EFFECTS OF EXPERIMENTAL FORAGER REMOVALS ON DIVISION OF LABOUR IN THE PRIMITIVELY EUSOCIAL WASP POLISTES INSTABILIS (HYMENOPTERA: VESPIDAE)

by

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Summary

Experimental forager removals were performed to assess the mechanisms by which Polistes instabilis colonies regulate their intake of nectar and water. Most foragers gathered nectar, while water was collected by a small number of fixated foragers. Removal of the most active water foragers led to decreases in water foraging, followed by recruitment of a single replacement water forager. Replacement water foragers were usually recruited from among the workers that had previously collected water at low rates. Water forager removals showed that some workers specialized on water collection, but these workers differed in their thresholds of response to colony need for nest cooling. Removal of the most active nectar foragers led to longer-lasting (one to three days) decreases in colony nectar collection rates, and resulted in replacement nectar foragers being recruited away from other foraging tasks or from nest tasks. Nectar forager removals were followed by increases in rates of dominance interactions among nest wasps; this response was not observed after water forager removals. Dominance interactions among workers appear to regulate nectar foraging in P. instabilis. The mechanisms of regulation of foraging differ among materials, and correspond to their maximum rates of collection, predictability of resources, and on the costs of short-term changes in supply to the colony.

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Introduction

To the extent that colony-level selection has shaped social insect worker behaviour, division of labour (polyethism) is assumed to be adaptive. Workers are expected to modify which tasks they perform in response to changes in colony needs, such that colony survival and reproduction are maximized (Oster & Wilson, 1978; Calabi, 1988). However, insect colonies are composed of idiosyncratic subunits (Jeanne, 1991): individual marking has shown that workers are not behaviourally identical. For example, even similarly aged nest mates can vary in specialization on tasks (O’Donnell & Jeanne, 1992) and rates of behavioural development (O’Donnell & Jeanne, 1993, 1995a). Because workers are idiosyncratic, individual behavioural differences are a key component to the structure of insect colonies (Robinson, 1992). A fuller understanding of insect colony function will depend on analysis of the regulation of individual worker behaviour. Quantification of how workers respond to experimental manipulations of colony need for task performance has become an important tool in studies of division of labour (Wilson, 1985).

Social insect workers must make such decisions as which tasks to perform and the rate at which to perform a given task. However, workers’ decisions are made based on incomplete information. Even in small insect societies, any individual worker is unlikely to be able to simultaneously and accurately assess the level of colony need for all tasks. This raises the question of which cues are used by workers when deciding which task(s) to perform. Workers may respond directly to physical cues that indicate the need to perform certain tasks (e.g. an increase in CO₂ concentration is perceived directly by workers and leads to nest fanning in honey bees; Seeley, 1974). Workers may also respond to social cues. For example, activity or task performance by nest mates (Dew & Michener, 1981), and dominance interactions (Akre et al., 1976; O’Donnell & Jeanne, 1995b), may be used as indirect social cues indicating the level of colony need for particular tasks.

Furthermore, workers often differ in their reactions to a given set of physical and social stimuli. Nest mates do not behave identically under the same or similar conditions, and recent models for the bases of individual differences in task performance have posited that workers differ in their thresholds of response to a given change in colony conditions (Page &
Different thresholds of response may be based on prior experience (Plowright & Plowright, 1988; Theraulaz et al., 1991) or on genetic variation among workers (Fewell & Page, 1993).

Eusocial wasps of the genus *Polistes* (Hymenoptera: Vespidae) are important but underutilized subjects for studies of regulation of division of labour. *Polistes* spp. are primitively eusocial relatives of solitary and advanced eusocial Vespidae (Carpenter, 1982). Information on worker behaviour in *Polistes* spp. may provide the basis for comparative inferences on how polyethism has evolved along with changes in colony size and social complexity in wasps (O'Donnell, 1995). *Polistes* spp. colonies are typically small (mature populations of fewer than 150 adults; Reeve, 1991), allowing accurate measurement of colony-wide behaviour. The exposed combs of *Polistes* spp. nests permit detailed records of individual behaviour (West-Eberhard, 1969). The present study focused on regulation of foraging behaviour, which has been the subject of prior studies of polyethism in *Polistes* spp. (Dew & Michener, 1981; Reeve & Gamboa, 1983; Theraulaz et al., 1992) and in other eusocial Vespidae (O'Donnell & Jeanne, 1990; Jeanne, 1996). Foragers must respond to both intrinsic (social and developmental) and extrinsic (environmental) changes in colony needs in order to maintain levels of food and building material input.

I quantified short-term individual and colony-level responses to experimental forager removals in the wasp *Polistes instabilis* de Saussure. Forager removal mimicked changes in colony social structure that might occur naturally when foragers are lost to senescence or to predators. I minimized the effects of long-term changes in colony foraging requirements that occur during colony development (West-Eberhard, 1969; Hoshikawa, 1981; Tsuchida, 1991) by quantifying behavioural changes that occurred over short periods of time (several hours to several days). As noted by Jeanne (1991), failure to account or control for colony developmental changes have made some studies documenting individual differences in *Polistes* spp. forager behaviour difficult to interpret.

Removal of foragers changed the level of colony need for performance of foraging tasks by temporarily reducing the rate of arrival of the materials they had collected. I assumed that the colonies’ need for the affected material would remain constant over the course of each experimental trial, and therefore expected changes in foraging behaviour of nest mates that
would adjust the colonies’ material collection rates toward pre-manipulation levels (the corrective response, in the terminology of Jeanne, 1996). The first goal of this study was to assess the roles of two aspects of individual behaviour (task specialization and thresholds of response) in the colonies’ corrective responses. The second goal was to test whether changes in social interactions among wasps on the nest, especially dominance interactions, play a role in the colonies’ adjustment of foraging rates.

**Forager specialization and thresholds of response**

Although *Polistes* spp. workers often engage in a diversity of tasks and exhibit little age polyethism, task specialization occurs in a number of species. Forager specialization on materials has been documented in un-manipulated *Polistes* spp. colonies (Owen, 1962; Strassmann *et al.*, 1984; Post *et al.*, 1988), but whether forager specialization persists following changes in colony conditions (O’Donnell & Jeanne, 1990) has not been tested in *Polistes* wasps. I tested for the existence of forager specialization on materials in *P. instabilis* through observation and experimental manipulations. During control observations, I asked whether individuals devoted most of their foraging effort to collecting a single material, and whether a disproportionate amount of colony foraging effort for that material was due to a subset of the active foragers. I tested experimentally whether forager specializations would persist following changes in colony need by removing nectar and water foragers. If forager specialization persisted, the individuals responding to forager removals would be recruited from among those that had performed the affected task, albeit at lower rates, prior to the manipulation (O’Donnell & Jeanne, 1990). Alternatively, if specialization did not persist, then switching among foraging tasks and activation of non-foragers would occur in response to forager removals.

Independently of task specialization, workers could differ in their thresholds of response to a given task-inducing stimulus (Page & Robinson, 1991). I tested for individual differences in response thresholds by removing the most active water foragers. If thresholds of response were similar or identical among the workers that collected water, then foragers would be replaced immediately following removal, assuming a constant or increasing level of colony need for nest cooling. Furthermore, the recruited workers would forage at the same rates as the original foragers. Alterna-
tively, if water foragers differed in response thresholds, the recruitment of new foragers would be delayed and/or their foraging rate would be diminished relative to the removed foragers, even though the stimulus or need for water foraging remained constant or increased following removal.

**Dominance interactions**

Gamboa et al. (1990) posited that queens are the principle organizers of colony foraging activity in *Polistes* spp. colonies. Queens appear to play a major role in regulating the foraging behaviour of workers in the temperate species *P. fuscatus* (Reeve & Gamboa, 1983, 1987). Queen activity, particularly aggression (dominance behaviour) directed toward certain workers, has been shown experimentally and observationally to influence foraging rates in *Polistes* spp. workers (Strassmann & Meyer, 1983; Gamboa et al., 1990). However, dominance interactions among workers have also been implicated in stimulation of foraging in wasps (reviewed in O'Donnell & Jeanne, 1995b). I tested for queen and worker dominance effects by measuring whether changes in rates of dominance interactions corresponded to the changes in foraging behaviour that followed nectar and water forager removals. If dominance interactions lead to increases in foraging, then rates of dominance would increase following forager removals, and would correspond to increases in foraging rates.

**Methods**

**Subject colonies**

Data were collected from five post-worker emergence *Polistes instabilis* colonies in Guanacaste Province, Costa Rica. Colony A was located at the Organization for Tropical Studies field station at Palo Verde (10°16'N, 85°14'W); colonies B through E were located at Centro Ecológico La Pacifica (10°25'N, 85°07'W), 5 km NW of the town of Cañas. Subject nests had been constructed on vegetation 0.5 to 1.5 m above the ground. Some obscuring vegetation was clipped from around colonies B, C, and E, which may have increased exposure to the sun; nest sites were otherwise unmanipulated. All adults present upon discovery of the colonies were individually marked with either model airplane dope (colony A) or paint pens (other colonies). Additional adults were marked on the days they emerged. The study was conducted between 19 July and 27 September 1988 (colonies A through D), and between 13 and 18 August 1997 (colony E). Colonies were observed one at a time for 3 to 11 days each. Queens were distinguished by the performance of egg laying; one female per colony laid eggs during the study.
Control observations

Control observations were conducted on 1 to 3 days immediately preceding each experimental manipulation. During observation periods I recorded behavioural data while seated 0.5-1 m from the nests, facing the cell openings. Data on all forager arrivals were recorded into a portable tape cassette player, comprising time to the nearest min, forager identity, and which material was transferred by the forager to nest mates, larvae, or onto the nest within 5 min of arrival. Times of forager departures were also noted to the nearest min in colonies B through E. Observations were continuous except during periods of heavy rain, when foraging usually ceased (pers. obs.). Daily observation periods (including experimental observations, below) lasted approximately 3:40 h on average. Behaviour of all wasps on the nests was recorded during scan samples every 10 min, following an ethogram similar to those of Post et al. (1988) and Tsuchida (1991). At colony B, only presence/absence of adult wasps was recorded during scans conducted every 15 min. Other than allogrooming, all behavioural acts involving physical contact among workers (e.g. biting and grappling), as well as chasing and lateral vibrations of the gaster against the nest (Gamboa & Dew, 1981), were classified as dominance interactions.

Rates of foraging and of dominance interactions during the control observations were used as a colony-specific baseline against which to compare rates of performance following experimental forager removals (below). Workers to be removed during experimental trials were selected on the basis of their high foraging rates during the control observations. Data on forager specialization and task partitioning collected during control periods were presented elsewhere (O’Donnell, 1995).

Water forager removals

One or two workers identified as the most active water foragers during control observations were removed from their nests. Foragers were removed by grasping them with forceps and allowing them to climb on, then lifting them from the nest (West-Eberhard, 1969). This was usually accomplished without visibly alarming their nest mates. Removed water foragers were held in a small mesh enclosure with ad libitum water and sugar solution until they were returned to their nests. Behavioural data were collected during the experimental trials as described above for 1:45 to 2:45 h following removals. During water forager removal experiments, the number of wasps engaged in fanning the nest was used as an additional measure of the colony’s need for nest thermoregulation. A total of four water removal trials were conducted on colonies A, B, and C (two trials). In trial 1 a second water forager was removed after she responded to the first removal.

Nectar forager removals

The two or three most active nectar foragers, which together had accounted for at least 25% of the total colony nectar foraging effort during control observations, were removed from their nests. Nectar foragers were removed either the evening before the trial began, or on the day of the trial within 0.5 h of the start of experimental observations. Behavioural data were collected as above for one to three days following nectar forager removals. A total of four trials were conducted on colonies C (two trials), D, and E.
Nest wasp removal

To test for effects of dominance interactions among workers on nectar foraging, two workers engaging in dominance interactions at high rates were removed from their nest in one trial. The workers that were selected for removal spent most of their time on the nest and rarely foraged (they did not collect nectar) during control observations. They were highly aggressive during control observations, biting and chasing nest mates more often than other wasps.

Statistical analyses

Foraging rates were calculated using time elapsed after the first observed water or nectar forager arrival at the start of each day's observations. Following Jeanne (1996), I divided the experimental observation period following each water forager removal into initial and corrective response periods. The initial response period began at the onset of observations and ended with the first ten min period where the number of forager arrivals equaled or exceeded the mean number per 10 min during control observations. The corrective response period followed the initial response period, and lasted until the end of a trial or until the next manipulation. Nectar foraging rates were analyzed on a per-day basis. I used the Kolmogorov-Smirnov test (Sokal & Rohlf, 1981) to test the null hypothesis that the cumulative distribution of water forager arrivals over time during each initial and corrective response period did not differ from the distribution of arrivals during the control period. The effects of water forager removals on colony-wide rates of nest fanning were assessed with the Kruskal-Wallis test corrected for ties (Sokal & Rohlf, 1981). For nectar forager ($N = 4$ trials) and nest wasp ($N = 1$ trial) removals, I tested for equality of nectar foraging rates between treatment days using survival analysis (SAS, 1985). I tested whether nectar foraging rates on the first day following forager or nest wasp removal were lower than rates on control days, and whether rates on subsequent days were higher than on the first day following removal (one-tailed tests). For nectar forager removals, multiple linear regression (GLM procedure; SAS Institute, 1985) was used to test for effects of the number of days elapsed since forager removal on rates of dominance interactions across colonies.

Results

Patterns of forager behaviour

Foraging rates were relatively low in the late afternoon (pers. obs.); all behavioural data presented were collected in the morning to early afternoon (between 06:40 and 12:45 h local time). Foragers collected four materials: wood pulp for nest construction, water for nest cooling, and food (nectar and insect prey). Water foragers spread their loads directly onto the nest surface; liquid loads that were spread on the nest were never shared with nest mates, nor were they offered to larvae. Nectar and prey loads were shared with other adults and/or given to larvae. Wood pulp loads were
either partitioned with nest mates or used by the forager to lengthen the walls of brood cells. Prey and pulp foraging rates were not analyzed. Within colonies, individuals varied widely in their rates of nectar and water collection (Fig. 1).

**Water forager removals**

Water was collected by foragers from colonies A, B, C, and E whose nests were exposed to direct sun for at least part of the day. Relative to nectar, few foragers (24-50% of all foragers in colonies that collected water; Fig. 1) collected water. When the nests were insolated, water was

![Graph showing foraging rates of Polistes instabilis workers from five subject colonies.](image)

**Fig. 1.** Distributions of nectar (hatched bars) and water (black bars) foraging rates of *Polistes instabilis* workers from five subject colonies. Each bar represents the foraging rate of one worker; workers are presented in decreasing order of their summed nectar and water foraging rates. Numbers of additional foragers that collected only prey and pulp were: colony A — 1, colony B — 1, colony C — 0, colony D — 5, colony E — 3.
collected at high rates, with a load arriving at the colony every 3.21 to 10.37 min on average during control periods (range of mean elapsed time between water load arrivals across colonies A, B, & C; O'Donnell, 1995). Foragers spent an average of 1.91 to 6.26 min away from the nest on water trips (mean time to collect a water load, colonies B & C, respectively; O'Donnell, 1995).

During all control periods, a single worker accounted for a disproportionate amount (at least 40%) of the colony's water collection (Table 1). When the most active water foragers were removed, they were not immediately replaced. Water foraging rates decreased following every water forager removal, and were significantly lower than the control rate during three of the five initial response periods (Fig. 2). In trials 1 and 4, water foraging rates did not recover to control levels following the first forager removal, and a corrective response period could not be defined. However, water foraging rates recovered and exceeded control foraging rates during corrective response periods, significantly so in trial 2.

Two types of evidence suggest that decreases in need for nest cooling did not cause lower water foraging rates following forager removals. First, weather conditions did not change noticeably, and nests remained insolated, throughout the experimental trials. Water droplets placed by the removed foragers evaporated within a few minutes, long before the end of the initial response periods (pers. obs.). Second, rates of nest fanning suggested that the need for cooling remained high following forager removals. In two of the three trials where nest fanning behaviour was recorded, median rates of fanning (number of wasps fanning per scan) did not differ significantly among treatments (Kruskal-Wallis test with correction for ties; trial 3, $H = 4.72$, df = 2, $p > 0.05$; trial 4, $H = 0.03$, df = 2, $p > 0.75$). In trial 1, the fanning rate did not differ between the control and first forager removal treatments ($H = 0.10$, df = 1, $p > 0.75$), but was lower during the second forager removal treatment ($H = 16.30$, df = 1, $p < 0.001$). However, water foraging rates were not significantly depressed during the second forager removal treatment (Fig. 2). Although queens typically spent more time on the nests than other wasps (O'Donnell, 1995), they were never observed fanning.

A single worker replaced the removed water forager(s) as the water specialist (accounting for $> 50\%$ of the colony’s water trips) following
### Table 1. Water foraging rates of Polistes instabilis workers during experimental manipulations

<table>
<thead>
<tr>
<th>Trial 1</th>
<th>Control</th>
<th>First forager removal</th>
<th>Second forager removal</th>
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<tr>
<td>Id</td>
<td>For. rate</td>
<td>% effort</td>
<td>Id</td>
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<tr>
<td>15</td>
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<td>*</td>
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<tr>
<td>6</td>
<td>3.49</td>
<td>(18.6%)</td>
<td>*</td>
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<tr>
<td>12</td>
<td>2.18</td>
<td>(11.6%)</td>
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<td></td>
<td>Total</td>
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<th>Forager returned</th>
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<tr>
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<td>% effort</td>
<td>Id</td>
</tr>
<tr>
<td>124</td>
<td>10.99</td>
<td>(76.5%)</td>
<td>*</td>
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<tr>
<td>33</td>
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<tr>
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<th>Forager returned</th>
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<td>For. rate</td>
<td>% effort</td>
<td>Id</td>
</tr>
<tr>
<td>3</td>
<td>10.22</td>
<td>(90.5%)</td>
<td>*</td>
</tr>
<tr>
<td>11</td>
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<td>(4.8%)</td>
<td>11</td>
</tr>
<tr>
<td>Total</td>
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<td>Total</td>
<td>5.54</td>
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<tr>
<td>3</td>
<td>1.92</td>
<td>(8.3%)</td>
</tr>
<tr>
<td>Total</td>
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<td>Total</td>
</tr>
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For each trial, the most active water foragers’ identity numbers are shown (Id), followed by their water foraging rate in trips/hour, and the percent of the colony’s water trips they contributed (% effort). Within a trial, manipulations are ordered temporally from left to right, starting with the control observation period. Foragers that were removed in a given manipulation are represented by an asterisk (*). The colony total water foraging rate (trips/hour) is shown for each treatment period.
Fig. 2. Effects of water forager removals on water foraging rates in *Polistes instabilis*. Cumulative numbers of water loads arriving at nests are plotted against time; the slope of each curve indicates the rate of water foraging. Observation time began with the first water forager arrival for each trial. Experimental manipulations are marked at the time of their occurrence with an arrow pointing up in the case of forager removals, and down in the case of foragers being returned to the nest. Treatments and response periods (see Methods) are indicated by symbols as follows: control observations — filled circles; first manipulation initial response — open circles; first manipulation corrective response — filled triangles; second manipulation initial response — open triangles; second manipulation corrective response — filled squares. Response periods where the water foraging rate differed significantly from the control rate are indicated by ** (Kolmogorov-Smirnov test, $p < 0.01$).

every water forager removal (Table 1). In some cases, a secondary water specialist also became active, accounting for $\approx 20\%$ of the colony’s water trips (Table 1). Replacement water foragers were usually individuals that had collected water at a low rate prior to the manipulation. The only exception to this pattern was seen in trial 2, where a worker that had previously collected nectar at a low rate became the water specialist. In trial 1, the first replacement water forager was removed after 1:20 h of observation, and was in turn replaced by another active water specialist
In trials 2 and 3, the original water specialists were returned to the nest after a replacement forager had become active. In both cases, the original forager resumed water collection. Replacement foragers also continued to collect water in both cases, leading to increases in the colony-wide rates of water foraging (Fig. 2; Table 1). Colony-wide rates of dominance interactions did not change consistently following water forager removals (effect of treatment period nested within trials on per-scan rate of dominance interactions: $F_{3,4} = 3.47, p > 0.10$).

**Nectar forager removals**

In contrast to water, nectar was gathered by most foragers in each colony (85-96% of foragers; Fig. 1). Nectar trips often required greater time away from the nest for individual foragers (29.97 to 46.71 min; range of mean time to collect a nectar load across colonies B, C, & D; O’Donnell, 1995) than did water trips (see above). Consequently, individual nectar foragers returned to the nest less frequently than did water foragers.

The removed nectar foragers contributed more of the nectar collection during control periods than expected if all workers had foraged at equal rates (percent of nectar foragers removed/percent of nectar foraging they contributed; trial 1: 33/78; trial 2: 50/70; trial 3: 12.5/25; trial 4: 20/39). Removals of the two or three most active nectar foragers were always followed by decreases in nectar foraging rates on the following day; these decreases were significant in 3 of 4 trials (Fig. 3; survival analysis Wilcoxon test, df = 1; trial 1: $\chi^2 = 9.53, p < 0.01$; trial 2: $\chi^2 = 8.86, p < 0.01$; trial 3: $\chi^2 = 2.10$, NS; trial 4: $\chi^2 = 4.62, p < 0.05$).

In the three trials where foraging was monitored for three days following nectar forager removal, colony-wide nectar foraging rates eventually increased significantly above the first post-manipulation day rates (Fig. 3; survival analysis Wilcoxon test comparing nectar foraging rate on the first day after manipulation with the third day after manipulation, df = 1; trial 2: $\chi^2 = 13.08, p < 0.001$; trial 3: $\chi^2 = 3.96, p < 0.05$; trial 4: $\chi^2 = 3.59, p < 0.05$). Nectar foraging rates eventually surpassed control rates in two trials (Fig. 3). Increases in individual nectar foraging rates accounted for little of the colonies’ recovery from forager removals. Only on the third day following removal in trial 2 did previously active foragers increase their total foraging rate by more than 10% above the control rate (Fig. 3).
Fig. 3. Effects of nectar forager removals on nectar foraging rates in *Polistes instabilis*. Contributions to total colony nectar foraging are indicated in each treatment period for the removed workers (black bars), other nectar foragers active during the control period (single-hatched bars), and new nectar foragers recruited after removal (double-hatched bars). Lines above the bars indicate results of statistical tests (survival analysis Wilcoxon test) for differences in foraging rates between the treatment periods overlapped by ends of the lines. Significant differences in nectar foraging rates are indicated by * (p < 0.05) and ** (p < 0.01).

Instead, the increased nectar foraging rates were due in large part to the recruitment of new workers (number of new nectar foragers following removal/total number of nectar foragers; trial 2: 11/14; trial 3: 7/15; trial 4: 6/15. In trial 3, the queen foraged for nectar on the third day after forager removal. This was the only observation of queen foraging in the study). Newly recruited foragers contributed substantially to the recovery of nectar foraging rates following removals (Fig. 3). Some of the recruited workers either switched from foraging for other materials or added nectar foraging to the set of materials they collected (trial 2: 2 foragers; trial 3: 3 foragers;
Fig. 4. Effects of nectar forager removals on rates of dominance interactions among workers in *Polistes instabilis*. Because absolute rates of dominance interactions varied among colonies, the per scan-sample rates are shown as proportions of the maximum rate observed for each colony. Dominance interaction rates increased significantly over time following nectar forager removals (linear multiple regression).

Queens did not engage in dominance interactions with workers in scan samples during nectar forager removal experiments. Workers engaged in dominance interactions, and rates per scan-sample of dominance interactions among workers increased over time following nectar forager removals (Fig. 4; effect of days from start of trial nested within trials on per-scan rate of dominance interactions $F_{3,8} = 5.39, p < 0.05$). One or two workers that spent most of their time on the nests became aggressive following nectar forager removals, biting and chasing nest mates at high rates and apparently stimulating forager departures (pers. obs.). In the trial where two aggressive nest wasps were removed, nectar foraging rates declined significantly on the following day (Fig. 5; survival analysis Wilcoxon test $\chi^2 = 5.62$, df = 1, $p < 0.05$). On the third day after removal, these wasps were returned to the nest and nectar foraging increased significantly (Fig. 5; survival analysis Wilcoxon test $\chi^2 = 4.87$, df = 1, $p < 0.05$). Colony-wide rates of dominance interactions also declined following removal of the aggressive workers, and increased again following their return.
Fig. 5. Effect of removing dominant workers on nectar foraging rate (upper bars) and rate of dominance interactions (lower bars) in *Polistes instabilis*. Lines above the top bars indicate results of statistical tests (survival analysis Wilcoxon test) for differences in foraging rates between the treatment periods overlapped by ends of the lines. Significant differences in nectar foraging rates are indicated by * (p < 0.05).

**Discussion**

*Forager specialization on materials*

Specialization on water collection by a small number of fixated foragers, at least on short time scales of several hours to several days, appears to be widespread in eusocial Vespidae, both in primitively eusocial (Itō & Yamane, 1992; this study) and in advanced eusocial species (Forsyth, 1978; O’Donnell & Jeanne, 1990, 1992). *Polistes instabilis* water forager specialization was an important component of the colony response to decreased water supply. Water was collected by a small number of fixated foragers, and the response to water forager removal usually involved changes in foraging rate, rather than switching among tasks. It is often assumed that differences in individual experience lead to worker fixation on tasks, but the possibility that genotypic differences among individuals play a role in determining task specialization (Page et al., 1995; O’Donnell, 1996) is untested in primitively eusocial wasps. Polyandry (queens mating with
more than one male) increases genotypic diversity within colonies, and is documented or suspected in a number of *Polistes* spp. (Metcalf & Whitt, 1977; Metcalf, 1980; Strassmann *et al.*, 1989).

In contrast to water, nectar collection did not depend on the efforts of a few, fixated foragers. In response to nectar forager removals, behavioural flexibility on the part of nest mates was important. Many recruited nectar foragers switched from on-nest tasks or from collecting other materials. Changes in the size and sugar concentration of loads collected by foragers were not measured, and increases in these variables may have compensated for reduced rates of nectar load arrival at the colony level caused by forager removals. However, bumble bee foragers did not change load size or concentration in response to manipulation of colony food stores that affected their colonies’ foraging rates (Cartar, 1992), suggesting that active foragers may already be collecting nectar as rapidly as possible.

**Individual behaviour and regulation of foraging rates**


Foraging is not a single task in *P. instabilis*. The materials that workers collect differ in degree of short-term individual task fixation, collection time, and the effects of decreases in collection rate on the colony. The results of this study suggest that the collection of nectar and water have distinct mechanisms of regulation at the colony level. Differences in the regulation of foraging correspond to the short-term effects on colony fitness of changes in the arrival rate of a given material. For example, there is an almost immediate cost to not cooling the nest, especially when the nest is isolated. Overheating can cause brood mortality and possibly failure of the colony in a very short span of time. Water for cooling can be collected rapidly from relatively stable, large sources by experienced foragers. The
need for a quick response to changes in the water supply to the nest, and
the ability of a small number of individuals to collect large amounts of
water quickly, may have selectively favored colony reliance on individual
water specialists to respond to changes in water arrival rates.

Conversely, the rate of flow of nectar to the nest may be more vari­
able, depending on the availability and ease of location of temporally and
spatially unpredictable nectar and honeydew sources. Active P. instabilis
nectar foragers showed little or no ability to increase their foraging rates in
response to forager removals. If nectar is difficult to locate and collect, ac­
tive nectar foragers may not be able to greatly increase their foraging rates.
Changes in the rate of arrival of one or a few nectar foragers, such as those
induced by this studies' manipulations, may often indicate changes in nec­
tar resource availability. Although Polistes spp. do not usually store large
amounts of food per se in their nest (but see Strassmann, 1979), changes
in the incoming food supply may be temporarily buffered by the larvae,
which can store and secrete nutritious fluids for adult nourishment (Hunt,
1984). These factors may have selected for decreased colony reliance on
specialized nectar foragers, and favored task switching over changes in
collection rate at the individual level.

Response thresholds

The colony responses to P. instabilis water forager removals suggest that
nest mates differed in their perception or assessment of colony need for
water collection. The stimuli indicating need for nest cooling, including
degree of exposure to the sun and presumably temperature, remained con­
stant or increased following water forager removals, yet there was a lag
before replacement foragers became active. In some cases, the recruited
forager(s) collected water at lower rates than the initial water specialist.
Most of the recruited foragers had previously gathered water, and therefore
were familiar with the location and handling of water. The lag in response
cannot be explained by the need for recruits to learn an unfamiliar task,
and suggests that water foragers differed in their thresholds of response to
colony need for water collection.

It appears that the responses to cues used by P. instabilis foragers in
deciding when to stop working are different from those that they use in de­
ciding when to start. Individuals' thresholds of response to a given colony
need (nectar or water collection) seemed to decrease once they began foraging, and they stayed active even in the face of increased overall levels of supply to their colonies. Positive feedback from successful task performance, as proposed by Plowright & Plowright (1988), could play a role in sustaining foraging activity in *P. instabilis*. Interestingly, Jeanne (1996) found the opposite pattern in *Polybia occidentalis* foragers responding to experimental nest damage: decreased need for foraging rapidly led to workers dropping out of the foraging force, relative to the amount of time of increased need for foraging that elapsed before they became active. It may be the case that the *P. instabilis* water and nectar foraging rates would have returned to pre-treatment levels if given sufficient time. However, changes in forager behaviour appear to last much longer in *P. instabilis* than in *P. occidentalis*. One possible reason for this difference is that *P. instabilis* foragers rely more heavily on information about colony need that they perceive directly from environmental cues. Unlike *P. occidentalis*, tasks are rarely partitioned among *P. instabilis* workers (Jeanne, 1986; O’Donnell, 1995), allowing less opportunity for social feedback among nest mates that could indicate changes in colony need for a given foraging task.

*The role of the queen and dominance interactions*

In small insect societies, the queen can play a large role in regulating worker behaviour via direct interactions. Queens are thought to act as regulators of colony activity (Gamboa *et al.*, 1990). However, this study does not support a direct role of queen dominance in regulating the activity of *P. instabilis* foragers. The correlative and experimental data suggest instead that dominance interactions among workers regulate nectar foraging rates, and the colony’s ability to respond to changes in resource input. These results must be interpreted with caution because the scan sampling method I employed may have missed important social interactions that were rare and short in duration. The role of the queen in regulating responses to forager removals could be studied further by measuring all occurrences of dominance at the nest and recording the identities of participants in dominance interactions.

Responses to water forager removals were not dependent on changes in rates of dominance interactions. Water collection must recover more quickly from changes in supply than nectar collection, and a corrective
response brought about through dominance interactions may be too slow to provide sufficient thermoregulation. The data presented suggest that water collection is regulated by direct assessment of need, which varies among individuals, and negative feedback from the results of nest mates’ labour.

References


