998a; Jha et al., 2006). We predicted that *P. instabilis* colonies would resemble self-organized societies, in which worker interactions regulate division of labor. We further predicted that worker competition over opportunities for direct reproduction would determine worker's roles. We extend previous research by quantifying individual changes in rates of social aggression and foraging behavior, and correlating these behavioral changes to workers' reproductive capacity. Queens should not manage colony activity, specifically not engaging in significantly more dominance interactions than the workers (O'Donnell, 1998a; Jha et al., 2006). In contrast to more derived societies (Robinson, 1987; Robinson et al., 1989; O'Donnell, 2001), we expected worker effects on task performance to be related to their reproductive physiology.

If worker competition affects task performance, we expected the following patterns. First, increased social aggression and increased foraging activity would be opposing responses to nest mate removals. The workers with better chances of replacing the queen should exhibit greater rates of aggressive interactions post-removal, and should also forage at lower frequencies. Second, reproductive physiology would correspond to individual's behavioral responses to dominant worker removal. Worker's ovary size and increased social aggression should be positively correlated (Pardi, 1948; West-Eberhard, 1969; Röseler et al., 1980; Strambi, 1985). We discuss the implications of our findings for individuals' direct and indirect reproductive fitness in *P. instabilis* colonies. We also develop further hypotheses for the evolution of the relationship between social aggression and task performance.

Materials and methods

Study site and subject colonies

The majority of *P. instabilis* colonies at our site are established at the beginning of the rainy season (e.g., the middle of May; Hunt et al., 1999). Data were collected from 27 June to 24 July 2005 from seven post-worker emergence *Polistes instabilis* colonies. Colony sizes ranged from 8 to 29 adult females, with all brood stages present throughout the study (eggs to pupae; Table 1). The nests were observed *in situ* near Cañas in Guanacaste Province, Costa Rica (10°26'N; 85°07'W; O'Donnell, 1998a). Nests were located at heights of 0.5 to 2.5 m above the ground in vegetation or on the eaves of buildings. All adult wasps on the nests were individually marked with paint pens 1–2 days before observations began. Colonies were observed daily for 4.5–5 hours per day for 3–4 days each.

Table 1. Number of individuals at the beginning of observation, times queens oviposited and number of offspring that were observed to emerge during observations for each colony.

Colony	Number of individuals	Number of times queen oviposited	Number of times offspring emerged
A	25	2	0
B	9	3	0
C	13	6	0
D	17	6	1
E	29	2	2
F	16	1	2
H	8	1	1

Behavioral data collection

We observed the colonies sequentially, collecting behavioral data on one colony exclusively before proceeding to the next. Behavioral data were collected continuously for three hours in the morning, between 0800 h–1200 h local time, and for two hours in the afternoon, between 1300 h–1700 h. We collected behavioral data using a portable tape cassette recorder while sitting 1 m from the nest, facing the cell openings. All occurrences of the following acts were noted: arrivals and departures from the nest, abdominal vibrations, chases/bites and number of times bitten, and oviposition (see O'Donnell, 1998a for ethogram). Biting and chasing nest mates are common *Polistes* aggressive interactions, but other possible forms of dominance communication include abdominal vibrations against the nest (Keeping, 1992; Brillet et al., 1999). There is only one type of abdominal vibration in this species (Downing and Jeanne, 1985): a series of rigorous abdominal waggings conducted as the wasp walks across the nest surface. We quantified each uninterrupted series of vibrations as a single occurrence. We followed O'Donnell (1998a) by scoring biting and abdominal vibrations as aggressive behaviors. We also scanned the nest surface every 15 min and recorded the identity of all adults present. Time spent on nest was calculated from the scan data (18–22 scans per day). Queens were identified based on observations of egg laying; one female per colony laid eggs during the study. Colony establishment is complex in this species (O'Donnell, pers. obs.). Workers could therefore have been offspring from the subject colony or from previous colonies or cofoundresses. No males were present on any of the colonies.

Behavioral criteria and methodology for dominant worker removals

Pre-removal observations were performed for 1 to 2 days before experimental manipulations on each colony. The workers selected to be removed were the individuals with the greatest overall sum of abdominal vibrations, bites and chases that did not oviposit during the pre-removal period. If individuals were tied in the number of bites and chases, the individual which bit and chased the greatest number of other wasps was selected. One individual was removed from colonies with fewer than 15 adult females, and two individuals were removed from larger colonies. The dominant workers were removed the night following pre-removal observations by grasping them with forceps and lifting them from the nests. Removed individuals were held in a small mesh enclosure with *ad libitum* water and 50% sugar water solution until they were returned to their nests. Post-removal behavioral data from colonies were collected the subsequent day (4.5–5 h), roughly ten hours following the removals. We returned removed dominant workers to their nests the same night, except for Colony H, which was collected the following night after removal. Behavioral data were recorded the day after the dominant workers were returned, also roughly ten hours following returns.

Collection of subjects and ovary dissections

After dark on the last day of observations, all adult females were collected. The gasters were dissected from the body and placed in an aldehyde-based fixative (Prefer fixative, Anatech, Ltd.). Wasps were fixed for at least 3 weeks and then transferred into 70% ethanol. The ovaries were dissected from each female's gaster and photographed through the 10X objective of a dissecting microscope using a digital camera. The two largest oocytes were measured from the digital photographs using the ruler tool in Adobe Photoshop software, and measurements were converted to millimeters. Because oocytes are roughly elliptical, area was calculated as: $\pi * \frac{1}{2} \text{length} * \frac{1}{2} \text{width}$. We used the mean area of the two largest oocytes as an index of ovary development (Markiewicz and O'Donnell, 2001; Keeping, 2000, 2002; Foster et al., 2004). We did not include body size in our analyses, because it had no significant effects on ovary development and behavior (Molina and O'Donnell, 2007).

Statistical analyses

Colony identity was included as a factor in all multivariate analyses. We used multivariate and univariate repeated-measure ANOVAs implemented in SPSS 14 to analyze treatment effects on social dominance and foraging performance at the colony level.

Individual rates of behaviors were calculated as frequency divided by the amount of observation time an individual spent on the nest, except for foraging rates, which was calculated as the frequency of arrivals per observation hour. The proportion of time spent on the nest was estimated from the number of scans an individual was present on the nest. If an individual, such as a forager, was not present for any scans on an observation day, we arbitrarily assigned her one scan on nest for that day. We calculated partial correlations to analyze changes in behavior across treatments. Hierarchical regression analyses were used to test associations between ovary development and square-root transformed rates of behavior. For all analyses, we first ran full multiple regression analyses including all behavioral covariates. When the overall model was significant, we tested the effects of individual predictor variables. Data plotted in figures represent residuals from regressing both variables against other covariates. All data points from these variables passed the box plot rule for outliers (Iglewicz and Hoaglin, 1993).

Results

Pre-removal and return rates of removed dominant workers

The removed individuals accounted for 42 to 65% of biting in pre-removal observations. These females did not significantly differ in rates of performing key behaviors when they were returned to the nest ($F_{4,2} = 1.15$, $p = 0.51$).

Queen responses to removal of dominant workers

During pre-removal observations, queens performed abdominal vibrations at higher rates than other females ($t_{53} = 4.16$, $p < 0.0001$) and queens were not observed to forage (queens significantly different from workers: $t_{53} = -3.60$, $p = 0.001$).

If queens act as central pacemakers, they should be the most responsive to changes in colony structure and activity. We therefore compared the absolute differences

in rates of key behaviors between different treatments in queens and workers. There were no caste differences in changes in rates of biting nest mates from pre-removal to post-removal days ($t_{53} = 0.24$, $p = 0.81$). However, queens did not change their rates of abdominal vibrations as much as workers in response to the removals ($t_{53} = -2.08$, $p = 0.04$). There were no significant caste differences in changes in the rates of biting ($t_{39} = 0.17$, $p = 0.86$) or abdominal vibrations ($t_{39} = -0.26$, $p = 0.79$) from post-removal to worker return treatments.

Worker responses to removal of dominant workers

Pre-removal behavioral profiles influenced how workers responded to dominant nest mate removals. Female workers with greater pre-removal rates of bites and abdominal vibrations significantly increased their rates of performing these behaviors after nest mates were removed (bites: $r = 0.40$, $df = 46$, $p = 0.005$; vibrations: $r = 0.61$, $df = 46$, $p < 0.0001$). Conversely, females with greater pre-removal foraging rates decreased rates of biting nest mates ($r = -0.36$, $df = 46$, $p = 0.01$) and foraged more frequently post-removal ($r = 0.72$, $df = 46$, $p < 0.0001$).

We next tested whether changes in the rates of dominance behaviors and foraging activity were negatively correlated. We first examined changes in worker behavior from pre-removal to post-removal treatments. Increases in individuals' rates of biting nest mates correlated with increases in their abdominal vibration rates ($r = 0.34$, $df = 46$, $p = 0.02$) and decreases in rates of being bitten by other nest mates ($r = 0.33$, $df = 46$, $p = 0.02$). There was also a non-significant negative association between increases in vibrations and times bitten by other nest mates ($r = -0.27$, $df = 46$, $p = 0.07$). Though increases in rates of vibrations and foraging were not related ($r = -0.10$, $df = 46$, $p = 0.49$), there were negative correlations between these behaviors between both pre-removal ($r = -0.36$, $df = 46$, $p = 0.02$) and post-removal rates of these behaviors ($r = -0.39$, $df = 46$, $p = 0.007$). The associations of these behaviors from the post-removal to the worker return treatments were also negative, but not significant.

Next, we examined the effects of worker return on individual behavior. We performed correlations on workers' pre-removal to post-removal changes in behavioral rates with their post-removal to worker return changes. Individuals that increased their rates of abdominal vibrations after nest mate removal later decreased their rates of vibrations once dominant nest mates were returned ($r = -0.34$, $df = 35$, $p = 0.04$). Increased foraging activity after removal also correlated with decreased rates upon return ($r = -0.50$, $n = 35$, $p = 0.002$). Pooling across the post-removal and return treatments, changes in worker's rates of foraging and abdominal vibration after worker removal (pre-removal to pooled post-removal) were also negatively correlated ($r = -0.34$, $df = 46$, $p =$

0.02 ; Fig.1). There were no significant relationships between behavioral changes in rates of biting ($r = -0.09$, $df = 35$, $p = 0.59$) or being bitten ($r = -0.28$, $df = 35$, $p = 0.10$) from pre-removal to removal and changes in rates from removal to worker return.

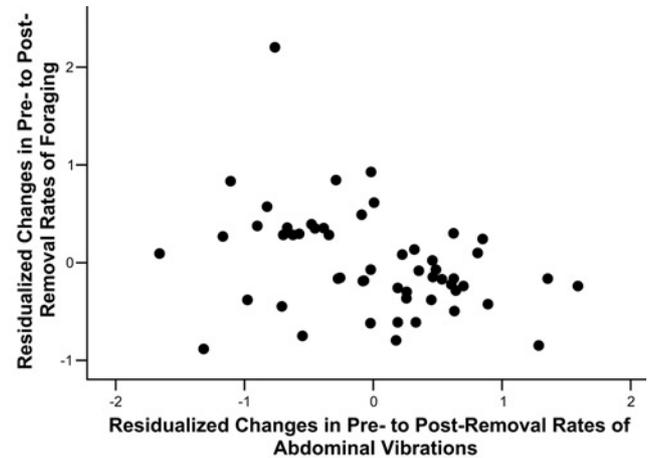


Figure 1. Scatterplot depicting the relationship between pooled post-removal rates of abdominal vibrations and foraging, after accounting for colony identity.

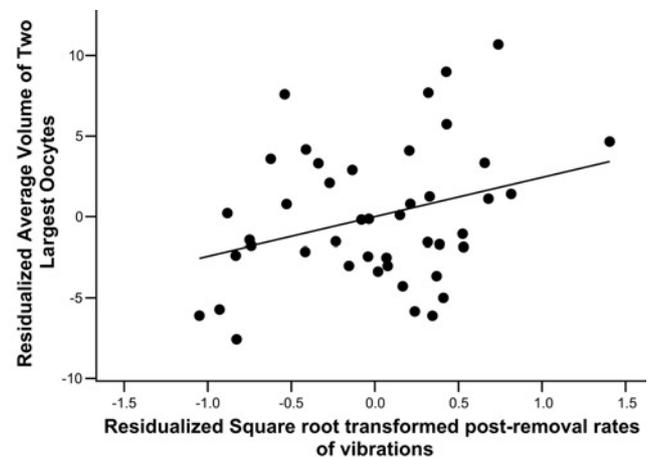


Figure 2. Partial regression plot showing correlation between ovary size and square-root transformed rates of vibrations during post-removal treatments, after accounting for colony identity, square-root transformed rates of biting other nest mates, foraging and times bitten by other nest mates.

Post-removal worker behavior as a predictor of ovary development

We examined worker reproductive capacity by measuring their ovary development. We compared worker ovaries to the ovary size needed for reproduction (worker ovary size/queen ovary size, within nest comparisons). We did not analyze colony D, because we were unable to collect the queen for physiological measurements. In each analyzed colony, some workers had minimal ovary

development ($n = 13$ (across colonies), 4% to 13% of queen oocyte size) while others had ovary development comparable to queens ($n = 6$ (across colonies, non-removed workers), 60–100% of queen oocyte size).

Ovary size did not correlate with pre- to post-removal changes in biting frequency ($r = -0.12$, $df = 36$, $p = 0.47$), but individuals with greater biting rates after dominant workers returned had larger ovaries ($r = 0.36$, $df = 28$, $p = 0.05$). Ovary development did not correlate with changes in the rates of abdominal vibrations ($r = -0.07$, $df = 36$, $p = 0.68$), foraging ($r = 0.22$, $df = 36$, $p = 0.20$), nor times bitten ($r = -0.04$, $df = 36$, $p = 0.81$) from pre-removal to post-removal treatments. There were no significant associations between ovary development and changes in behavioral rates between removal and return treatments.

Rates of abdominal vibrations and ovary development were positively associated throughout treatments. There was a non-significant positive association between ovary development and pre-removal rates of vibrations ($t_{32} = 1.88$, $p = 0.07$). Both post-removal and worker return rates of vibrations were significant positive predictors of ovary development (removal: $t_{32} = 2.75$, $p = 0.01$, Fig. 2; return: $t_{23} = 2.52$, $p = 0.02$).

Discussion

Social interactions are important for regulating overall colony activity and distributing tasks among individuals in a diversity of social insects (Gamboa et al., 1990; Gordon, 1996; Fewell, 2003; Wenseleers et al., 2006; O'Donnell and Bulova, 2007). In some *Polistes* paper wasps, queens participate in the majority of social interactions, acting as central pacemakers of colony activity (Reeve and Gamboa, 1983, 1987; Gamboa et al., 1990). However, recent studies suggest that the workers of at least some species of IF paper wasps can influence each other's task performance (Chandrasekara and Gadagkar, 1992; O'Donnell, 1998a; Jha et al., 2006). Our findings, building on those of O'Donnell (1998a) and Jha et al. (2006), suggest that *P. instabilis* colony activity is decentralized. Previous research on IF paper wasps may have overlooked the importance of worker-worker interactions in task performance because of an emphasis on competition between queens and workers for current reproduction. Our research suggests that competition among workers for future reproductive opportunities may actually contribute to the decentralized aspects of division of labor in *P. instabilis*.

Unlike other *Polistes* species (Reeve and Gamboa, 1983, 1987; Gamboa et al., 1990), *P. instabilis* queens do not initiate the majority of interactions, and our data suggest that workers responded to changes in colony structure more than queens (e.g., greater changes in abdominal vibration rates than queens). Our data also show that worker responses to changes in social structure are highly variable. Many workers modified their rates of

foraging and abdominal vibrations following the dominant worker removals, and again once the dominant workers were returned. Our study suggests that, as predicted, dominance and foraging behaviors are opposing individual responses to colony changes. Pre- and post-removal rates of foraging and abdominal vibrations were negatively associated. This parallels findings in queen removal/return studies (Premnath et al., 1996), in which workers increased rates of aggression once queens were removed, and then reduced them once queens were returned. Furthermore, the individuals that vibrated at higher rates post-removal also decreased their rates of foraging. When dominant nest mates return to the nest, these female workers then appear to revert to previous behavioral profiles, reducing their aggressive behaviors and increasing their rates of foraging.

Like previous research on queen removal/replacement, our data on worker removal/replacement suggest that individual behavioral and physiological changes following nest mate removal are related to shifts in the reproductive queue, with some workers replacing the dominant workers that were removed. First, females with greater rates of physical aggression and abdominal vibrations increased rates of dominance behaviors after nest mate removals, whereas more subordinate nest mates responded to nest mate removals with increased foraging. Second, the individuals that increased their aggression rates post-removal also received less aggression from nest mates. Third, workers responded to the removals with a greater change in abdominal vibration rates than queens, and worker's rates of vibrations were consistently positively associated with greater ovarian development. The rate of abdominal vibrations was the only significant behavioral correlate of ovary development, suggesting that abdominal vibrations function in worker reproductive competition.

Besides aggressive interactions such as antennal clashing and biting (Pardi, 1948; West-Eberhard, 1969; Röseler et al., 1980), queens and workers may indicate their dominance status via abdominal vibrations (Wasps: Downing and Jeanne, 1985; Keeping, 1992; Bees: Schneider et al., 1998; Schneider and Lewis, 2004; Hyland et al., 2007; but see Savoyard et al., 1998; Cummings et al., 1999). The patterns we observed suggest that abdominal vibrations indicate social status in *P. instabilis*. Abdominal vibrations may not only signal dominance, but may also influence task performance. Because abdominal vibrations are transmitted through the nest, they potentially reach all wasps present on the comb. Such broadcast signals can presumably advertise colony needs to a large number of individuals, and therefore be more effective than biting interactions which can enlist only one individual per interaction (Brennan, 2007). Alternatively, abdominal vibrations may be used in adult-brood interaction to increased larval saliva secretion for newly dominant workers (Savoyard et al., 1998; Cummings et al., 1999; Brennan, 2007). Further studies examining rates of vibrations in single versus multiple *P.*

instabilis foundresses and overall rates throughout the colony cycle are necessary to more fully identify the recipients of these signals (e.g. Brennan, 2007).

Competition among reproductively capable, but not currently ovipositing, individuals may have preceded the decoupling of social and reproductive dominance in more advanced eusocial societies, such as worker policing of nest mate reproduction (Gobin et al., 2001; Kawabata and Tsuji, 2005; Wenseleers et al., 2004a,b, 2006) or worker regulation of foraging (O'Donnell, 2001, 2006). Conflict over current (queen-worker) and future reproduction (worker-worker) may be the ancestral basis for many communicative interactions that affect task performance (O'Donnell and Bulova, 2007). Increases in colony size, and the evolution of preimaginal caste determination in highly eusocial species, may have obscured or negated hierarchical reproductive queues. Larger colonies may have required a more even distribution of pathways for information about colony needs. Future studies investigating the effects of colony size on worker reproductive conflict may provide useful information about shifts from centrally controlled to self-organized societies.

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