Behav Ecol Sociobiol (1986) 19:333–341

**Behavioral Ecology and Sociobiology**


# The organization of work in *Polybia occidentalis*: costs and benefits of specialization in a social wasp

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Received September 12, 1985/Accepted May 6, 1986

**Summary.** Nest construction, a complex social activity requiring the coordination of 3 tasks (Fig. 2), was compared in large (>350 adults) and small (<50 adults) colonies of *Polybia occidentalis*. The 3 tasks – water foraging, pulp foraging, and building – are performed by 3 separate groups of workers (Fig. 4). Of the 8 acts comprising the 3 tasks, 5 regularly involve the transfer of water or pulp from one worker to another on the nest.

Small colonies required nearly twice as long (35.4 worker-min) as large colonies (20.1 worker-min) to complete a unit amount of construction work. Behavioral acts involving material transfer among workers were responsible for most of the increase in small colonies. In other words, the waiting times experienced by material donors and recipients were greater in small colonies. In small colonies workers switched among the three tasks more frequently than in large colonies (Fig. 4). This was the result of more frequent switching by generalists (workers that performed 2 or 3 of the tasks), rather than by a decrease in the proportion of specialists (workers performing only 1 task type) (Fig. 3).

The series-parallel system by which *Polybia occidentalis* organizes nest construction has a major advantage over the series operation of solitary wasps. Pulp foragers collect and carry loads that are 6.1 times as large as builders can work with at the nest, and water foragers bring in loads that appear to be limited only by crop capacity and that provide all the moisture necessary for the complete processing of 0.74 of a foraged pulp load. As a result *P. occidentalis* can collect and process a given amount of nest material using 2.6 times fewer foraging trips than would be required by the series system. This in turn means that *P. occidentalis* not only achieves an energy saving that probably more than offsets the increased costs of material handling at the nest, but it reduces the exposure of its foragers to predators in the field.

## Introduction

Nest construction in wasps is a complex activity, that is, one involving the coordination of two or more tasks. Solitary wasps perform the requisite tasks in series (Oster and Wilson 1978). In mud wasps, for example, the sequence begins with the collection of water. This is used to moisten soil material to form a mud pellet, which is then incorporated into the nest (Evans and West Eberhard 1970). Because each female works alone on her own nest, there is no alternative to this pattern. In social wasps, however, the presence of many workers opens up the possibility of organizing nest construction activities in series-parallel, wherein each individual performs only one act in the sequence (Oster and Wilson 1978).

I investigated nest construction in the social wasp *Polybia occidentalis* (Olivier) to determine how a complex social activity is organized in an advanced eusocial insect. I was particularly interested to learn how workers divide up tasks during a round of nest construction. In other words, the intent was to analyze task partitioning, or specialization over the short term (several days or less) (Jeanne 1986), rather than division of labor in the usual sense. A second purpose was to determine whether the organization observed is fixed and unvarying, or if it changes in response to reduced worker number so as to approach the in-series performance of behavioral acts characteristic of solitary wasps.

**Fig. 1.** Young nest of *Polybia occidentalis* under construction. The cells of the third comb are visible. The nest entrance is the small hole near the center. The large opening in the envolope covering the third comb will be narrowed to form the new nest entrance, below the current entrance

## Methods

Colony founding in *Polybia occidentalis* is by means of a swarm consisting of up to several hundred workers accompanied by numerous queens. The workers construct the initial nest in a matter of days and the cells are provided with eggs by the queens. Thereafter the nest is enlarged in discrete pulses that are timed by growth in the brood and worker populations (Forsyth 1978).

The nest (Fig. 1) is of the phragmocyttarous type. The first horizontal comb of cells is built under a twig or other substrate. This is enclosed with an envelope, which forms the substrate for the second comb of cells, and so on. The nest entrance is near the bottom, on the side facing the clearest flight path to and from the nest. As the nest grows, the upper walls are thickened by application of pulp to the outer surface.

The study was conducted at Hacienda La Pacifica, near Cañas, Guanacaste Province, Costa Rica, in September and October 1982 and June and July 1984. Colonies were located in shrubbery in pastures and other areas of low second growth vegetation and on buildings, and were studied in situ.

Colony populations at this site typically numbered several hundred adults, but much smaller colonies occasionally occurred. Extremely small colonies probably result when a colony suffers brood loss to predators one or more times before it can produce its first worker offspring. Observations were made on three large colonies and four small colonies (Table 1). At the end of the study the large colonies had adult populations of more than 350; small colonies had populations of less than 50 adults. All colonies were in the founding stage of development, that is, they had not yet produced adult offspring.

A total of 256 workers were individually marked on the thorax with Testor's model airplane enamel as they engaged in nest construction tasks. Sequences of behavioral acts were recorded from among these individuals using the focal animal technique (Altmann 1974). The duration of observations on each individual varied, but usually lasted as long as the worker remained visible on the outside of the nest. If an individual switched to a task unrelated to nest construction or entered the nest the sequence was terminated. Individual acts for focal animals were timed to the nearest second using a digital stopwatch.

Task diversity indices were computed for individual workers, based on the three construction-related tasks of pulp foraging, water foraging, and building. Only workers for which observations totalled 15 tasks or more over at least two observation days were included. The index used is the Shannon-Wiener information theory parameter $H$:

$$H_T = -\sum_{i=1}^{T} p_i \log p_i,$$

where $p_i$ is the frequency of task $i$.

Crop capacity was measured by allowing water foragers to imbibe water from the tip of a calibrated capillary tube. Pulp and prey loads were collected by removing laden foragers from the nest with forceps and holding them over a clean sheet of paper until the load was dropped. Pulp loads were stored

**Table 1.** Data for colonies used in the study. Workers were marked during the first days of observation of each colony. Colony size data are as of the date of collection at the end of study of each colony

| Colony no. | No. of workers marked | Collection date | Total adult population | No. of queens | Oldest brood | No. of combs | No. of cells |
|---|---|---|---|---|---|---|---|
| Small colonies | | | | | | | |
| 162 | 14 | 7-23-84 | 8 | 1 | larvae | 1 | 66 |
| 117 | 26 | 10-31-82 | 33 | 6 | pupae | 2 | 223 |
| 103 | 50 | 10-16-82 | 42 | 1 | larvae | 2 | 109 |
| 93 | 16 | 10-14-82 | 44 | 9 | pupae | 2 | 144 |
| Large colonies | | | | | | | |
| 85 | 40 | 10-16-82 | 371 | 46 | pupae | 4 | 1,083 |
| 76 | 79 | 10-29-82 | 567 | 10 | pupae | 6 | 2,286 |
| 16 | 31 | 10-06-82 | 598 | 13 | pupae | 6 | 2,496 |

dry, while prey loads were preserved in alcohol. Loads were dried for two days in an oven at 60° C and then weighed individually on a Cahn 29 automatic electrobalance. A sample of workers from each colony was dried in the same way and weighed in groups of ten.

## Results

### *The tasks and their coordination*

Nest construction in *Polybia occidentalis* was normally limited to the morning hours. While nest construction was going on, the workers engaging in it rarely switched to other activities, although other workers concurrently foraged for nectar or prey or tended the brood. In the afternoon the workers that had been involved in nest constructing during the morning may well have engaged in non-construction-related activities, but no observations were made on this.

Nest construction involves three tasks: water foraging, pulp foraging, and building. In large colonies on any given day these three tasks are performed by three separate groups of workers. That is, the tasks are performed in series-parallel (Oster and Wilson 1978). The coordination of the three groups and the flow of materials between them are summarized in Fig. 2.

Each task and its component acts are defined below:

*(1) Water foraging.* Worker leaves nest, flies to water source (standing water or dew or rain droplets on vegetation), imbibes water filling the crop, returns to nest, regurgitates to nestmates. $W_{o-l}$= time spent in the field, from take-off from the nest to landing. $W_{l-o}$= time spent on the nest, from landing to take-off on the next trip; during this interval the water forager transfers its crop water to nestmates. The landing zone is above and to the sides of the entrance (Fig. 1) but water foragers move about if necessary, offering regurgitated water until their croploads are exhausted.

*(2) Pulp foraging.* Worker obtains water at the nest (from a water forager or builder), flies to fiber source (e.g. dead twig or fencepost), searches on foot for a suitable spot, wets the site with regurgitated crop water, then scrapes up a ball of wood fiber using the mandibles and returns with it to the nest. As do water foragers, pulp foragers land above and to the sides of (rarely below) the entrance (Fig. 1). If the load is not taken by a nestmate within a few seconds, the forager may move about, first on this area of the nest, then down into the zone of construction, offering the load

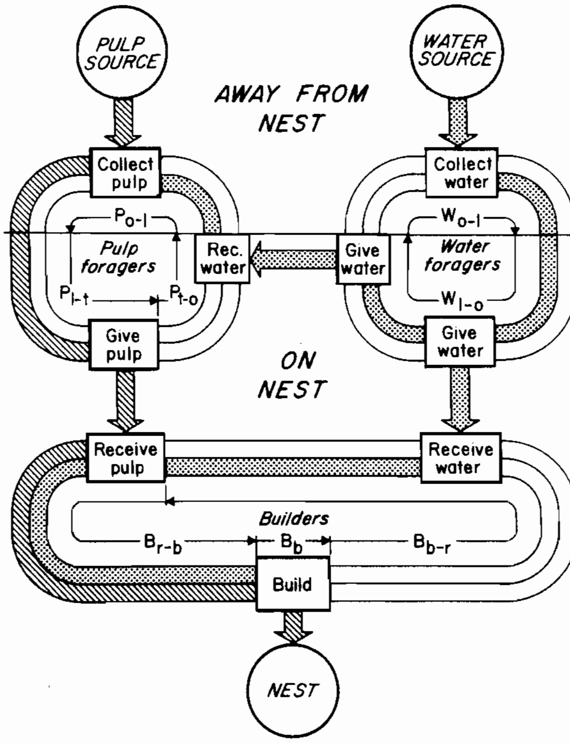


**Fig. 2.** Interactions of workers and materials in a large colony of *Polybia occidentalis* engaged in nest construction. Materials generally flow from top to bottom of the diagram. Each of the three categories of workers is represented by a cycling loop with two tracks. The inner track represents the crop: *blank* = empty, *stippled* = water-filled; the outer track represents the mandibles: *blank* = empty, *hatched* = carrying pulp. Symbols inside each loop refer to the timed acts comprising each task and are defined in the text. Water foragers (*upper right*) collect water in the field and return to the nest, where they give it to pulp foragers and builders. After filling the crop with water, pulp foragers collect pulp in the field, using some or all of the water to soften the fibers. At the nest they transfer the pulp to builders. Builders further wet the pulp mass with water from their own crops prior to adding it to the nest. Not shown are interactions among builders whereby pulp loads are subdivided

to any worker it encounters. $P_{o-l}$= time spent in the field, from take-off to landing. $P_{l-t}$ = time from landing at the nest to completing of transfer of its pulp load to nestmates, or, if the forager builds with the residue of its own load, until start of building. $P_{t-o}$= time from completion of transfer of pulp load to take-off from the nest for the next trip; during this interval the pulp forager seeks and imbibes water from nestmates.

*(3) Building.* Worker obtains water (from a water forager or another builder) then pulp (from a pulp forager or another builder). Worker wets pulp with crop water and malaxates it. After subdividing the load by sharing it with other builders, she moves

to an area of the nest under construction, searches for a building site, and works the wet pulp into the nest using her mandibles. $B_{r-b}$ = time from receipt of the first load of pulp to the initiation of building; this interval typically includes numerous exchanges of pulp with nestmates until load size is appropriate for building. $B_b$ = time spent building, from the moment the pulp is touched to the surface to which it will be added until the mandibles are empty; especially on small colonies, this interval may include interruptions to adjust load size by sharing with other builders. $B_{b-r}$ = time from the end of a building act (mandibles emptied) until the receipt of the next pulp load.

Most building activity takes place on the lower part of the nest, where construction of new cells and new envelope proceeds (Fig. 1). Smaller amounts of nesting material are used inside the nest to heighten pre-existing cells to keep pace with the growth of larvae in them, and on the upper parts of the outer envelope, where pulp is added to the surface to thicken and strengthen it to bear the growing weight of the nest. Builders move to the landing zone above the entrance, first seeking water either directly from water foragers or from nestmates who in turn have received water from foragers. After obtaining water, a builder takes a load of pulp, either from a forager or from another builder in the area. As she moves toward the zone of active construction, she subdivides the load several times with other builders until the load is small enough for her to work with (see below). Upon finding a site suitable for the receipt of a fresh load of pulp, she works the material into the nest, shaping it repeatedly with the mandibles. Upon completion, she may suck excess water from the newly-constructed surface, or she may fan her wings to dry the carton, before moving back up the nest for another load.

### *Weights of loads carried by foragers*

The mean dry body weight of *Polybia occidentalis* workers is 5.33 mg ($n = 5$ colonies, 510 workers, weighed in groups of 10). The range in dry body weights of a sample of 40 workers from 2 colonies was 3.80–6.71 mg. Since a balance was not available in the field, it was not possible to determine a mean wet weight. For *Polistes fuscatus*, a temperate zone social wasp, wet weight averaged 2.31 times that of dry weight ($n = 12$). Using the same proportion gives an estimated mean wet weight for *P. occidentalis* of 12.80 mg.

Pulp foragers carry loads averaging 0.66 mg (dry weight), or 12.0% of their own dry weight. Water loads imbibed by water foragers averaged 6.65 mg (range: 4.52–8.48 mg, $n = 18$), or 52% of their estimated wet weight. Water foragers typically imbibed enough water to distend the gaster to its apparent limit: clear liquid could be seen through taut intersegmental membranes. Prey foragers brought in prey averaging 1.01 mg dry weight (range = 0.01–5.16 mg, $n = 96$), or 18.3% of their mean dry weight. Assuming that the heaviest prey load recorded (dry weight of 5.16 mg for a geometrid larva) was brought in by the heaviest worker recorded (6.71 mg), *P. occidentalis* workers appear capable of carrying loads conservatively estimated at 75% of their own weight. This estimate would probably be even higher if it were based on wet weight, since percent water content is considerably greater for caterpillars than for adult wasps (Wigglesworth 1972). Since the maximum water load carried by workers was 8.48 mg, or only 66.3% of estimated mean wet weight, the limit on water loads carried by workers appears to be set by crop capacity rather than by weight. Likewise, pulp foragers appear not to be carrying the heaviest pulp loads of which they are capable. The limit could be set by the size of the pulp mass they can efficiently collect and secure during transport to the nest.

### *Relative efficiency of nest construction in large versus small colonies*

One way to measure the cost of an operation such as nest construction is to measure the time required to carry out a given amount of work. I computed the time required to complete the collection and addition to the nest of one average foraged pulp load using the following equation:

$$T = P_{o-l} + P_{l-t} + P_{t-o} + (W/P)\,[W_{o-l} + W_{l-o}] + (B/P)\,[B_{r-b} + B_b + B_{b-r}] \qquad (1)$$

where

$W/P$ = the average number of foraged water loads required to supply enough water for pulp foragers and builders to collect and process one foraged pulp load, and

$B/P$ = the average number of builders required to process one foraged pulp load.

The remaining parameters are the geometric means of durations in seconds of the acts comprising each of the three tasks defined above. The data were log-transformed because the means and variances of the raw data were highly correlated. These values for large and small colonies are given in Table 2.

**Table 2.** Durations, in seconds, of construction-related acts for large and small colonies. Data are from 3 large and 4 small colonies. Acts are as defined in the text. Based on log-transformed data. Tests to determine if small colonies take longer than large colonies for each task were performed using log-transformed data. Means are geometric with 95% (retransformed) confidence intervals. "Ratio $S/L$" is the mean for small colonies divided by the mean for large colonies

| Act | Small colonies | | | Large colonies | | | Ratio $S/L$ | $t$-value | $P<$ |
|---|---|---|---|---|---|---|---|---|---|
| | $n$ | Mean | 95% confid. limits | $n$ | Mean | 95% confid. limits | | | |
| $P_{o-l}$ | 240 | 219.0 | 206.3–232.5 | 414 | 188.8 | 181.8–194.8 | 1.16 | 4.13 | 0.001 |
| $P_{l-t}$ | 330 | 16.1 | 14.1– 18.4 | 477 | 6.7 | 6.3– 7.1 | 2.40 | 11.90 | 0.001 |
| $P_{t-o}$ | 207 | 44.4 | 38.3– 51.6 | 270 | 27.7 | 24.5– 31.2 | 1.60 | 4.82 | 0.001 |
| $W_{o-l}$ | 295 | 41.3 | 38.9– 43.8 | 467 | 42.9 | 41.5– 44.4 | 0.96 | −1.13 | 0.8 |
| $W_{l-o}$ | 283 | 45.4 | 41.1– 50.2 | 465 | 34.6 | 32.7– 36.6 | 1.31 | 4.71 | 0.001 |
| $B_{r-b}$ | 129 | 69.9 | 60.8– 80.4 | 42 | 44.3 | 36.6– 53.8 | 1.58 | 3.76 | 0.001 |
| $B_b$ | 218 | 96.6 | 87.6–112.2 | 87 | 61.9 | 53.3– 71.9 | 1.56 | 4.89 | 0.001 |
| $B_{b-r}$ | 49 | 116.6 | 78.4–173.5 | 34 | 37.7 | 21.9– 65.1 | 3.09 | 3.28 | 0.01 |

The ratio $B/P$ was computed by taking the ratio of the weight of pulp loads handled by pulp foragers to those handled by builders. The mean dry weight of foraged pulp loads was 662.2 μg (SE = 74.3; $n=29$ loads), while that of loads utilized by builders was 108.6 μg (SE = 25.7; $n=5$ loads). Therefore, the value of $B/P$ used in Eq. (1) is 662.2/108.6 = 6.1.

Since the volume of water utilized by pulp foragers and builders could not be feasibly measured, a different approach was used to compute $W/P$. The numbers of pulp and water loads arriving at the nest per 10-min interval were counted during periods of steady-rate nest construction. It was assumed that the incoming water was a representative sample of the volume required to supply both the pulp foragers and builders active during the same interval. Eleven 10-min samples yielded a mean ratio of 1.35 water trips per pulp trip.

Solving the equation using values for the geometric means for large and small colonies (Table 2) and adjusting units to wasp-minutes yields

$T_{(\mathrm{large})} = 20.1$ worker-min
$T_{(\mathrm{small})} = 35.4$ worker-min.

Thus, small colonies required more worker-minutes to add an average foraged pulp load to the nest than did large colonies.

*Organizational differences between large and small colonies*

Workers in small colonies were more likely to switch among pulp foraging, water foraging, and building. This difference in the degree of specialization between large and small colonies was quantified by three methods.

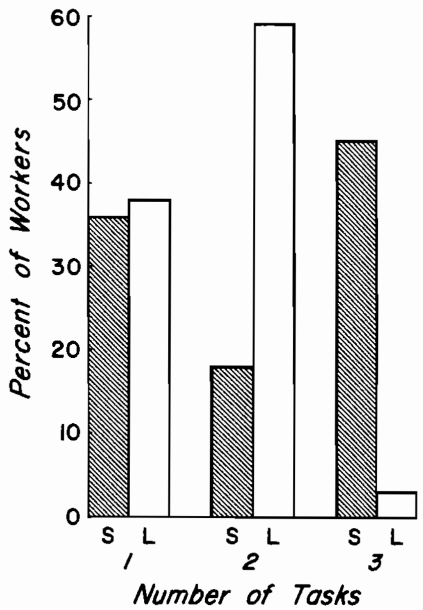


**Fig. 3.** Frequency distribution of degree of specialization among workers engaged in nest construction. *Bars* give the percent and number of workers seen to perform 1, 2, or all 3 tasks during the period of observation. $S$ = small colonies, $L$ = large colonies

*(1) Short-term individual specialization*

"Specialists" are workers that performed only one of the three nest construction tasks during the period of observation (minimum observation: 15 tasks performed over 2 days). That is, their task diversity indices, $H_T$, were equal to zero. "Generalists" are those seen to perform two or all three tasks by the same criterion. The proportion of specialists was similar for both large and small colonies ($\chi_1^2 = 0.02$, $P<0.9$) (Fig. 3). If specialists are removed from the analysis and only generalists considered, a greater proportion of the generalists on small colonies performed all three tasks than on large colonies ($\chi_1^2=16.56$, $n=38$, $P<0.005$). This is reflected in a higher mean task diversity index for generalists on small colonies ($H_T=1.039$; $n=21$) than on large colonies ($H_T=0.582$; $n=17$) ($t_{36}=165.5$, $P<0.005$). This means that the degree of short-term specialization among workers engaged in nest construction is significantly less in small colonies than in large. Interestingly, all 12 specialists on small colonies were builders, while on large colonies 4 were builders, 4 were water foragers, and 3 were pulp foragers ($\chi_2^2=10.98$, $n=23$, $P<0.005$).

The specialist category appears not to be merely an artifact of sampling error, i.e. made up of those individuals for which the number of tasks observed were small. The average number of tasks observed for generalists was 62.4 ($n=39$) and for specialists 32.1 ($n=23$). However, most of the specialists (16) were builders, and since building tasks were repeated less rapidly than were water or pulp foraging tasks, fewer of these observations were accumulated over a given observation period, thus pulling down the average number of tasks observed for specialists. The 7 pulp and water specialists averaged 56.4 observed tasks per worker, similar to the value for generalists.

### *(2) Transition frequencies*

In large colonies marked workers switched among the three tasks only rarely. In small colonies, in contrast, the frequency of transition between tasks was significantly higher for each task ($\chi_6^2=363.7$, $P<<0.005$) (Fig. 4). Since the proportion of specialists was similar on large and small colonies, this means that the generalists on small colonies switched more frequently than did those on large colonies. The probability of a generalist's switching tasks averaged 0.38 per task on small colonies (range = 0.05–0.53, SD = 0.19, $n=1193$ tasks, 21 workers) and only 0.10 per task on large colonies (range = 0.01–0.50, SD = 0.13, $n=0.13$, $n=1241$ tasks, 18 workers).

The most common transitions were between pulp foraging and building and between pulp foraging and water foraging; transitions between building and water foraging were rare (Fig. 4). Transitions from pulp foraging to water foraging were discrete; that is, all acts within a pulp foraging sequence were completed before water foraging was begun. The same was true in most instances for transitions from water foraging to pulp foraging, although on several occasions I saw a pulp forager stop for water on a wet leaf near the nest

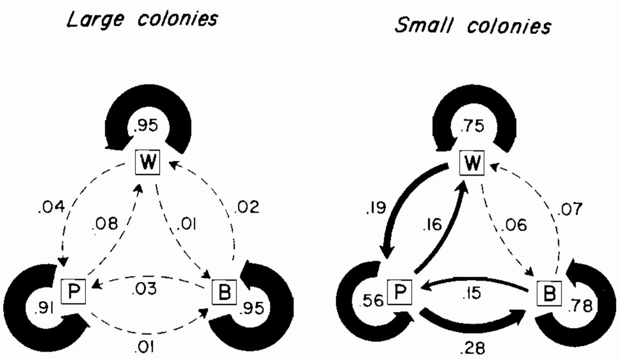


**Fig. 4.** Frequencies of transition among the three construction-related tasks, 3 large colonies compared to 4 small colonies. Values are conditional probabilities. *Line thicknesses* are proportional to the magnitude of the probability, except for very small values (*dashed lines*). $W$ = water foraging, $P$ = pulp foraging, $B$ = building. The differences between large and small colonies were tested using a $2\times3$ contingency table, 2 degrees of freedom. First task pulp foraging: $\chi^2=216.8$, $n=952$, $P<0.005$; first task water foraging: $\chi^2=117.3$, $n=1394$, $P<0.005$; first task building: $\chi^2=29.6$, $n=536$, $P<0.005$. Total tasks observed: large colonies, $n=2085$, small colonies, $n=797$

before going on directly for pulp. On the other hand, when a pulp forager switched to building, it was rare for it to complete the entire pulp foraging sequence (i.e. give up the entire load) before receiving pulp from a nestmate and building with it. More commonly, transitions from pulp foraging to building involved the pulp forager's building with the last bit of its own pulp load. These differences in pulp flow between large and small colonies are detailed below.

### *(3) Pulp flow*

On large colonies pulp foragers almost always found willing takers for their loads within seconds after arriving at the nest (Table 2). The receiving builders typically accepted the entire pulp mass, leaving the forager free to seek water from a water forager, then take off for its next pulp load. Only 0.2% of pulp foragers retained a part of their loads and switched to building to add it to the nest themselves; the remaining 99.8% transferred the loads completely to builders (Fig. 5). Eighty-six percent of incoming pulp loads were taken in entirety by the first receiver encountered ($n=547$); the mean number of recipients per pulp load was 1.16 (range = 1–5, $n=547$).

In contrast, pulp flow through small colonies was much less smooth and rapid. It was not uncommon in a small colony for one of the two or three active pulp foragers to land just after the previous one had arrived and given up its load. The new arrival then found all or most of the build-

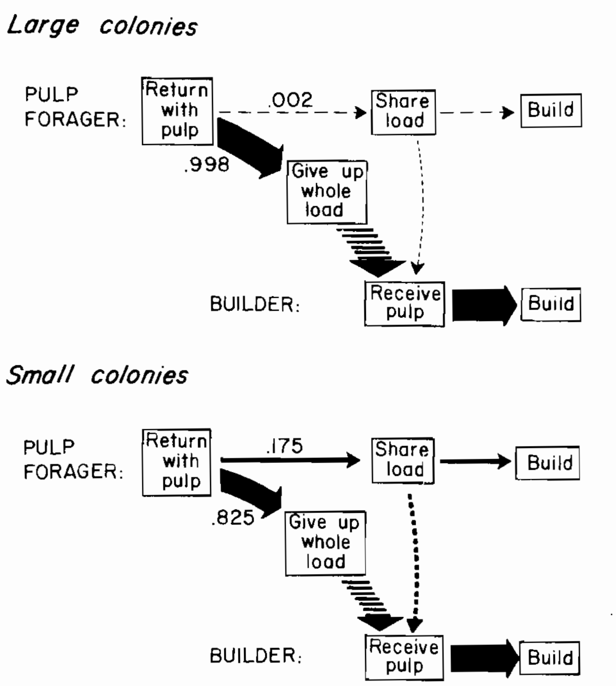


**Fig. 5.** Pulp flow in 3 large and 4 small colonies. Values are conditional probabilities. *Line thicknesses* are proportional to the magnitude of the probability, except for very small values (*long-dashed lines*). *Solid arrows* represent behavioral transitions for a given worker. *Short-dashed lines* represent transfer of pulp from one worker to another. Pulp loads observed: large colonies, $n=920$, small colonies, $n=485$

ers occupied and had to wait, sometimes for several minutes, for them to finish building before it could transfer all of its load. Furthermore, the behavior of pulp receivers in these situations suggested an unwillingness to take more pulp than they could build with: the pulp-receiving builder appeared to resist the efforts of the pulp forager to give it the whole load, instead chewing off only a small bit while pushing the bulk of the mass back into the face of the forager. This was reflected in an increase in the average number of receivers per pulp load on small colonies to 1.55 (range = 1–8; $n=455$), significantly higher than the 1.16 (range = 1–5, $n=547$) for large colonies ($\chi^2_7=69.9$; $P<0.001$). On small colonies only 64% of loads were taken entirely by a single recipient ($n=451$), again significantly lower than the figure of 86% for large colonies ($\chi^2_1=62.38$; $n=998$; $P \ll 0.001$). When a pulp forager experienced delays in finding takers for the last bit of her load, she frequently switched to building, adding the residue to the nest herself, rather than continue waiting. On small colonies the percentage of incoming pulp loads for which this was the case jumped to 17.5% (Fig. 5). On the smallest colony (162), where pulp foragers frequently had long waits to transfer their loads and often ended up adding the last fragments themselves, they sometimes returned with loads that were visibly smaller than average. However, in every case these were still too large for them to build with and had to be subdivided among nestmates.

## Discussion

The organization of nest construction work on large colonies of *Polybia occidentalis* is distinctly different from the performance of tasks in series by solitary wasps in that workers typically perform one or the other of the three tasks repeatedly, only rarely switching to another task. There are at least two ways in which this system leads to gains in efficiency over the series system. First, workers probably improve their performance efficiency (Seeley 1982; Jeanne 1986) for the tasks they specialize on, although no attempt was made to measure this. Second, and potentially more important for *Polybia occidentalis*, the system has enabled gains in what I have called "materials handling efficiency" (Jeanne 1986). If instead *Polybia occidentalis* followed a parallel-series form of organization, wherein each worker first foraged for water, then for pulp, then built with its own load, foraged water load volume would be limited by the amount it needed to collect pulp and add it to the nest, and foraged pulp load size would be limited by the amount the worker could built with. By specializing, each worker can handle the size of material load that is most efficient for the task it is performing. Thus water foragers collect loads that appear to be limited only by crop volume and not by the lesser amounts required by each pulp foraging or building act. Similarly, pulp foragers collect loads that average 6.1 times larger than those handled by builders. As a result, compared to the series system, the *P. occidentalis* system results in a 2.6-fold reduction in number of trips flown per unit of nest material [6.1 water-pulp trips under the series system divided by (1.35 water trips + 1.00 pulp trips) under the *P. occidentalis* system]. In terms of total distance flown to collect water and pulp, the advantage of *P. occidentalis* over the series operation ranges from 2.6 (if water is available next to the pulp source) to 6.1 (if water is available next to the nest).

There are two benefits to the reduced number of foraging trips. One is a corresponding reduction in foraging time, and undoubtedly an even greater proportionate saving in energy cost to the colony, because flight is a particularly expensive activity.

Thus, foraging efficiency (amount of work accomplished/calorie expended) is greater than under the series system. Second, the reduced number of foraging trips means a consequent reduction in exposure of workers to risk of accidental death while foraging. Since in social insects mortality rates for foragers are higher than for on-nest workers (Wilson 1985), fewer trips mean a lowered rate of mortality per mg of nesting material added to the nest.

On the other hand, associated with the *P. occidentalis* form of organizing nest construction work is a cost that is absent from the in-series system. Because loads have to be passed from one worker to another at the nest (Fig. 2), a finite transfer time is introduced into the system. As the data show (Table 2), transfer time is a substantial factor in the estimate of worker-minutes per mg of nest material added to the nest (Eq. 1), expecially in small colonies.

The fact that in small colonies the greatest increases in worker-minutes occur in acts involving transfer of material from one worker to another (Table 2) strongly suggests that these increases are due largely to greater waiting times experienced during these transfers. In other words, the cost associated with the *P. occidentalis* system of work organization – that incurred by the transfer of material between workers – is much greater on small colonies.

Why should waiting times increase on small colonies? The answer may lie in the differential effects of variance in arrival times on waiting times in queueing systems of different sizes (Law and Kelton 1982). The system could operate at maximal efficiency only if waiting times were zero. Waiting times of zero could be realized only if a receiver becomes available to take a load just as a forager lands. Such a perfect temporal meshing of donors and receivers would require (1) optimal numbers of workers engaged in each of the three tasks, and (2) no variance in task duration. The second condition, at least, is clearly not met in *P. occidentalis* colonies (Table 2). According to this hypothesis, waiting times are $>0$ primarily because variance in task durations causes unevenness in the spacing of arrival times of foragers and finishing times of builders. In a large colony the effect of this unevenness is partially damped out by large numbers of workers active in each task category. But when numbers of workers are very small, as in small colonies, the effects of the unevenness are greater, causing average waiting times to increase.

When costs and benefits are taken into account, is the series-parallel system of *Polybia occidentalis* more efficient in terms of worker-minutes than the series operation of solitary wasps and some primitively eusocial wasps? Since acts involving transfer of materials (excluding $B_b$) represent approximately 48% on large colonies (59% on small colonies) of the worker-minutes required for collecting and processing one foraged pulp load (Equation 1 and Table 2), the answer to this is probably no. However the more realistic currency is energy, not time, and here there is probably a considerable gain in efficiency for the *P. occidentalis* system, because metabolic rates during flight are so high (20–50 times resting metabolic rates for *Apis* and *Bombus*, Kammer and Heinrich 1974). Thus in terms of the energy balance sheet for the colony as a whole, the energy savings and reduced mortality accruing under the *P. occidentalis* system by virtue of the reduction in number of foraging trips probably more than offset the relatively cheap energetic and demographic costs of the introduction of material transfer times into the equation.

What is the selective advantage of switching? The *P. occidentalis* system of organizing nest construction will run at optimal smoothness (minimization of waiting times) if the numbers of workers are optimally allocated among the three tasks. If there are too few water foragers to service the pulp foragers and builders that are active, for example, then pulp foragers and builders will experience longer than usual waits to obtain water. This could trigger a switch to water foraging by one or more builders or pulp foragers, the effect being to reduce the wait for water. In this way the system could fine-tune itself to reduce mean waiting times and increase efficiency.

Although the phenomena of specialists and generalists appear not to be artifacts of sampling differences, there remains the question of whether or not they represent two discrete behavioral types. The fact that some workers were characterized as generalized on the basis of only one switch suggests that the two kinds of workers may lie on a continuum of switching rates (switches/task), and that if longer sequences of tasks had been observed more of the specialists would have been seen to perform more than one task, putting them in the generalist category. On the other hand, three observations circumstantially support the notion of two discrete behavioral types: (1) a relatively large proportion of workers were specialists, (2) similar proportions of workers in large and small colonies were specialists, and (3) the increase in overall transition frequencies observed in small colonies was the result of increased switching rates on the part of the same proportion of generalists as in large colonies, and not by an increase in the proportion of generalists.

It should be emphasized that these apparent differences between generalists and specialists are based on short-term observations (in some cases as little as two days' observation), and do not necessarily reflect longer term differences. Age polyethism does occur among *Polybia occidentalis* workers (Forsyth 1978). Workers typically work on the nest when they are young, then switch to foraging when they are older. The interval during which the transition is made may be several days for some workers (Jeanne, unpublished data). It is possible that the generalists observed to perform building plus one or both kinds of foraging were workers that were in this transition period, while specialists were workers sampled either before entering or after leaving it.

Thresholds of response to each of the three tasks considered in this study undoubtedly differ among individual workers. Although the interactions analyzed here no doubt are constrained by such differences, it was not the purpose of this study to determine the sources of these differences or the extent of the constraints they impose. This will have to await future work.

Two patterns seen in small colonies seem to be partial throw-backs to the series operation typical of solitary wasps: the switching by pulp foragers to building to use up the residue of their own foraged loads, and the occasional collection of water from a leaf by an outgoing pulp forager. Yet certain behavior patterns are not flexible enough to revert to the in-series system of solitary species. Most notably, pulp foragers always collect loads that are too big for them to build with until they are shared with nestmates.

In sum, the *Polybia occidentalis* system of organizing nest construction work is well adapted to colonies of several hundred workers or more, and works more efficiently there.

*Acknowledgements.* Appreciation is expressed to Holly A. Downing for assistance in the field. Dr. Brian Yandell provided statistical advice. Jeffrey Baylis and Deborah Gordon suggested ways to improve the manuscript. Research supported by the College of Agrucultural and Life Sciences, University of Wisconsin, Madison, and by National Science Foundation grant BNS-8112744.

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