Organization and Regulation of Nest Construction Behavior in *Metapolybia* Wasps

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Field observations and experiments revealed that construction behavior of Metapolybia *wasps is based on parallel processing and distributed decision making. Sixteen behaviors were used to separate five behavioral groupings: specialized water forager, flexible pulpforager, active builder, active generalist, and idle. The idle category proved to be the source and the sink of the other task groups, although specialist foragers tend to retain their duties or take over other active roles. Nest construction is partitioned into three tasks. Pulp foragers transfer wood-pulp to the nest where other wasps (builders) distribute and process it further. The builders incorporate this material into the nest structure on the basis of individual decisions. Water foragers provide the extra water necessary for both building and pulp collecting. Material exchange takes place on the nest between pairs or in small groups. The duration and frequency of different behaviors, the number of wasps belonging to different behavioral groups, and the different scale of specialization in different groups suggest that the colony-level performance and speed are governed by the activity of the pulp foragers, who receive information about both the water saturation level of the colony and the activity of the builders through local interactions. Several predictions of this hypothesis were supported by disturbing the normal construction behavior through removing or decreasing the number of individuals belonging to different behavioral groups or supplying additional building material.*

KEY WORDS: organization; regulation; specialization; building behavior; social wasp.

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111

INTRODUCTION

Social insects coordinate many colony-level performances without any evidence of central control. Oster and Wilson (1978) highlighted parallel processing as one reason for the great success of social insects, because the colony has the capacity to conduct all of its operations concurrently instead of sequentially. Reliability theory states that redundancy at a subunit level is more efficient than redundancy at the system level (Barlow and Proschan, 1975), reinforcing the significance of insect colonies with redundant components. Behavioural castes emerge through specialization for more efficient performance: labor is divided by tasks, and these more or less separate tasks are concatenated to form a complete sequence. This system demands explanations of three kinds that can be aligned with one another: "the relative adaptiveness of the colonies as superorganismic operating units within their natural environment, the ergonomic matrix that determines an optimal or at least evolutionarily stable mix of castes and communication systems, and the details of the castes and communication systems themselves" (Hölldobler and Wilson, 1990).

Cooperative phenomena may emerge at the colony level from simple behavioural rules and interactions at individual level (Grassé, 1959; Deneubourg, 1977; Deneubourg and Goss, 1989; Camazine, 1991; Franks *et al.,* 1991; Karsai and Pénzes, 1993, 1998; Theraulaz and Bonabeau, 1995; Bonabeau *et al.,* 1997; Theraulaz *et al.,* 1999). While the individual behavioural repertoire of a social insect is small and its behaviour has some random component, the great number of (nonlinear) interactions lead to complex, adaptive, colony-level performance. These interactions can be both direct (e.g., antennating) and indirect (e.g., through nest structure or foraging trail), and behaviors with strong random components may be controlled by local constraints and locally perceived information (Theraulaz *et al.,* 1999). The nests of social wasps, for example, are generally much larger than what a single individual could construct. These structures can reach considerable complexity and size, but usually only beyond the lifespan of any individual builder (Jeanne, 1975; Wenzel, 1991; 1998) and therefore require some integration of information across both time and space. The information may be "stored" by way of the nest itself (as an external map), thus requiring no central control or learning, but using decentralized decision making based on stigmergy (Karsai and Pénzes, 1993; Theraulaz and Bonabeau, 1995; Karsai, 1999). Examples of such emergent phenomena concerning nest construction behavior of wasps include isotropic growth of combs (Karsai and Pénzes, 1993), correspondence between nest design and subsequent construction (Karsai and Theraulaz, 1995), origin of nest diversity (Theraulaz and Bonabeau, 1995; Theraulaz *et al.,* 1999, Karsai

and Pénzes, 1998), and nest size and its relation to brood demography (Karsai *et al.,* 1996).

In a separate study (Karsai and Wenzel, 1998), we examined complexity and specialization in task partitioning at both individual and colony levels. Consistent with models of Oster and Wilson (1978) we predicted that in small, risk-tolerant colonies, behavioral flexibility of individual workers would be preferred, whereas at the other end of the spectrum, species characterized by large colonies should rely upon a high rate of exploration and exploitation of the environment by numerous small specialized workers. In primitive, small societies (e.g., *Polistes*), the nests generally grow gradually through the season coupled with the colony dynamics (Karsai *et al.,* 1996). There is no specialization in material transport (each forager collects first water, then pulp), and wasps seldom share the load with other wasps upon return to the nest (Fig. 1a). The regulation of building activity is mainly achieved by the nest structure: behavior is controlled by spatial constraints and perceived local information (Downing and Jeanne, 1988; 1990; Karsai and Pénzes, 1993; Karsai and Theraulaz, 1995; Karsai and Wenzel, 1995). On the other hand, the nests of advanced, large societies (e.g., *Polybia occidentalis*) are built in short bursts with long calm periods. Workers specialize in either water or pulp foraging, and both materials are distributed to other individuals on the nest (Fig. 1f). Specialized builders execute the construction behaviour (Forsyth, 1978; Jeanne, 1986; 1996). Large colony size allows redundant, parallel organization for higher reliability at the level of the system. Jeanne (1996) proposed that the control mechanism was a chain of information from one task group to the next (in reverse order of material flow), e.g., the level of pulp foraging activity is determined by information about demand from builders. However, generalizations regarding the evolution of the organization of work remain inconclusive as long as they are based only on studies of very primitive and very advanced species; data from intermediate species are critical (Fig. 1e).

Species such as those of *Metapolybia* possess characteristics intermediate between *Polistes* and *Polybia* for both colony size and nest complexity. These are easily observed and may be particularly informative for discovering transitions in more intangible properties, such as those of organization of work (see Fig. 1). Using data from field observations and experiments, the present paper addresses the following problems:

1. How are the different colony tasks linked?
2. What degree of specialization (behavior groups) emerges in building behavior?
3. How flexible are the individual- and colony-level construction behaviors?
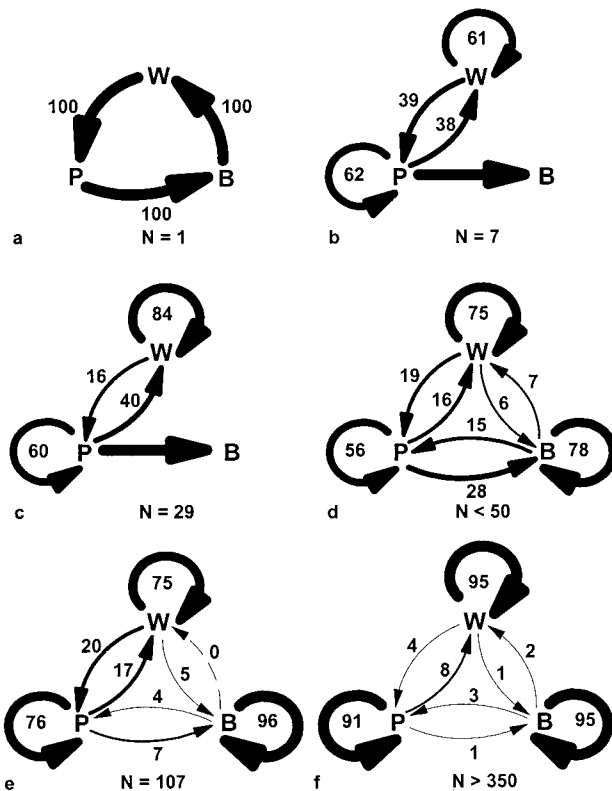4. How is nest construction regulated?

Fig. 1. Frequency of transitions between three construction tasks, building (B), pulp foraging (P) and water foraging (W). a. Single foundress, as in *Polistes.* b. *Vespula sylvestris,* c. *Polistes* fuscatus, colony of 29 individuals, d. *Polybia occidentalis,* data pooled from four colonies of less than 50 individuals, e. *Metapolybia mesoamerica,* colony of 107 individuals, (this study). f. *Polybia occidentalis,* data pooled from three colonies larger than 350 individuals, Width of arrows corresponds to frequency, numerals indicate exact values. In Figs. 1a, b, and c, every pulp forager also built with her pulp (regardless of sharing) as indicated by the large arrow between P and B. (Figure from Karsai and Wenzel 1998, *Proc. Nat. Acad. Sci. USA* **95:** 8865–8869, Fig 4: see also references for the original studies).

MATERIALS AND METHODS

Study Site and Population

Field studies were conducted at the research station on the island of Barro Colorado Nature Monument, Panama, in the tropical lowland forest (Rau, 1933) and at Gamboa in suburban-successional vegetation. The observations were made in November 1995 during the rainy season. A colony of 63 individuals of *M. aztecoides* was observed at Gamboa Research Station (GAM colony). A colony of 107 individuals of *M. mesoamerica* (Smethurst and Carpenter, 1997) was observed on Barro Colorado Island (BCI colony). Voucher specimens are deposited at Museum of Biological Diversity, OSU Columbus and at the American Museum of Natural History, New York.

The two species were examined separately with the same methods. The data of the two species were examined separately and we are reporting the results on behavior of both species separately here. There is no profound differences in the behavior of individuals or in organization and regulation at colony level across species. In a previous study we showed that these properties are so robust that they show a predictive pattern across different wasp genera (Fig. 1). In a few cases, (indicated) the data for the two species were pooled (the scale of analysis is the behavior and interactions among individuals, not the colony as a whole). As our goal was to find commonalities that might be general across a diversity of paper wasps, we believe that finding commonalities across species within a genus is an appropriate start (see Fig. 1). Furthermore, the continuity between colony size and organization of work has been shown in previous work (Karsai and Wenzel, 1998).

Metapolybia builds a nest of one oval comb and an envelope with an upward-pointing, spout-like opening (Wenzel, 1991). The comb is built sessile upon a flat surface (here, the vertical walls of two buildings), and the bottom of each cell rests firmly on the surface. Wasps were accustomed to the presence of human activity, therefore close observation of the activity of the wasps was convenient. To induce more extensive nest construction behavior, the envelope was removed (keeping intact its eaves around the margin of the comb) with a razorblade in late afternoon. This technique has long been used to study swarming wasps by other researchers (West Eberhard, 1978a, Jeanne, 1986, 1996), and is well-respected. Over the next few days (examination period) the behavior of the wasps was followed without new perturbation. The reconstruction of the envelope resembled the normal construction of the envelope of natural swarms of *Metapolybia,* in which the wasps (after constructing the cells and the sides of the envelope) complete the central sheet that covers the comb (Karsai and Wenzel, personal observations). To ensure good visibility of the individuals the partly-

rebuilt envelope was removed again in a few days, if necessary. To decrease disturbance of the colonies, but to obtain information for a given individual for the longer term (3 weeks), the observations were organized into the observation periods as follows: Zero day: removing envelope, first day marking individuals, registering already marked individuals from previous marking, 2–7 days observations and experiments, 5- to 10-day pause for the given colony (working with other colony), then new observation period with removing of envelope.

From those wasps that showed building activity and foraging, we marked as many as was practical for individual recognition at least 1 day prior to collection of behavioral data. The marking was done without anaesthesia by grasping the wasp with forceps. A small drop of correction fluid was applied to the thorax, then this spot was painted with a unique combination of colors, and the wasp was immediately released near the comb. The behavior of all colored wasps was recorded according to a predefined behavioral set (Table I) every 5 min. One observation period consisted of 7 scanning periods (total 35 min). Observation periods were separated from the experimental manipulation or from other observations by a pause of at least 15 min. During observations, every wasp arriving on the nest was examined and the type of load was registered. At the end of each 5-min scanning period the rate of building activity was measured as the instantaneous number of builders (either marked or not) actively adding pulp to the nest. On the BCI colony 21 marked wasps were scanned 287 times, and on the GAM colony 18 marked wasps were scanned 133 times.

Table I. Observed Behaviors

Acronym	Description
LW	Land with water
LP	Land with pulp
LK	Land with protein food
LN	Land without load
BU	Build
MP	Malaxate pulp
GL	Give liquid to another wasp
RL	Receive liquid from another wasp
MK	Malaxate protein food
FE	Feed larvae
EX	Examine cells
SI	Sit on the surface of comb or an edge of envelope
WA	Walk on surface of comb or on edge of envelope
GR	Groom
FA	Fan nest with wings
NO	Undetected, wasp outside or hidden between side of comb and envelope, or other behavior

Thus the total observation time excluding pilot studies, manipulations, and markings was 2100 wasp-minutes.

Manipulations

Before each manipulation, the baseline activity (for control) was registered for one observation period. Then the actual manipulation was carried out with minimal disturbance: capturing 10–15 builders or 2–3 pulpforagers with forceps, or spraying 0.5 ml water on the nest with a small syringe. Data from the observation periods preceding and following manipulation were compared using a Wilcoxon rank test. Captured wasps were released immediately after the experiment. A subsequent observation period allowed us to study the effect of returning the system to baseline conditions. Even if the reaction of the system was clear (e.g., after removing pulp foragers, the number of pulp loads and construction became zero), at least four replicates were carried out. In case of water addition seven replicates were made due to the supposed importance in the regulation of the water. Each replicate itself comprised data from 14 scans of 18–21 marked wasps and all building related activity at colony level.

Durations of behaviors were measured (in seconds) by a stopwatch. Unloading time is defined from landing on the nest with a load to the dispensation of the load by the forager. Building time is defined from the application of material to the nest to the end of this process. Distributing and malaxating the pulp load were considered different behaviors. When numbers of arriving loads were low, the distribution process (number of recipients, time necessary for distribution) and the solicitation of water (number of wasps from which water was solicited and the duration from first solicitation to the last) were also followed.

For hierarchical cluster analysis, individual behavioral profiles were standardized according to absolute activity. To prepare the dendrogram, the squared Euclidean measure with the centroid method was used (Norusis/SPSS Inc., 1993). To define behavioral profiles, we clustered by variables to find what behaviors are associated with each other. Behavior "NO" (Table I) was omitted from this analysis. Independently, we clustered by cases to find which wasps fell into each group (assigning groups trivial names according to features of their respective profiles). This method of defining behavioral profiles and groups in swarm founding wasps contrasts with earlier research (Jeanne, 1986, 1996) in that the data form patterns prior to our designation of task-group identity. Additionally, the patterns include all observed behaviors, not just those immediately preceding or following a given observation. This technique uses more information than

earlier methods and reduces the influence of axiomatic or accidental assign-ment of individuals to one or another group [for similar approach see examples in Gadagkar and Joshi (1983, 1984) and in Corbara *et al.* (1989)]. These methods permitted discriminant analysis to test the probability that wasps would be correctly assigned to named behavioral groups.

RESULTS

Behavioral Profiles

Cluster analysis of behaviors revealed several groups (Fig. 2). In both colonies, general colony maintenance behaviors clustered tightly together (e.g., returning with protein, feeding larvae, exchange of liquid, malaxating food and pulp) and separately from behaviors associated with building or patrolling the comb. In the GAM colony, water foraging was extremely enhanced in one individual, causing the separation of this behavior from all others. If this individual is excluded from the analysis, the association of behaviors is even more similar across the two colonies, except that sitting and walking are connected in GAM, as are receiving liquid and building.

Main clusters of wasps according to behaviors were also similar in the two colonies. Clusters are given trivial names here based upon the common behavioral profiles characteristic for the group. A specialized water forager emerged in the GAM colony (Fig. 3). The activity of this individual corre-sponded almost exclusively (95% of the examined time) to water transport. In both colonies, a fundamental division grouped about half the marked wasps as "idle" and half as active. The general activity of a given group can be easily followed by the magnitude of "NO" behavior, which is defined as an observation when the wasp was not detected on the surface of the nest (but we used the whole behavioral profile to characterize the individu-als (see Methods and Table I)).

Idle wasps performed wide variety of behaviors, but did so only rarely (NO = 83 ± 12%, $N = 11$ in GAM, and NO = 84 ± 9%, $N = 17$ in BCI). Protein foragers were a specialized subset of this group: one or two wasps occasionally transported a load of meat to the nest, but they spent the majority of their time resting or in nonspecific behaviors (e.g., grooming, examining cells). The majority of wasps which that never marked belonged to this idle group; they did not show any building or foraging activity.

The active wasps are divided into pulp foragers versus all others. Pulp foragers were very active individuals (NO < 36%, $N = 3$). The pulp foragers spent more than a third of their total activity transporting cellulose pulp to the nest. In the BCI colony, where there was no specialized water forager,
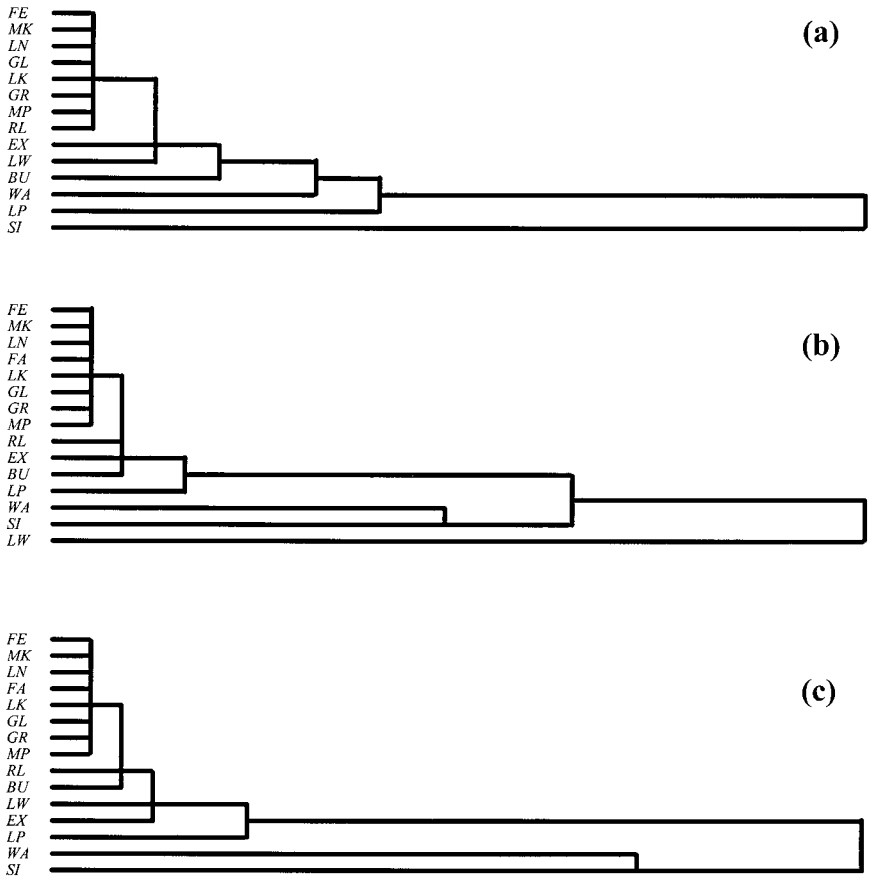
Fig. 2. Linkage of behaviours in *Metapolybia* colonies. a: BCI (*M. mesoamerica*). b: GAM (*M. aztecoides*). c: GAM, after removing the specialized water forager. Acronyms and description of behaviors in Table I. Especially when the specialized water forager of GAM colony was excluded, the two colonies showed general agreement regarding which behaviors were linked most tightly and which were most apart from the others.

the pulp forager commonly collected water too, or solicited and received water from nestmates that were sitting or walking on the nest (see Discussion).

In the larger BCI colony the final cluster of active wasps is divided in two subgroups. The more active of these subgroup (NO = 24 ± 9%, N = 4) performed the majority of building behaviors (Figs. 4, 6) and remained on the most active zone of the nest (top of the comb and edge of the envelope) between the building bursts. The less active subgroup (NO =
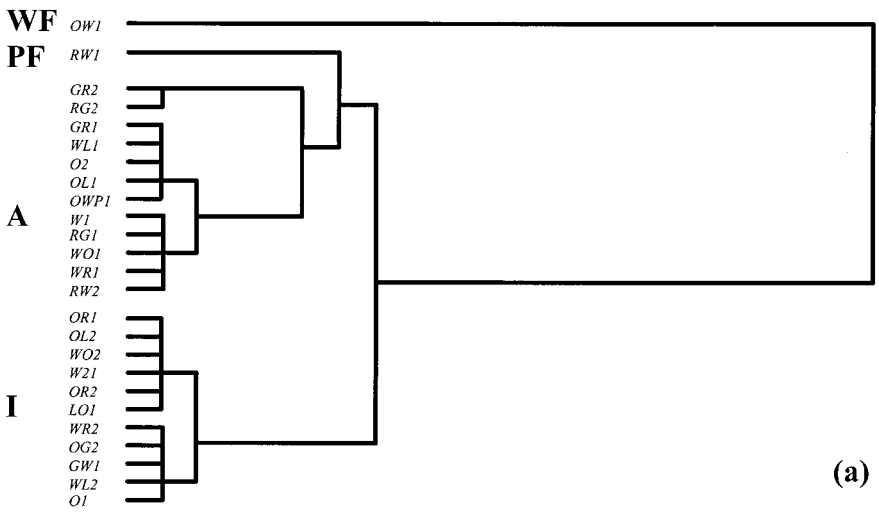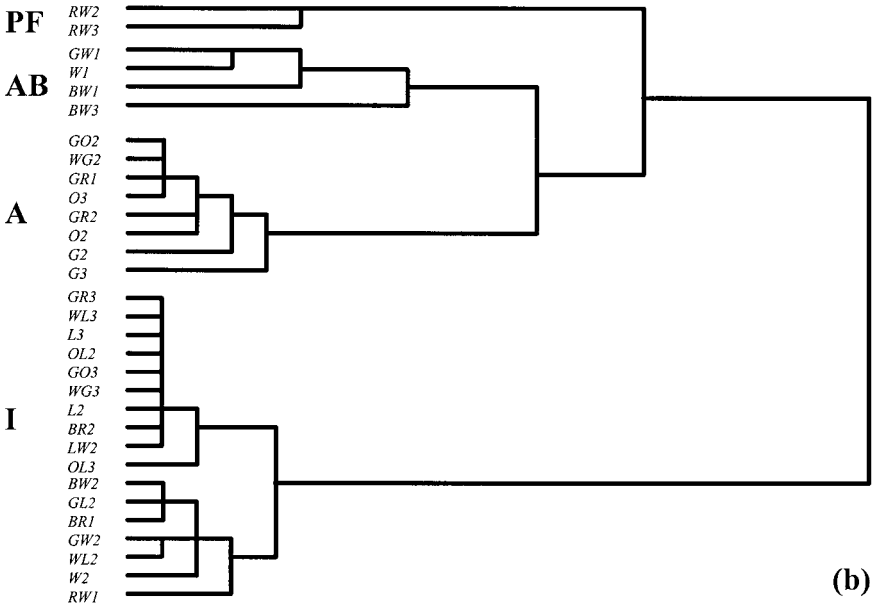
Fig. 3. Behavior groups of *Metapolybia* colonies: a: GAM. b: BCI. Individual wasps identified by their color codes (letters, here). First letter denotes the behaviour observed just before marking (R: pulp foraging, O: water foraging, L: protein foraging, G, B, W: building). Second letter is corresponds to unique identification of each wasp within each colony (letters represent the actual color code). The numeral denotes consecutive observation periods to follow long term (5–10 days) changes (see Fig. 5). Groups (large bold letters) derived from the multivariate analysis: WF: water forager, PF: pulp forager, A: active, AB: active builder, I: idle. As an example, in BCI colony: RW wasp was marked with red-white color after it was caught while returning with pulp. In the first period, this wasp was rather idle (RW1), but in the second (7 days later) and third observation periods (5 days still later) it worked as pulp forager (RW2, RW3). The figure shows that this individual was similar behaviourly to other idle wasps initially, then it was rather distinct from all other wasps, and it retained this distinction through time.
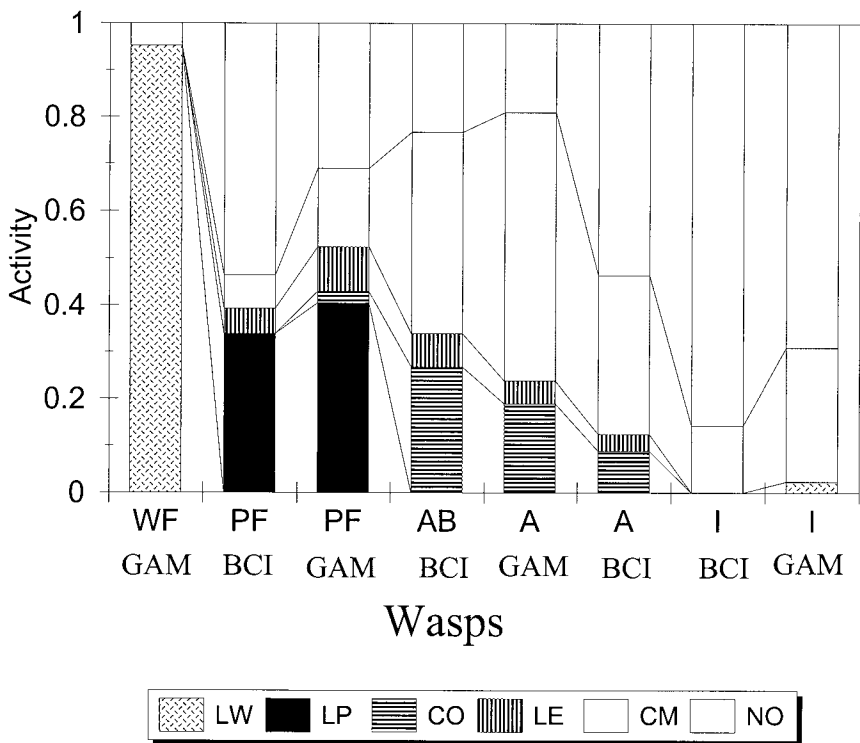
Fig. 4. An example of the percentage distribution of daily activity of wasps belonging to different behavioral groups and colonies (see Fig. 3). WF: water forager, PF: pulp forager, A: active, AB: active builder, I: idle. Behaviors: LW: landing with water, LP: landing with pulp, CO: construction (BU+MP), LE: exchange of liquid (GL+RL), CM: colony maintenance behaviors (MK+FE+WA+SI+EX+GR), NO: not any of other behaviors. See Table I for definitions of behavioral abbreviations.

$53 \pm 6\%$ $N = 8$) is composed of generalists performing all kinds of colony maintenance behaviors without specialization, including building and foraging for water. In the smaller GAM colony, the general activity level of the active group is between that of the two active subgroups of the BCI colony (NO = $31 \pm 18\%$, $N = 12$). This group performed colony maintenance behaviors, including building and occasional pulp and water foraging.

Assignment of individuals to these nominal groups was tested by discriminant analysis, and for every individual the probability of correct assignment exceeded 99%. The best discriminative behaviors (Wilks' Lambda <0.5 and significance of univariate F-ratio $p < 0.05$) in the BCI colony were NO, BU, MP, LP, RL, SI, WA and in the GAM colony were NO,

LP, LW, LN, RL, SI (see Table I for acronyms). Changes of behavioral profile between observation periods (5–10 days) were common. The ''idle'' group served as source and sink of the other groups. Most specialized foragers retained their status until they disappeared from the study or assumed other active tasks without returning to the pool of idle wasps (Fig. 5).

Nest Construction

If we focus only on the behaviors linked directly to construction (building, landing with pulp and water) interesting specializations can be found (Fig. 6). There are only a few active builders, and these rarely forage for water or pulp. Wasps that spend a considerable time with water-foraging are usually highly specialized. They neither build nor take part in colony maintenance behavior. Wasps that carry pulp to the nest seem to be less specialized, because they occasionally both build and forage for water (Fig. 7). Changing tasks is common both over the short term (as in a single observation period) and over the long term (encompassing several days) (Figs. 5, 7). The flexibility of these pulp foragers is valid for construction behaviour only, because they rarely perform any other type of colony maintenance behaviour (e.g. feeding).
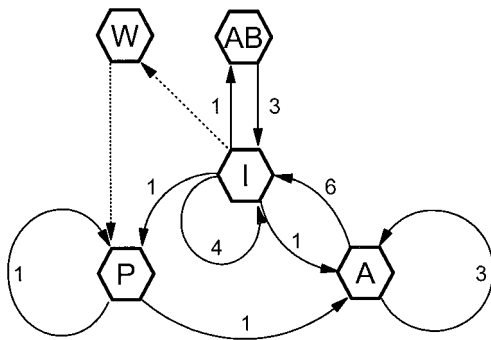

Fig. 5. Transitions among different behavioral groups between two consecutive observation periods (interval between observations was between 5 and 10 days), data of colonies are pooled. Transitions established from cluster and discriminant analyses. A: active, AB: active builder, I: idle, P: pulp forager, W: water forager. Transitions to and from water forager (broken arrows) somewhat speculative, based on short-term behavior of one wasp.
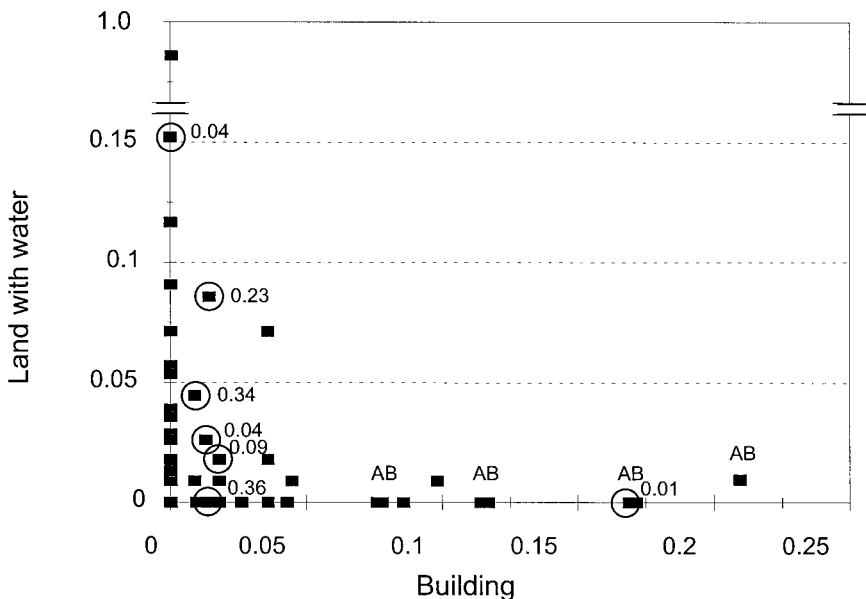
Fig. 6. Building versus land-with-water scattergram of the marked individuals ($N = 47$) of the two colonies. Data are expressed as the relative occurrence of given behavior among all scans for each individual. AB denotes the active builders (see also Fig. 3). Circle denotes individuals who transported pulp loads to the nest, numerals representing for these a third axis: the proportion of all scans in which they had pulp. LW = 0.95 shows the value of the specialized water forager, which is off scale.

A great number of wasps performed at a very low rate both building and water foraging. Among these those wasps that prefer water foraging mainly belong to the idle group and those that prefer building mainly belong to the active group. The idle wasps are not necessarily young, unspecialized individuals. For example, some of them were very active in building 6 days earlier (e.g., in BCI colony, individuals GW, W and BW; in GAM colony, individuals WO, WR, and WL, see Fig. 3).

Each of the construction behaviors is discussed in turn below.

1. Water foraging (characterized by behavior "Land with water"). The worker that specializes in water foraging leaves the nest, flies to a water source where she imbibes water, than carryies it to the nest (Fig. 8). The water forager regurgitates the water to several wasps at the nest, taking a little longer than a minute. The relationship between the handling time and the number of nestmates receiving liquid fits an exponential function ($Y = 35.8e^{0.15x}$, $R^2 = 0.56$***,
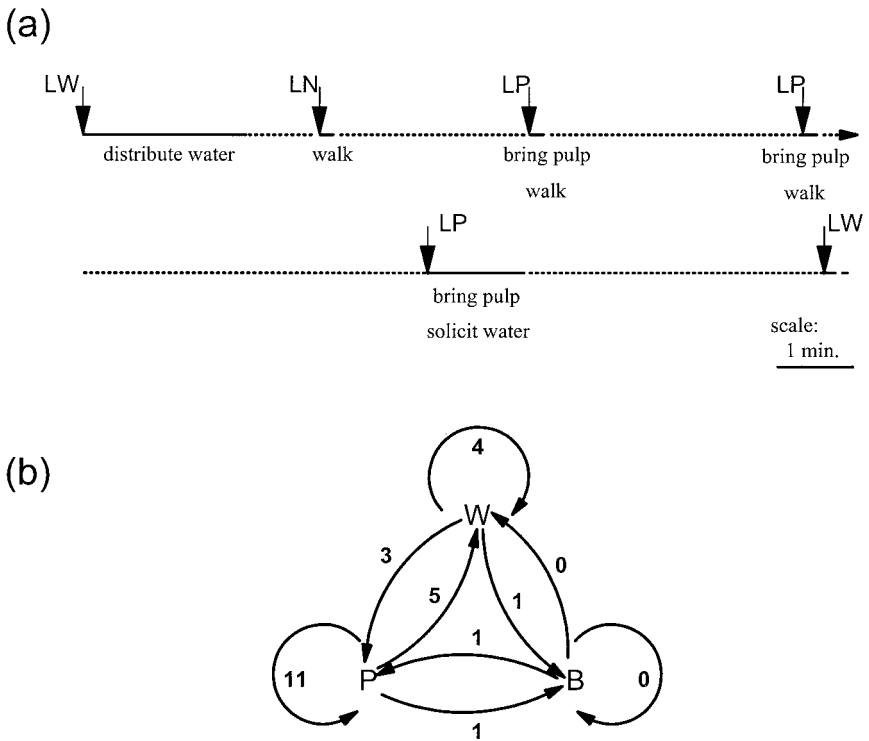
(a)

(b)

Fig. 7. (a) Time line: short-term flexibility of a pulp forager's activity (about 30 min total). Upper line wraps around to lower line. LW: land with water, LP: land with pulp, LN: land without load, solid line: wasp on nest; broken line: wasp off nest. (b) Transitions between different tasks concerned with building for the same wasp illustrated in Fig. 7a, summed over four days. W: water foraging, P: pulp foraging, B: building.

df = 25) as expected from the mechanism of transfer (because distributing water becomes more difficult as colony saturation increases). This suggests (assuming that the quantity of the load is near constant) that water transport is controlled by a value determined as [stored water quantity]/[water storage capacity] of the colony. This value approximates 1.0 when the colony is saturated with water, and approximates 0.0 when it is dehydrated. If the colony saturation is low, foragers are able to deliver water with great frequency because nearly any wasp will take the forager's load. The maximum rate of delivery observed in GAM colony was performed by a specialized wasp that transported 101 water loads during 210 min, i.e., it completed a trip in every 2.08 min with a minimum turn-
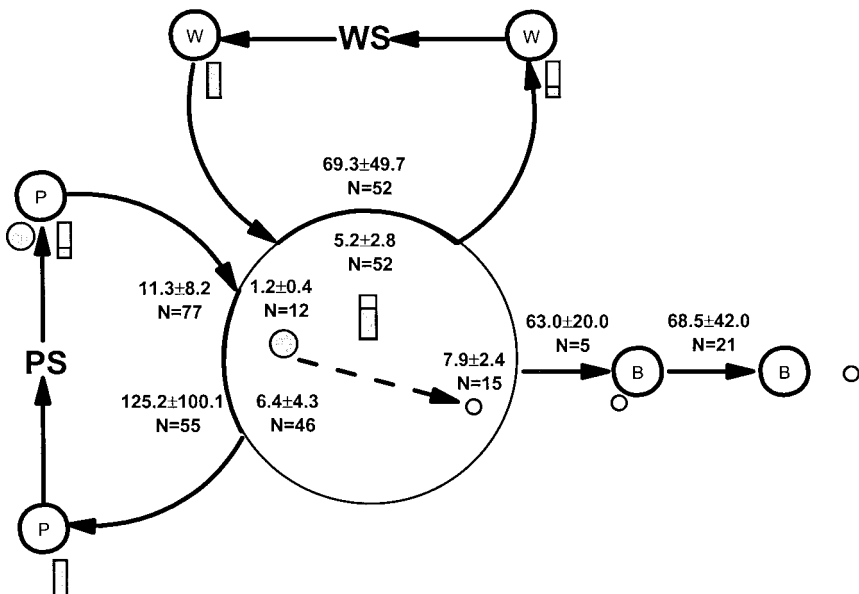
Fig. 8. Timing of construction process and interaction of workers and materials in nest construction of *Metapolybia* (data pooled from two colonies). Big circle in the center represents the pool of wasps (colony members). Numbers inside the circle denote the number of wasps involved in the interactions (mean ± standard deviation, N = sample size). Numbers outside the circle show the duration of different behaviors in seconds (mean ± standard deviation, N = sample size). Small circles around a single letter represent a given individual: P: pulp forager, W: water forager, B: builder. Thick arrows shows the cycle involving pulp source (PS) or water source (WS). Shaded figures represent relative quantities of pulp (circles) and relative water level (box) of a reference individual. Broken arrows within the big circle represent sharing pulp (one pulp shared among 7.9 individual in average).

around time (highest number of "landing with water" behavior per 5 min) calculated at 1.25 min.

2. Pulp foraging (characterized by behavior "Land with pulp"). The wasp that forages for pulp generally flies to a fiber source, wets the surface, scrapes up a ball of wood fiber using the mandibles, and then returns with it to the nest (Fig. 8). The majority of the pulp (56% ± 20%, calculated from 8 observation periods including 400 pulp trips) is delivered by a single individual. After landing, the pulp forager actively offers the load to one or two workers. Sometimes the pulp forager retains some pulp and builds. Usually after distributing the pulp, the pulp forager starts to solicit water for the next trip. Soliciting water is generally a very time-consuming behavior. As was found for water distribution, the time necessary for collecting

water by solicitation increases exponentially with the number of wasps solicited ($Y = 27.4e^{0.19x}$, $R^2 = 0.59$***, df = 27). This suggests (assuming that the quantity of water necessary for the next pulp foraging trip is near constant) that the speed of soliciting water (and therefore the activity of pulp foraging) is controlled by the colony saturation of water. Delivery of pulp to the colony is never as frequent as water foraging. A specialized pulpforager arrives with a new load on average every 14.7 min (19 pulp loads during 280 min). However, if the colony is saturated with water, this time can drop to 2.5 min (see below).

3. Building (characterized by behavior "build"). A builder receives water from water foragers or another wasp, or it forages for water independently. A builder receives pulp from a pulp forager or from other active workers. One pulp load is generally subdivided by the builders into several pieces (7.87 ± 2.4, from direct observation of the subdivisions of 15 pulp loads). After processing (malaxating the pulp with water), the builder moves to an area of the nest under construction and works the wet pulp into the nest using its mandibles. Time from the arrival of a pulp load to its complete incorporation into the nest is almost 7 min (411.3 ± 12.5 seconds; $N = 3$).

Colony Level Activity

Because observation bouts (3.5 and 4 h total) were evenly distributed throughout the active period of the colony (7:00 a.m.–5:30 p.m.), the total activity of colony BCI can be calculated as: ((observed in day1 + observed in day2)*2.8)/2. Thus daily water foraging is estimated as 117.6 trips and pulp foraging as 92.4 trips. The water/pulp foraging ratio is 1.27. From the ratio of pulp sharing (Fig. 8) and the number of pulp loads the number of building efforts can be calculated as: 92.4*7.87=727.19. Removing 15 builders from a colony of 107 individuals showed that building continued with seven builders (observed maximum). This means that at least 20% of the colony can take part in the construction behavior as builders. If we assume that construction behavior has the highest priority and that these 22 putative builders would be able to perform the work continously (63.0 sec. processing + 68.5 sec. building) during the active period, then the daily maximum of building events is ((10.5*3600)/131.5)*22 = 6324. This is more than nine-fold of the estimated value; thus, it seems that the builders could build more than they actually do. Starting from a different point, if building continously, these 22 builders would require: (35*60)/131.5*(22/7.87) =

44.6 pulp loads every 35 min. This is ten times larger than the observed (4.4 ± 2.3, max $= 11$, $N = 15$) pulp foraging activity.

Perturbation Experiments

1. Which Behavioral Group Controls the Tempo of Construction Behavior?

The removal of two or three pulp foragers had a drastic effect, completely stopping pulp foraging (new pulp foragers did not emerge within the studied 50-min period), and no building behavior was observed (Table II). However, there was no significant change in the number of water loads that arrived at the nest. Thus, as a behavioral group, pulp foragers control the tempo of the construction behavior.

2. Is There Any Feedback from Building to Pulp Foraging?

The removal of the most active 10–15 builders had no effect on the number of water loads, but significantly decreased building activity, indicating that few if any new builders were recruited. The number of pulp loads also decreased (Table II), indicating the link between the two tasks. When the number of builders is small, the pulp foragers need significantly more time to unload pulp (35.3 ± 54.5 seconds, $N = 12$ instead of 12.0 ± 10.5 seconds, $N = 25$).

3. What is the Key Factor in the Control of the Construction Behavior?

Addition of water to the nest significantly decreased the number of water trips. On the other hand, both pulp foraging and building activity increased significantly (Table II). Sometimes pulp foraging seems to be triggered by water supplementation. With water supplemented, pulp foragers received water required for pulp collection two times faster than the baseline rate, dropping from 110.4 ± 87.3 to 63.9 ± 32.1 seconds (Wilcoxon signed-rank test: $Z = -1.771$, $N = 19$, $p = 0.077$). However, the number of wasps solicited only slightly decreased, from 6.7 ± 5.1 to 4.4 ± 2.7, (Wilcoxon signed-rank test: $Z = -1.528$, $N = 19$, $p = 0.126$). Thus, as a medium, water controls the global tempo of construction activity because as colony water saturation increases, pulp foragers can increase the pace of their own activity.

Table II. Perturbation Experiments[a]

	Removing pulp foragers					
	Pulp loads		Water loads		Building	
Replicate	Control	Manip.	Control	Manip.	Control	Manip.
1	4	0	1	2	26	0
2	5	0	9	3	28	0
3	9	0	6	2	53	0
4	8	0	2	7	46	0
Wilcoxon	$Z = -1.826, p = 0.068$		$Z = -0.365, p = 0.715$		$Z = -1.826, p = 0.068$	

	Removing builders							
	Pulp loads		Water loads		Building		Unload time (sec.)	
Replicate	Control	Manip.	Control	Manip.	Control	Manip.	Control	Manip.
1	7	3	4	4	45	13	5.4 ± 2.2	12.8 ± 8.2
2	6	3	2	5	43	14	7.4 ± 1.7	15.3 ± 2.5
3	7	2	4	2	20	7	14.4 ± 4.4	32.7 ± 34.4
4	5	5	0	6	32	19	17.0 ± 16.6	114.5 ± 119.9
							SN = 25	SN = 12
Wilcoxon	$Z = -1.604, p = 0.110^b$		$Z = -1.069, p = 0.285$		$Z = -1.841, p = 0.066$		$Z = -1.826, p = 0.068$	

| | Water addition | | | | | |
| | Pulp loads | | Water loads | | Building | |
Replicate	Control	Manip.	Control	Manip.	Control	Manip.
1	5	7	6	5	19	39
2	1	7	5	8	9	16
3	3	7	11	8	29	38
4	10	10	24	5	55	55
5	0	3	8	5	4	18
6	0	2	12	4	2	9
7	0	4	11	7	5	18
Wilcoxon	$Z = -2.214, p = 0.027$		$Z = -1.873, p = 0.061$		$Z = -2.207, p = 0.027$	

[a]The effects of independent removal of pulp foragers, builders and water foragers on the construction activities (number of pulp loads, water loads, building events, or the time to unload pulp). Control values were measured just prior to each manipulation. Matched pairs are compared by Wilcoxon ranked-sign test. See text for discussion.

[b]After release of the captured builders, arriving pulp loads increased to 9, the highest measured in this set of manipulations. Including this value as a comparison with the loads delivered during manipulation gives $Z = -1.841, p = 0.068$.

DISCUSSION

The ability of social insect colonies to allocate labor in response to changing colony conditions demonstrates behavioral integration and suggests that insect colonies seem to act as cohesive biological entities. Apparently, optimal or close to optimal colony level performance (Robinson, 1992; Franks, 1993) can be observed in the absence of a decision-making leader. How does colony organization evolve and work in social insects, if there is no colony-level ''genome'' or organizer to orchestrate activity? Decentralized decision making and self-organizing processes at the individual level seem to be the best candidates for this role (Bonabeau *et al.,* 1997; Bonabeau *et al.,* 1996). This paradigm for regulation and integration of colony performance has inspired several theoretical and experimental studies mainly in the field of foraging (Deneubourg *et al.,* 1989; Seeley, 1989, 1995; Camazine and Sneyd, 1991; Seeley *et al.,* 1991; Robson *et al.,* 1995) and construction behavior (e.g., Denebourg, 1977; Skarka *et al.,* 1990, Franks *et al.,* 1992; Karsai and Pénzes, 1993, Karsai and Theraulaz, 1995; Theraulaz and Bonabeau, 1995; Karsai *et al.,* 1996; Karsai, 1997; Karsai and Pénzes, 1998; Karsai, 1999). Such new perspectives have provided diverse and provocative insight into these classical issues.

The importance of interactions between individuals is revealed by empirical studies of Gordon *et al.* (1993), who show that the encounter rate is regulated by setting up a local density that allows a high interaction rate. High interaction rate allows quick rescanning of the environment and colony needs and may allow further specialization of workers (Karsai and Wenzel, 1998). Division of labor is considered to be adaptive because specialized workers increase colony efficiency (Oster and Wilson, 1978). Interplay between individual behavioral flexibility and specialization for higher performance (caste) is one of the key problems in sociobiology (Oster and Wilson, 1978; Robinson, 1992; Karsai and Wenzel, 1998; Naug and Gadagkar 1999). If we want to understand how colonies integrate and regulate labor in the face of changing conditions, first we have to identify the behavioural profiles of the individuals to find the linkage between tasks that determine identity of the behavioral groups

Tasks and Behavioral Groups in *Metpolybia* Construction

The first detailed study of division of labor during construction in swarming paper wasps was by Forsyth (1978) on *Metapolybia* and *Polybia,* showing that there are separate groups with differing fidelity to their tasks. Jeanne (1986, 1996) focused on the regulation of nest construction behavior

in *Polybia occidentalis.* He named several castes, such as builder or pulp and water forager for his studies. Using multivariate techniques on two *Metapolybia* species separated behavior profiles corresponding to colony maintenance, water and pulp foraging, building, and patrolling behavior (Fig. 2). Because the present study focused on the regulation of construction behavior, the following behavioral groups were described: water forager, pulp forager, active, active builder, and idle (Fig. 3). By following the behavior of 39 individuals in detail, we found that the first behavior recorded for a marked wasp (that is, the behavior performed just prior to marking) was not a good predictor of the general performance of the given individual. Several individuals showed considerable flexibility and their profiles changed with time (Figs. 3, 5, 7a). Individual variability in "task fixation" was observed in *M. azteca* and *P. occidentalis* by Forsyth (1978) and in *P. occidentalis* by Jeanne *et al.* (1988). For example, Jeanne (1991) showed that 75% of pulp and 94% of water was collected by three and two individuals respectively, but the existence of 118 other "pulp and water foragers" was also mentioned. In the present paper, it is clear that although many wasps sometimes leave the nest to forage, they perform other duties more commonly or are idle. For the present paper, these individuals are assigned to groups other than "forager" such as "idle" or "active" on the basis of their whole performance including behaviors unrelated to foraging. Robinson (1992) pointed out that worker behavioral flexibility must be considered along with colony caste structure. After all, the workers' decisions are made in the context of the colony, not simply as a predetermined schedule, and they are affected by such constraints as the availability of certain resources and the distribution of workers already in place.

In *Metapolybia,* we found only one water forager that we may call a "specialist" in the strict sense. Independent of the general activity level, wasps usually showed diverse behavioral profiles with occasional repetitive behaviors in the short term. This does not mean that all of the wasps should be called generalists, because more active individuals tended to perform a given behavior more repetitively. The pulp foragers are the best example of this flexibility, even in short term (Fig. 7a). They were very active, and although they brought mainly pulp to the nest, sometimes they suddenly changed to building or to forage for water. In contrast, Forsyth (1978) found in *P. occidentalis* higher specialization because of infrequent transitions between types of materials collected by each forager. Jeanne (1986) suggested the existence of two behavioral types of about the same proportions: a group of flexible generalists and a group of specialists. Comparing "small" (< 50 wasp) and "large" (> 350 wasp) colonies, he demonstrated that behavioral transitions are more frequent and the proportion of generalists is higher in small colonies. The correlation between specialization and

colony size appears to be a general rule even across different genera of wasps, with greater specialization only favored in colonies with more numerous workers (Oster and Wilson, 1978, Karsai and Wenzel, 1998). Similarly, the emergence of a parallel system for building would likely impede the nest construction in a small colony, such as a *Metapolybia* colony of seven individuals reported by Forsyth (1978). In this situation, a sequential, individually based organization of work (*Polistes* model) would be more efficient because there would be less time wasted waiting for two specialists to interact.

Following the behavior of several individuals for 3 weeks demonstrated that the idle wasps are the source and the sink of other behavioral groups. However, specialized foragers tend to keep their status or take over another active role. These findings agree with the existence of temporal polyethism (Forsyth, 1978, Jeanne, 1991, Robinson, 1992, Naug and Gadagkar, 1999) and the ''reserve workers'' (Michener, 1964, Gordon, 1989; Robinson, 1992) hypotheses. In our two colonies, half of the colony members spent the majority of time motionless between the comb and the envelope. These individuals are generally considered as excess labor that can be mobilized to defend the nest or substitute for loss of active workers (e.g., Wilson, 1983; Breed *et al.,* 1991; Lenoir, 1987). This reserve pool may contain idle, experienced workers (awaiting appropriate stimuli) as well as young workers that do not respond to colony needs in their first few days. In *Metapolybia,* Forsyth (1978) and West Eberhard (1978b; 1981) outlined the temporal polyethism as follows: 0–6 days idle, 6–10 days nest construction, and brood care, 10–15 days onset of foraging. Although the present paper does not include animals whose ages are known definitively, the length of observation indicates that such a schedule is only a general trend with individual flexibility.

Organization of Nest Construction

The existence of different behavioral groups and the task partitioning in building behavior in *Metapolybia* showed more similarity with highly eusocial swarm founding wasps (e.g., *Polybia*) than with primitive independent founding colonies (*Polistes* model, Karsai and Wenzel, 1998). From the interaction of different groups, a complex building network emerged. The majority of wasps remain always on the nest, while only a few (more or less specialized) individuals carry out the majority of foraging. Limiting the high risk of mortality due to foraging duties (Sakagami and Fukuda, 1968; Schmid-Hempel and Schmid-Hempel, 1984) to certain, usually older individuals is well-known as an adaptive strategy, but the colony must

nonetheless distribute some workers into the roles of foragers and strike a balance between the demands of the different tasks.

The ratio of water trips per pulp trip during construction in this study (1.27) was close to what Jeanne (1986) observed in *Polybia* (1.35). Foraging for water was a frequent behavior because the colony needs water for several purposes outside of construction behavior (e.g., cooling the nest), and water collection continues even when there is no construction. Distributing water was generally more time consuming than unloading pulp because it usually required to contact with more wasps to distribute a water load (Fig. 8). Soliciting water from nest mates for the next pulp foraging trip was a very time-consuming process and requiring contact with a great number of nestmates. Sometimes the pulp forager stopped soliciting and collected water by itself.

When pulp is brought to the nest, one or two wasps (mean of 1.6, identical to Jeanne's estimate for *Polybia*) take it from the pulp forager and distribute it further. This pulp sharing allows release of the constraints that would stem from the next construction step. For example, the size of pulp mass that a wasp can carry is considerably larger than what it can use to build paper. Thus task partition allows larger loads to be brought back in fewer foraging trips than if each builder had to get its own pulp. One pulp load is enough for approximately 8 builders, one third larger than the six builders Jeanne (1986) calculated for *Polybia* (our value is based on observation of the fate of loads, not dry weight ratio). If this discrepancy is not due to the difference between methodologies alone, this may reveal some optimization problem of the material handling. The two wasps have similar size (the *Polybia* is a bit smaller), but the colony size of *Polybia* is generally much larger. If everything else is equal, it would be expected that smaller wasps with larger colony size should transport a load that is enough for more builders. It is yet unclear what limits the size of pulp carried to the nest. It is likely not the size or weight of the pulp, because wasps can transport much larger and heavier food parcels (unpublished data I. Karsai). As we observed, the number of putative builders does not seem to be a constraint against processing larger loads. It is possible that the size of the load is a result of an optimization problem concerning energy or time minimization. Alternatively, the load size may be constrained by a prerequisite material (e.g., water) or in an other way (e.g., scraping and holding large quantity of material is difficult).

Although all wasps took part in exchange of liquid, only 20% of the colony accepted pulp and built. As was found among foragers, some of the builders were very active and performed the majority of building acts. Processing of material and the application of material to the nest required the same time as the total for soliciting water by the pulp forager. Material

processing and construction required some water beyond that contained in the original pulp load. Interacting with other nestmates or foraging for water balanced the demand and the stored water among these wasps quickly. Due to sequential pulp sharing and the duration of processing, the total time elapsed from arrival of a pulp forager and completion of the last building act with that pulp was about 7 min. This is why even with maximal pulp input, some building sites and several builders always remain free. If the pulp input is very low, some builders may remove some small empty outer cells and rebuild the extracted material into the envelope (unpublished data I. Karsai).

Regulation of Nest Construction

Studying *Polybia occidentalis,* Jeanne (1996) concluded that there is flow of information from one task group to the next, in reverse order of material flow, that regulates building behavior. This would mean that the builders received information about the nest damage by direct contact with the nest, that pulp foraging is determined by demand for pulp by builders, and, finally, that water foraging is adjusted in response to feedback received from pulp foragers and builders about the demand for water. Jeanne stated in an earlier study that the water forager set the pace for the operation (Jeanne, 1987), but in a more recent paper (1996), he reports that feedback between builders determines the level of building activity, which in turn sets the magnitude of the entire operation. Building activity would emerge from individual decisions of the builders on the basis of both positive feedback (stimulus from nest damage) and negative feedback (inhibition from active builders). Although our results in *Metapolybia* construction agree in some details with those of Jeanne (above), we found no evidence for information flow among behavioral groups, nor for the feedback mechanisms that are supposed to affect builders and water foragers. Consequently, we propose a regulation mechanism different from Jeanne's, one based on a minimal number of assumptions and coherent with our data and general theory of caste determination.

Removing the envelope of the nest changes the microclimate of the nest considerably (such as by exposing the comb to light, decreasing humidity, or decreasing CO_2 levels). In this context, it seems unecessary to invoke a specific and construction-related stimulus affecting only the group that physically contacts the damaged structure. The new situation would affect all colony members, and the colony has to readjust its activity accordingly. However, as Lenoir (1987) pointed out, age polyethism makes the colony vulnerable to fluctuations in age structure, because different age cohorts

may not be available in proportions appropriate for the colony's immediate need. The difference between the optimal performance and the actual performance (allowed by age distribution and previous specialization) may be reduced by behavioral flexibility and accelerated development, but the colony may not always reach ratios optimal for the given situation (Robinson, 1992; Nakata, 1995, 1996). Hence, if the number of builders was largely determined by factors preceding the experimental removal of envelope, there may be no need to invoke a direct negative feedback for regulating the number of builders (see Bonabeau *et al.,* 1996, for analysis of a similar problem). A more simple approach, the so called ''fixed threshold'' model (Calabi, 1988, Robinson, 1987a,b, 1992, Bonabeau *et al.,* 1996), uses thresholds adjusted by reinforcement processes to account for the number of builders (and, by the same logic, for the other groups too). Individual interactions may *modify* this ratio according to colony needs to increase efficiency.

One of the best examples for fine-tuning ratios of behavioral groups is the interaction between pulp foragers and builders. Removing a large number of builders increased the unloading time of pulp foragers and the summed activity of pulp foragers decreased significantly. This indicates that pulp forager activity may be regulated by the demand for pulp; long unloading time may indicate to the pulp forager that the builders are busy with another load, or the stimulus for accepting pulp is low. The behaviour of the pulp foragers changed in these cases (they rested more, or collected water, or built instead), but their pulp foraging activity returned quickly when the builders were released (Table II). This interpretation is consistent with studies of *Polybia occidentalis* (Jeanne, 1996): In presence of excess pulp, the activity of pulp foragers decreased, more time was need for each forager to unload its pulp, and it encountered more wasps that rejected the pulp during the unloading period.

Removing two or three pulp foragers completely impeded building, because no pulp arrived at the nest. Within the timescale of the observation (35 min), no new pulp forager was recruited despite the fact that demand for pulp was high. This result agrees with general theories of caste determination based on age polyethism (Robinson, 1992) and also shows that the pace of building is determined through the activity of the most flexible task-group (pulp forager), not by the builders sensing construction needs (*contra* Jeanne, 1996). Although the behavior of the pulp foragers is influenced by interactions with builders, their numbers are determined by more complex factors. The low number of pulp foragers is noteworthy in this regard. Although the envelope was removed regularly for 3 weeks to stimulate building, there was no increase in the number of pulp foragers during this period.

Jeanne (1987), in a preliminary study, suggested that building in *P. occidentalis* is regulated by the supply of water brought by water foragers, and in a more recent study (Jeanne, 1996: 486) he suggested that ''water foragers are two steps removed from the ultimate source of information. . . . {they} obtain information about the need for their material through feedback from water users, namely, the pulp foragers and the builders.'' Our results in *Metapolybia* disagree with both suggestions, because the quantity of water arriving at the nest (and taken up by the colony) did not change significantly when either pulp foragers or builders were removed from the nest. This suggests that in *Metapolybia* a large quantity of water is used for purposes other than building (cooling, drinking), and that water foraging cannot be linked directly or strongly to building behavior. Of course, this does not mean that water is neutral for building behavior. Our experiments demonstrated that addition of water to the nest surface, in addition decreasing water foraging activity, significantly increased the number of pulp loads collected and the rate of building behavior. In several cases when there has been only water foraging (no building or pulp foraging), pulp foraging started when water was experimentally supplied to the colony. Thus, although water maybe used for other purposes first, water beyond a certain level can promote building. Analyzing water distribution and solicitation shows that water is given to (or solicited from) any kind of wasp, and the frequent trophallaxis between individuals produces a common watertank. Thus, water users and water foragers are not necessarily linked physically and directly.

In the case of water addition, two changes in the system increased pulp foraging and building activity. First, as observed in the analysis of behavioral profiles (Fig. 7), pulp foragers are important water foragers too, for they may collect water when the colony needs it or when the pulp forager is unable to solicit enough water for the next pulp trip. Applying excess water released the pulp forager from the duty of collecting water; under these conditions it may then collect more pulp per unit time despite no change in general activity level. Moreover, the time necessary for soliciting water for the next pulp trip dropped significantly, making shorter turnaround times possible. We interpret that this effect is more important for regulating colony-level building behavior than is the feedback of demand from builders.

CONCLUSIONS

This study demonstrates that in *Metapolybia* there can be five behavioral groups, three of which actively take part in construction behavior.

This study indicates the importance of flexible behavioral groups in the regulation of colony-level performance. Accordingly, caste definitions must be based on linkages between suites of behaviors rather than on predetermined classes oriented toward single behaviors.

Several parts of the regulation of building behavior in *Metapolybia* can be derived from the primitive *Polistes* model (Karsai and Wenzel, 1998), wherein a queen may solicit liquid from a nestmate, then take pulp from another to initiate a cell without leaving the nest. There is also some similarity with the *Polybia* model proposed by Jeanne (1996), wherein building is partitioned into three tasks with feedback loops.

Studying a species with intermediate complexity (such as *Metapolybia*) provides a concise explanation of the organization and regulation of building behavior: a baseline caste ratio may be determined primarily by age structure and colony needs other than building, and then fine-tuned according the activity of the flexible pulp forager group. While interacting with other individuals, the activity of this behavioral group is regulated by the water saturation of the colony and the activity of the builders.

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