Forager specialization and the control of nest repair in *Polybia occidentalis* Olivier (Hymenoptera: Vespidae)

S. O’Donnell and R.L. Jeanne
Department of Entomology, University of Wisconsin, Madison, WI 53706, USA

Received December 1, 1989 / Accepted June 26, 1990

**Summary.** We measured patterns of individual forager specialization and colony-wide rates of material input during periods of response to experimental nest damage and during control periods in three colonies of the tropical social wasp *Polybia occidentalis*.

1. Most foragers specialized on gathering a single material. While active, foragers rarely switched materials, and most switching that did occur was between functionally related materials — prey and nectar (food materials) or wood pulp and water (nest materials).

2. Individuals differed greatly in activity level, here expressed as rate of foraging. Workers that foraged at high rates specialized on a single material in almost all cases. Specialized, highly active foragers comprised a minority (about 33%) of the working foragers in each colony, yet provided most of the material input.

3. Individuals that responded to experimental nest damage by foraging for nest materials did not gather food on days preceding or following manipulation.

4. On the colony level, nectar and prey foraging rates were not affected by foraging effort allocated to nest repair within days, or when comparing control days with days when damage was imposed. The emergency foraging response to nest damage in *P. occidentalis* did not depend on effort recruited away from food foraging.

---

**Introduction**

A defining feature of caste in social insects is the phenomenon of specialization among workers; not all nonreproductive individuals in an insect colony are equally likely to perform a given task (Wilson 1971; Oster and Wilson 1978). The caste to which a given worker belongs can be influenced by its age (Seeley 1982; Calabi et al. 1983) or morphological features (Herbers 1980; Wilson 1983). Individual variation in the rate of behavioral development, activity level, and degree of specialization are often superimposed on more rigid caste-delimiting traits (Oster and Wilson 1978; Gordon 1984; Jeanne et al. 1988).

Such variability is especially interesting in light of recent theoretical and empirical studies linking individual worker behavior patterns to colony function in social insects. Interindividual differences in behavioral specialization and activity level enhance efficiency of task performance (Heinrich 1976; Plowright and Plowright 1988) while allowing for rapid and reliable colony responses to changing social and environmental conditions (Herbers 1981; Calabi and Traniello 1989; Gordon 1989). Specialization by individuals on a subset of the tasks normally performed by their caste has been documented in many taxa of social Hymenoptera. For example, in some ants social carrying (Abraham and Pasteels 1980) and foraging behavior (Lenoir and Ataya 1982; Schmid-Hempel 1984) are characterized by greater variability among than within individual workers of similar age. Foraging bees (Apidae) are well-known for their propensity to specialize on a specific nutritional material (pollen or nectar) and on particular flower species (reviewed by Eickwort and Ginsberg 1980; Kolmes 1985). A current challenge to insect sociobiology is to establish how specialization by individuals interfaces with changing colony needs. In addition to their dynamic population structure, insect societies in nature are faced with such contingencies as attacks by predators and the appearance of ephemeral food sources. There are two mechanisms of flexible colony response to rapidly changing conditions. The first is reallocation of labor, whereby active workers switch among tasks. In this case, ongoing work is interrupted at some cost to the colony (Gordon 1989a). The second involves changes in activity level. Here, the rate of task performance by workers is predicted to increase. This implies a maintenance cost for an inactive reserve force, or that active workers usually perform their duties at less than maximum rates (Verron 1981; Kolmes 1985b). These mechanisms of colony flexibility are not mutually exclusive, and both methods may be employed in concert.
Recent work on the tropical swarm-founding wasp *Polybia occidentalis* showed that the tasks associated with nest repair are partitioned among workers, with little inter-task switching by individuals (Jeanne 1986b, 1987). Forsyth (1978) found that some *P. occidentalis* foragers were specialized or 'fixed' on gathering a specific material, and further noted that material fixation was sometimes long-lasting relative to the life of the individual worker. The purpose of this study was twofold: (1) To learn how an experimentally imposed contingency (nest damage) is met by members of the foraging caste in *P. occidentalis*. (2) To learn how the emergency foraging response to damage affects the flow of food to the colony. To these ends we documented the extent to which foragers specialize on materials in *P. occidentalis*. By experimentally damaging the nest, we determined whether foraging specializations change in response to changing colony conditions. We measured the rate of food foraging on the colony level to establish whether it decreases because of effort allocated in response to nest damage.

**Materials and methods**

**Study site and animal.** We studied three colonies of *P. occidentalis* (one in 1988, two in 1989) at Hacienda La Pacifica, near the town of Cañas in northwestern Costa Rica. *P. occidentalis* is common at this site; many colonies can be found in vegetation at heights of less than 2 m. Observations were made during the rainy season when all study colonies were actively rearing brood. The colonies used in this study were chosen to represent a range of medium-sized nests, with populations of several hundred workers.

*P. occidentalis* colonies are readily induced to repair damage of the nest envelope (Jeanne 1986b). Nest repair entails three distinct tasks: foraging for water, foraging for pulp, and building. Workers rarely switch between building and foraging (Jeanne 1986a, b). Repair of envelope damage usually begins at dawn and rarely continues past noon, even if the damage is not fully mended.

**Experimental manipulations and data collection.** Before the start of observations, we enclosed each nest in a plastic bag with a cotton ball soaked in diethyl ether then shook the nest to incite many of the wasps to exit. Adults were removed from the bag after light anesthetization and transferred to a refrigerator to await marking. Xylene-based paint pens were used to apply colored dots to the thoracic dorsum, providing each individual wasp with a unique numerical code. Marked wasps were returned to their nest within 2 h of removal.

We induced nest repair each morning by removing a 5 × 7 cm portion of the nest envelope. This was done at least 1 h before the start of observations. If the previous day's damage had not been fully repaired, we enlarged the remaining hole to 5 × 7 cm. Colony A was damaged daily from 2 to 9 October 1988; the colony was observed daily for 120–180 min in the morning, during active nest repair, and for 15–120 min each afternoon, after nest repair had ended, for a total of 21.5 h in the morning and 11.8 in the afternoon. Colony B and (in parentheses) colony C were observed daily from 28 June to 10 July 1989 for 60 to 90 min before and 30 to 90 min after 1200 h, for a total of 18.3 (18.5) h in the morning and 11.3 (11.5) h in the afternoon. The 1989 colonies were observed undisturbed for 5 days, then damaged daily from 3 to 8 (3 to 9) July.

The characterization of individual specialization is dependent on the time scale over which behavior is measured. For example, a worker that performs one task exclusively during a single observation period may switch to another task later in the same day, or in other days. *P. occidentalis* colonies rarely engage in nest construction in the afternoon, suggesting that important changes in worker behavior occur over the course of the day. We quantified changes in foraging specialization within observation periods, within days (morning vs afternoon observation periods), and among days (control vs experimental days), since material specialization that occurred on any one of these time scales might not be detected by analysis of specialization on the other time scales.

We recorded all occurrences (Altmann 1974) of forager arrivals at the nest by noting time of landing (5 min interval 1988, 10 min interval 1989), forager identity, and material carried. *P. occidentalis* workers foraged for four materials. Prey and nectar provided nutrition for the colony and are referred to as "food materials." Pulp and water were used in nest construction (water was also used for nest cooling); these are referred to as "nest materials." The two solid materials (pulp and prey) were carried in the mandibles and could be identified when a forager landed. Liquids (water and nectar) were carried in the crop, and were distinguished by the posture of the forager when transferring her load (Hunt et al. 1987). Water foragers extend their antennae to the sides when passing liquid and hold them still. Nectar foragers vigorously stroke the head and mouthparts of the recipient wasp with their antennae. If a returning forager made no material transfers to other workers on the nest before leaving again or entering the nest, material was recorded as unknown.

Because mean times required by foragers to collect loads differed among the four materials (see Results), relative foraging effort devoted to the materials is not represented accurately by the relative numbers of trips. To correct for this, we weighted the trips for each material (x) by the mean trip duration for that material relative to the mean duration of a water trip:

\[
\text{Weighted number} = \frac{\text{Number of trips for } x}{\text{Mean time for } x} \times \frac{\text{Mean time for water}}{\text{Mean time for water}}
\]

The mean time for each material is mean time elapsed between successive arrivals at the nest by the same forager. Weighted numbers of trips were computed independently for each colony. Henceforth the term "foraging effort" refers to the weighted number of trips for each material.

To quantify the degree to which individuals specialized on materials we used the Shannon-Wiener information variable 'H' (Lehner 1979) as an index of specialization:

\[
H(x) = - \sum p(x) \log p(x)
\]

where \( p(x) \) is the proportion of a forager's effort devoted a given material \( x \).

In some cases our categorical data did not meet the assumptions of parametric contingency tests due to small expected values in many cells of our contingency tables (Colgan and Smith 1978). When this was the case we performed analogous tests for association among variables based on information theory, as described in Steinberg (1977).

**Results**

Among individual workers, the maximum total numbers of foraging trips for nest materials were higher than those for food materials (Fig. 1). Pulp and water were often gathered near the nest from relatively predictable supplies such as fence posts and ditches, to which the foragers returned repeatedly. Mean time elapsed between successive arrivals by workers carrying building materials was significantly less than mean time between successive food arrivals during bouts of continuous individual foraging activity (Table 1).
Table 1. Mean *P. occidentalis* forager round-trip times for each material. Values are mean ± one SD of time elapsed between successive arrivals in minutes; sample size in parentheses. Trip times differed significantly over materials (Overall Kruskal-Wallis test, $\chi^2 = 466$, $df = 3$, $P < 0.001$; in addition, the sum of scores statistic for each material was >3 standard deviations from the value expected under $H_0$ of similar distributions of trip times)

<table>
<thead>
<tr>
<th>Colony</th>
<th>Material</th>
<th>Nectar</th>
<th>Prey</th>
<th>Pulp</th>
<th>Water</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td></td>
<td>46.5±16.6 (30)</td>
<td>24.8±11.5 (25)</td>
<td>6.6±3.7 (70)</td>
<td>1.7±1.8 (40)</td>
</tr>
<tr>
<td>B</td>
<td></td>
<td>30.0±14.9 (27)</td>
<td>19.6±16.8 (34)</td>
<td>5.7±2.4 (61)</td>
<td>2.4±1.3 (100)</td>
</tr>
<tr>
<td>C</td>
<td></td>
<td>40.0±23.9 (29)</td>
<td>25.0±20.5 (8)</td>
<td>5.4±2.3 (52)</td>
<td>2.1±0.7 (86)</td>
</tr>
<tr>
<td></td>
<td>Overall mean</td>
<td>39.13</td>
<td>22.19</td>
<td>6.00</td>
<td>2.16</td>
</tr>
</tbody>
</table>

Forager specialization

We analyzed the matrices of (individual worker) $\times$ (total effort devoted to each material over the course of the study) using information theory techniques. Knowing worker identity reduced uncertainty about total effort devoted to materials by A: 76.1%, B: 68.0%, C: 66.3% (normalized transmission). Variables with normalized transmissions of > 50% can be considered tightly linked (Steinberg 1977). Thus effort devoted to particular materials is highly dependent on worker identity. This means that foragers were significantly specialized on materials over 8 observation days in colony A and over 13 observation days in colonies B and C. Although most foragers were specialized, few gathered one material exclusively. When a forager devoted at least 50% of her total effort to one material we refer to that material as her major (*sensu* Heinrich 1976); other materials gathered by these workers are their minors.

There was little switching among materials within observation periods (Table 2). Which material was gathered on a given trip was highly dependent on the

Table 2. Frequencies of transitions among materials by *P. occidentalis* foragers. Only consecutive foraging trips within uninterrupted observation periods were used to calculate transition frequencies. Transitions where material was unknown are not included

<table>
<thead>
<tr>
<th>Preceding material</th>
<th>Following material</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nectar</td>
<td>Prey</td>
</tr>
<tr>
<td>Colony A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nectar</td>
<td>261</td>
<td>14</td>
</tr>
<tr>
<td>Prey</td>
<td>13</td>
<td>29</td>
</tr>
<tr>
<td>Pulp</td>
<td>2</td>
<td>424</td>
</tr>
<tr>
<td>Water</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>276</td>
<td>43</td>
</tr>
<tr>
<td>Colony B</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nectar</td>
<td>129</td>
<td>19</td>
</tr>
<tr>
<td>Prey</td>
<td>10</td>
<td>26</td>
</tr>
<tr>
<td>Pulp</td>
<td>2</td>
<td>263</td>
</tr>
<tr>
<td>Water</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>142</td>
<td>48</td>
</tr>
<tr>
<td>Colony C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nectar</td>
<td>70</td>
<td>6</td>
</tr>
<tr>
<td>Prey</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>Pulp</td>
<td>2</td>
<td>278</td>
</tr>
<tr>
<td>Water</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>77</td>
<td>13</td>
</tr>
</tbody>
</table>

Fig. 1. Frequency distribution of the rate of foraging for each of four materials by marked *P. occidentalis* workers from 3 colonies. Only individuals that made trips for a given material are included in the histogram for that material. Rates were calculated for each individual by dividing its unweighted number of trips by total observation time. Note the differences among materials in the maximum foraging rate, shown by the scales of the X-axes. The distributions of rates for materials differed significantly in all colonies (Kruskal-Wallis test with $df = 3$; A: $\chi^2 = 13.0$, $P < 0.005$; B: $\chi^2 = 30.0$, $P < 0.001$; C: $\chi^2 = 13.0$, $P < 0.005$). Mean foraging rates in trips per hour with standard deviations (sample size in parentheses) for each material were as follows: A: nectar 0.22±0.25 (92), prey 0.10±0.13 (29), pulp 1.37±2.43 (19), water 1.99±5.01 (150); B: nectar 0.21±0.20 (120), prey 0.09±0.13 (55), pulp 0.80±1.16 (23), water 1.51±2.21 (17); C: nectar 0.18±0.19 (72), prey 0.08±0.07 (15), pulp 0.92±1.10 (22), water 1.03±2.73 (19)
previous trip (Chi squared test, $\chi^2 > 1500$, $df = 9$, $P < 0.001$ for all colonies). The vast majority of transitions involving food and nest materials were to the same material (A: 95.7%, B: 96.0%, C: 94.9%). Transitions to the other material of the same functional type (food or nest material) were next most common (A: 3.9%, B: 2.9%, C: 4.2%), while transitions to the other type (from a food to a nest material or vice versa) were rare (A: 0.4%, B: 1.6%, C: 0.9%). A striking feature of the transition frequency matrices is that they are nearly symmetrical around the diagonal of transitions to the same material (Table 2). This indicates that transitions between any two materials are almost equally likely in both directions (from material X to Y and vice versa).

**Activity level**

In all colonies, the distribution of total number of trips per worker was skewed toward high foraging rates (Fig. 1). For each material there was a small number of exceptionally active foragers, while many foragers made relatively few or no trips (Fig. 1). To test the relationship between individual activity level and material specialization we used the Shannon-Wiener information variable ‘H’ as an index of material specialization. Because there were four materials, this index could range in value from 0 (complete specialization on one material) to 2 (equal effort to all materials); an index value of 1 results if, for example, a worker devotes equal effort to two materials and none to the others. For every wasp that made at least four foraging trips, we plotted its index value against its total foraging rate (Fig. 2). Workers with high activity levels (>10 weighted trips/h) all had index values of 1 or less. Thus high individual foraging effort does not correspond to a high diversity of materials collected. Furthermore, foragers with relatively low activity levels (<10 weighted trips/h) did not differ significantly in specialization from more active foragers (Wilcoxon rank sums test, $Z = -1.37$, $P > 0.10$).

Although less active foragers appear to be more variable in their degree of specialization (Fig. 2), this may be an artifact of sample size. Higher variance in H is expected at low activity levels since index estimates for less active workers are (by definition) based on fewer observed foraging arrivals.

To quantify material input attributable to specialized foragers, we examined workers who devoted at least 50% of their total foraging effort to one material (their major). We further stipulated that these foragers must have made at least 10 trips where material was known, thus avoiding spurious classification of rarely-observed workers as specialized. The percentage of marked foragers that met these criteria was similar for all three colonies (A: 31.1%, B: 35.2%, C: 33.3%). In all colonies the majority of foragers performed fewer than 10 trips over the course of the study. Except for two individuals from Colony A and one from Colony C, all workers that made at least 10 foraging trips also majored on one material. The contributions to colony effort by majoring foragers are summarized in Table 3. The predominance of material input by these workers is most striking for nest materials, where a small number of highly active foragers met much of the colony demand. Averaged over the colonies, 36.9% of the few marked workers that made pulp trips majored on pulp; these accounted for 89.3% of the total pulp input. Water majors comprised 22.8% of the workers that collected water, yet these majoring foragers accounted for 88.2% of the water loads delivered to the colonies. Over the course of the study.

### Table 3. Contribution to colony foraging by specialized workers in *P. occidentalis*. Workers that devoted at least 50% of their foraging effort to a single material majored on that material. Only workers that made a total of 10 or more foraging trips are counted as majoring. The total number of marked foragers observed was A: 122, B: 159, C: 96.

<table>
<thead>
<tr>
<th>Material</th>
<th>Number of marked workers gathering</th>
<th>Number (%) of workers majoring</th>
<th>Number of trips by colony</th>
<th>Percent of colony effort by majoring workers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nectar</td>
<td>A 91</td>
<td>27 (29.7)</td>
<td>722</td>
<td>63.3</td>
</tr>
<tr>
<td>B 121</td>
<td></td>
<td>40 (33.1)</td>
<td>883</td>
<td>59.7</td>
</tr>
<tr>
<td>C 71</td>
<td></td>
<td>17 (23.9)</td>
<td>581</td>
<td>40.3</td>
</tr>
<tr>
<td>Prey</td>
<td>A 29</td>
<td>3 (10.3)</td>
<td>99</td>
<td>44.4</td>
</tr>
<tr>
<td>B 35</td>
<td></td>
<td>3 (5.5)</td>
<td>158</td>
<td>30.4</td>
</tr>
<tr>
<td>C 14</td>
<td></td>
<td>1 (7.1)</td>
<td>40</td>
<td>17.5</td>
</tr>
<tr>
<td>Pulp</td>
<td>A 19</td>
<td>6 (31.6)</td>
<td>585</td>
<td>88.9</td>
</tr>
<tr>
<td>B 24</td>
<td></td>
<td>7 (29.2)</td>
<td>340</td>
<td>87.9</td>
</tr>
<tr>
<td>C 22</td>
<td></td>
<td>11 (50.0)</td>
<td>375</td>
<td>91.2</td>
</tr>
<tr>
<td>Water</td>
<td>A 13</td>
<td>2 (15.4)</td>
<td>929</td>
<td>94.2</td>
</tr>
<tr>
<td>B 17</td>
<td></td>
<td>6 (35.3)</td>
<td>771</td>
<td>87.2</td>
</tr>
<tr>
<td>C 17</td>
<td></td>
<td>3 (17.6)</td>
<td>581</td>
<td>83.3</td>
</tr>
</tbody>
</table>

*This is a conservative estimate, since some unmarked workers may have been specialized foragers, though their effort would not be counted as such.*

![Fig. 2. Index of specialization on materials (Shannon Wiener information variable ‘H’) as a function of total weighted foraging rate of *P. occidentalis* foragers from three colonies. An index value of 1, indicated by dashed line, results when equal effort is allocated to two materials, and none to the other materials. Only individuals that made four or more foraging trips are included, as this is the smallest number that allows one trip for each material. Rates were calculated for each individual by dividing total foraging effort (see Methods) by total observation time.](image_url)
the largest number of foragers (approximately 75% in each colony) made trips for nectar, while the other materials were gathered by only 10% to 35% of the active marked foragers (Table 3).

Material flow to the colony

The colony-wide rates of foraging for nectar and prey, after the daily round of nest construction stopped, were not significantly different from the rates during construction in colonies A and C (Paired t-test, A: $T = -0.38, P > 0.25$; C: $T = -0.32, P > 0.50$); in colony B, the colony food foraging rate during nest repair was slightly but significantly higher than the rate after nest repair ended ($T = 3.65, P < 0.001$). Nest material majors gathered food materials at significantly lower total rates than all other foragers during the afternoon when no building occurred (Wilcoxon rank sum test; A: $Z = -2.42, P < 0.05$; B: $Z = -2.66, P < 0.01$; C: $Z = -2.62, P < 0.01$). On the individual level, mean morning foraging rate was highly correlated with mean afternoon rate for workers from all three colonies (A: $r = 0.84, df = 111, P < 0.01$; B: $r = 0.77, df = 144, P < 0.01$; C: $r = 0.73, df = 79, P < 0.01$). Pulp foragers were not included in this analysis as they rarely foraged after construction ended.

Response to imposed nest damage

Colonies B and C both repaired naturally occurring nest damage on 2 of 5 control observation days preceding experimental damage (Fig. 3). The small amount of pulp brought in on other control days was probably used to heighten brood cells inside the nests. Water is used for nest cooling as well as for construction and, unlike pulp, was collected at times when building did not occur (Fig. 3). On the days of imposed nest damage, pulp majors gathered pulp at higher mean rates than on control days (Fig. 3; paired t-test, B: $T = -2.84, P < 0.05$; C: $T = -2.25, P < 0.05$). In contrast, pulp and water majors' mean rates of food foraging were unaffected by experimental nest damage (comparison between treatment and control days; B: $T = 1.08, P > 0.25$; C: $T = 0.89, P > 0.25$). Food foraging by all other workers also showed no significant change between control and experimental days (B: $T = 1.12, P > 0.25$; C: $T = -1.47, P > 0.10$).

Discussion

P. occidentalis foragers tended to specialize or major (sensu Heinrich 1976) on one of four materials over the course of several days. Comparably stable individual material specializations within foraging castes have been noted in bumblebees (Heinrich 1976) and seed-harvester ants (Rissing 1981). Heinrich (1976) showed that a bee's ability to extract nectar and pollen from a given type of flower improves with experience. Such increases in task performance efficiency are thought to be a major advantage of individual worker specialization (Oster and Wilson 1978; Franks 1987). However, specialization on one material does not necessarily imply rigidity. In P. occidentalis, as in bumblebees and harvester ants, most foragers devoted some effort to other materials (minors) to a lesser degree. Bumblebee and harverster ant workers rapidly shifted to new specializations in response to changes in resource quality and colony demand (Heinrich 1976; Rissing 1981). Most switching among materials by P. occidentalis foragers was within a single functional type (food or nest materials), rather than between types. Food and building material foraging are task-sets, or groups of social acts which are functionally related (Secley 1982; Jeanne et al. 1988). Possible advantages of switching within rather than between task sets include minimizing travelling distances and waiting times between jobs, as has been shown for nest-worker honeybees (Secley 1982), and exposure of foragers specializing on one material to cues indicating colony need for the other material in the task set. Since pulp and water are delivered to builders, and nectar and prey to nurse wasps and brood, specialists on one material may have ready access to information on colony demand for the most functionally similar material.

The colony rate of foraging for food materials was unaffected by effort devoted to nest repair. Workers that responded to nest damage by foraging for pulp and water were not recruited away from food foraging. These workers may have been drawn from a pool of inactive reserve foragers or from workers previously engaged in nest work. Furthermore, they did not switch to food foraging on the days following experimental damage, and subsequently either returned to nest work or became inactive. Previous work on age polyethism in this species (Jeanne et al. 1988) concluded that foragers rarely revert to nest work, lending support to the latter alternative.

Similar patterns have been found in leafcutter ants (Wilson 1983) and honeybees (Kolmes 1985b; Winston...
and Fergusson 1985), where active workers did not switch among tasks in response to contingencies. In these cases, a reserve of less active workers was present which reacted to the novel labor demand by increasing their rate of work. These results contrast with patterns in several species of *Pheidole* (Wilson 1984) and harvester ants (Gordon 1989b), where already active workers switch among tasks in response to rapid changes in colony conditions.

Some authors have recently emphasized the importance of behavioral flexibility in enabling an insect colony to respond successfully to unpredictable changes in the environment (reviewed in Calabi 1987; Gordon 1989a). Empirical studies suggest that in diverse hymenopteran societies behavioral flexibility constrains and may even obscure the expression of ergonomically efficient behavior (Kolmes 1986; Gordon 1989a). Insect colonies alter their behavior in response to contingencies through changes in the behavior of individual workers. These changes include modification of activity levels, reallocation of effort, or some combination of both. The relative reliance on these two mechanisms appears to vary among species. Further efforts to measure the relative importance of these two mechanisms of response to contingencies in different species (or in different populations) will increase our understanding of the control of division of labor in insect societies.

**Acknowledgements.** We extend our deepest thanks to Larry Phelps for good ideas and companionship in the field. The Hagnauers were most gracious in providing assistance and allowing us to work on their land. Susan Bulova is gratefully acknowledged for writing the computer program used for transition probability analysis. This paper benefited from Dennis Heiney's advice on statistical analysis, and from the careful and thoughtful suggestions made by J.P. Hallman, G.D. Henderson, J.F.A. Trianni, and two anonymous reviewers. Financial support was provided by NSF Grant BNS-8517519 to R.L. Jeanne.

**References**


Gordon DM (1989b) Dynamics of task switching in harvester ants. Anim Behav 38:194–204


