



Organization of Work via a Natural Substance: Regulation of Nest Construction in Social Wasps

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In social insects, colony-level complexity emerges from simple individual-level behaviors and interactions. In the evolution of insect societies, selection has acted to promote efficiency through division of labor. Nest construction of social wasps is an excellent model system to study division of labor and the performance of a decentralized behavioral regulation. After re-examination of Jeanne's (1996) demand-driven "non-taskmates feedback" hypothesis, an alternative mechanism is suggested whereby the regulation of behavior is based on a natural substance (water) which is itself also a building material. By experimenting with a simple model system, we show that the model's predictions agree with observational data and cover a wide range of evolutionary transitions. According to the internal and external parameters, the colony builds up storage of water that is used both as regulator and building material. Through individual interactions, pulp foragers and water foragers emerge from general laborers and their ratio becomes balanced. The emergent foragers ensure both the stabilization of the quantity of stored water and the steady construction of the nest according to the given conditions. Perturbations of the system alter colony-level dynamics in a similar way as was observed in nature: water and pulp addition increase pulp arrivals and building rate; removal of pulp foragers decreases pulp input and construction rate, but not the water influx; removal of water foragers causes overcompensation of water input after a delay. After comparing the predictions of the model to natural data, assumptions found in the literature on organization of work and regulation of behavior are re-examined. A new, more parsimonious model of organization of work is proposed that may cover wide variety of cases where hormones and learning cannot be accounted for the regulation of behavior.

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Introduction

Social insect societies provide some of the most thoroughly studied biological systems in which both the strategy and tactics of decision making have been analysed (Camazine *et al.*, 2001). These societies generally develop into parallel

processing systems where the colony conducts all of its operations concurrently instead of sequentially (Oster & Wilson, 1978; Karsai & Wenzel, 1998; Anderson & Franks, 2001), and where frequent adjustment of the worker force undertaking different tasks is required (Oster & Wilson, 1978; Robinson, 1992; Seeley, 1995; Gordon, 1996). The organization and regulation of construction behavior of social wasps has proven to be a very useful and tractable system

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for the study of general rules of behavioral regulation, division of labor, and task allocation (Forsyth, 1978; Jeanne, 1986, 1987, 1996, 1999; O'Donnell & Jeanne, 1990; Karsai & Wenzel, 1995, 1998, 2000) (Fig. 1).

Jeanne (1996) proposed a detailed explanation of how regulation of task force allocation occurs in the social wasp *Polybia occidentalis*. He showed that water and pulp are collected by two groups of foragers which is later used by a third group, the builders (water foragers also supply pulp foragers with water). Thus, these groups are interacting with each other while

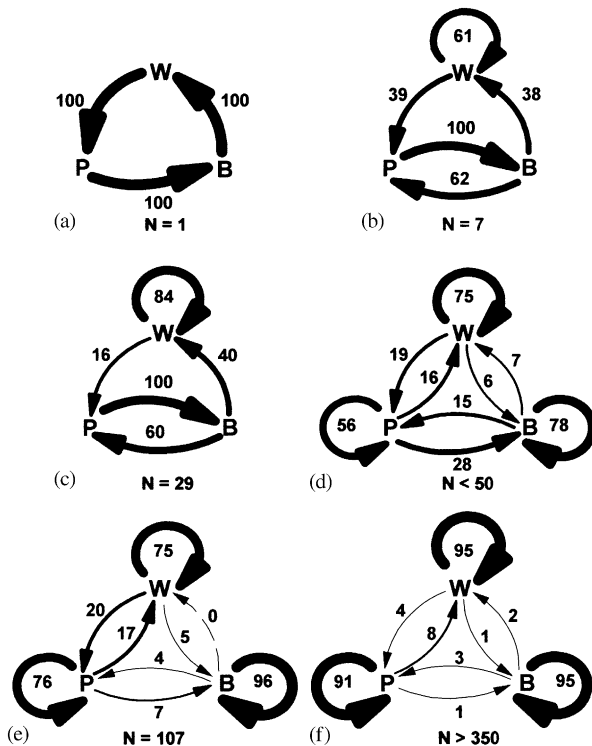


FIG. 1. Frequency of transitions between three construction tasks, building (B), pulp foraging (P) and water foraging (W). The transformation of the system suggests a general fundamental mechanism that is fine-tuned by a parameter that relates to colony size. (a) Single foundress, as in *Polistes*. (b) *Vespa 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, (f) *Polybia occidentalis*, data pooled from three colonies larger than 350 individuals. Width of arrows corresponds to frequency; numbers indicate exact values. In Fig. 1(a–c), every pulp forager also built with its pulp (regardless of sharing). (Figure redrawn from Karsai & Wenzel 1998, *Proc. Natl Acad. Sci. U.S.A.* **95**, 8865–8869, Fig. 4; see references therein for the original studies).

transferring materials, and the proportion of the three groups is kept in balance and queueing delays are kept to a minimum to ensure optimal performance (Jeanne, 1986). Perturbation experiments (removing wasps belonging to given task groups and adding or depriving materials) were performed to test three hypotheses he put forth: 1, “nest feedback hypothesis”, where individuals differ in their probability of working in response to a given degree of nest damage; 2, “task-mates feedback hypothesis”, where low-level activity by a task group increases, but high-level activity reduces the number of idle wasps belonging to the given task group; 3, “non-task mates feedback”, where the activity of the individual of a given group depends on the activity of the group with which the individual interacts through material transfer. He concluded that his data mainly supported the third hypothesis. Jeanne (1996) presented a schema (Fig. 2), to summarize his findings: (1) builders have a self-regulation component via the extent of accessible building site, and only builders receive information on nest damage directly from the nest; (2) forager activities were determined by the demand of the task group to which the forager unloaded the material; (3) a chained flow of information from one task group to the next, in reverse order of material flow, was concluded to regulate task allocation; (4) change in ease of unloading (unloading delay, unloading duration and rejected offers) was suggested as the information source used by the wasps for their decision.

Recently, Karsai & Wenzel (2000) carried out studies on *Metapolybia aztecoides* and *M. mesoamerica*, which possess characteristics intermediate between *Polistes* and *Polybia*. Studying *Metapolybia*, with its intermediate complexity, may provide a concise explanation of transitions of behavioral regulation and task allocation mechanisms (Karsai & Wenzel, 1998, 2000). There are differences in the results and interpretation made for the *Polybia* and *Metapolybia* systems: (1) in *Metapolybia*, pulp foragers set the pace of operation (Karsai & Wenzel, 2000) whereas in *Polybia* (Jeanne, 1996), it was the role of builders; (2) Jeanne (1996) proposed that water foragers obtained information about the need of water through

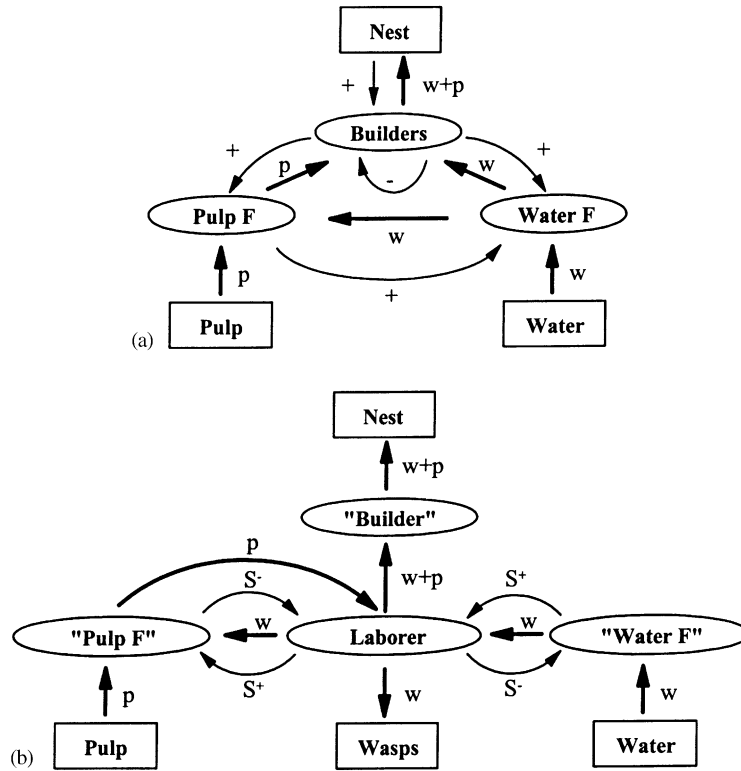


FIG. 2. Regulation of construction behavior in wasps. (a) Schema of Jeanne (Figure redrawn from Jeanne 1996, *Anim. Behav.* 52, 473–488, Fig. 11) (b) Flow diagram of Karsai & Balázs (current study). Task groups (oval boxes): Pulp F—pulp forager; Water F—water forager; quotation marks indicate temporal assignment of a given worker, while groups without quotation marks are predefined. Source or sink of materials are in square boxes; material flow (thick arrow): p—pulp; w—water. “Nest” means material is built into the nest structure and “Wasps” means the consumption of material by insects (e.g. for drinking and cooling). Information flow between task groups (thin arrows): S⁺—positive or stimulatory effect; S⁻—negative or inhibitory effect depending on the water saturation level of the colony. See the text for detailed comparisons and discussions of these two regulation mechanisms.

feedback from pulp foragers and builders, however, removing neither pulp foragers (Jeanne, 1996; Karsai & Wenzel, 2000), nor builders (Karsai & Wenzel, 2000) significantly decreased the number of water arrivals. (3) Although Karsai & Wenzel (2000) confirmed the finding of Jeanne (1996) that pulp forager activity is determined by the demand for pulp imposed by the builders, they also found that pulp foraging is additionally governed by the water saturation of the colony (e.g. water addition increased pulp arrivals significantly). We believe that these differences can be resolved by using a general model for the regulation of task allocation. Our previous analyses (Karsai & Wenzel, 1998) revealed that a general global pattern emerges across different species and genera, indicating that common fundamental processes must govern the organization of work

(Fig. 1, see also Karsai & Wenzel, 1998, 2000; Bourke, 1999). We believe that the regulation mechanism is universal, and the differences between species or genera can be explained as a result of fine-tuning of the same mechanism. The degree of specialization of workers in construction behavior seems to be fine-tuned by the colony size rather than by their taxonomic relationships (Fig. 1). The mechanism controlling such adaptive allocation of individuals in the face of variable internal and external conditions is therefore one of the crucial questions in sociobiology (Gordon, 1996).

In the current paper we propose a new hypothesis regarding how nest construction is controlled in social wasp colonies. Our explanation for regulation of nest construction can be conceptualized as an alternative to the schema of Jeanne (1996) (Fig. 2). We demonstrate that

our current hypothesis is based on fewer assumptions, is coherent with the data of both experimentally well-studied systems (*Polybia* and *Metapolybia*), and avoids the majority of the problems and contradictions outlined above. We investigate this problem by building a simple model and examining its predictions in full agreement with Franks & Tofts (1994): “The benefit of formal mathematical models is that they can show whether proposed causal mechanisms are at least theoretically feasible and can help to suggest experiments that might further discriminate between alternatives.”

The Model

Our aim is to present a model of the regulation of behavior, based on a natural substance (water) [Fig. 2(b)], that can produce robust performance where its predicted results show good agreement with the observed data of both *Polybia* (Jeanne, 1996) and *Metapolybia* (Karsai & Wenzel, 2000)

wasps. The behavior of this system was described by differential equations. Fourth-order Runge–Kutta method (Burden & Faires, 1997) was used to approach the solution of the equations in a simulation program written in “C” using continuous variation of all variables.

ASSUMPTIONS AND PARAMETERS

(1) The colony of wasps consists of N individuals from which a given proportion (Ry) is passive (Table 1). They sit motionless almost all day on the comb without interacting with others or performing any activities. The active wasps ($Ra = Na/N = 1 - Ry$) either forage for water ($Rw = Nw/Na$), pulp ($Rp = Np/Na$) or carry out other duties (building, brood care, patrolling, thermoregulating and so forth) as a laborer ($Rl = Nl/Na = 1 - Rw - Rp$). Every active wasp carries out all kinds of activities, but with different intensities and sometimes with some specialization (Karsai & Wenzel, 2000).

TABLE 1
Parameters of the model

Description	Acronym	Estimated	Used	Reference
Number of adults	N	107	100	1
Proportion of passive adults	Ry	0.68	0.7	1
Proportion of active adults	Ra	$1-Ry$	0.3	1
Active individuals				
Proportion of laborers	Rl		0.98	$1-Rw + Rp$
Proportion of water foragers	Rw		0.01	var
Proportion of pulp foragers	Rp		0.01	var
Water saturation	S		0.01	var
Time for collecting water (s)	Tw	41.3, 42.9	40	2
Time for collecting pulp (s)	Tp	219, 188	200	2
Time for downloading pulp (s)	Tu	16.1, 6.7, 11.3*	10	2, 1*
Time for water download (s)	Td	32.29	35	1, Fig. 3
Time for water uptake (s)	Tk	33.43	35	1, Fig. 3
Maximal time between two successful encounters (s)	Ta	9.74, 9.02	10	1, Fig. 3
Successful encounters for water download	Nw			var
Successful encounters for water uptake	Np			var
Water needed to process 1 pulp	Wp	1.35, 1.27*	1.3	2, 1*
Consumption of water/wasp/time	C	0.0000781	0.0001	1
Probability of becoming water forager	Pw		0.001	
Probability of becoming pulp forager	Pp		0.001	
Coefficient of Weibull distribution	$k2$		10	Fig. 5
Coefficient of Weibull distribution	$k3$		1	Fig. 5

Note: Sources of parameter estimation are: 1—Karsai & Wenzel (2000); 2—Jeanne (1986) (if there is estimation from both sources then * indicates the corresponding reference); Fig. 3—current study Fig. 3; Fig. 5—graph of the function in Fig. 5. Column “Used” shows the values that were actually used as standard start parameter sets for simulations. Any divergence from this set is indicated at the given simulation. Acronym “var” indicates those variables that were calculated and/or followed during the simulations. Their value in the “Used” column shows the initial value.

Foragers can emerge from laborers simply by carrying out more foraging than others, and builders are laborers that actually accept pulp and build it into the nest [Fig. 2(b)]. The dynamics of these task groups (i.e. the activities of the linked behaviors: water and pulp flow) are the variables used for comparing the predictions of the model to field observations.

(2) For the sake of simplicity, we assume that there is no individual variation either in load size or duration of activities. All foraging trips are successful and all foragers return with 1 unit of pulp or a maximal quantity of water ($W_{max} = 1$). All loads will be processed, i.e. there is a sufficient number of laborers to accept the loads and process them. However, the actual processing time depends on other parameters (the mechanism of water exchange and the equations discussed later). By this assumption we simply neglect those very rare occasions when in the course of normal construction activity the water or pulp load is discarded. In *Metapolybia* we showed that there were at least 10 times more wasps willing to build than the general pulp influx required (Karsai & Wenzel, 2000). We also suppose that other activities or duties carried out by the laborers do not impede or compete with the building behavior because the workforce is sufficient to cope with the general demand. Strong disturbance of the colony (water spraying, removing large numbers of wasps) may result in the discarding of loads (Karsai & Wenzel, 2000).

(3) The influx rate of materials is calculated as the number of foragers per turnaround time of foraging. Turnaround time is defined as the total time required for a complete foraging cycle including all necessary foraging, searching, downloading and uploading times. For simplicity, we assumed that foraging cycles start again as soon as the previous one is finished if the wasp remained in a forager status. Collecting pulp (T_p) costs more time than collecting water (T_w) (Table 1). Both foragers spend time on the nest while downloading material (T_u and T_d). For simplicity, pulp downloading time is assigned a constant value. Although we are aware that pulp downloading time shows some increase (approximately 9 s see Jeanne, 1986) in cases where a great number of builders were removed from the system or extra pulp was added

(Jeanne, 1996; Karsai & Wenzel, 2000), we concluded that the time increase was insignificant compared to other durations such as time spent with water solicitation (pulp downloading time = 11.3 ± 8.2 s; water solicitation duration = 125 ± 100.1 s; Karsai & Wenzel, 2000). As for the role of this parameter in the regulatory mechanism of laborer–pulp foragers' interactions, we combine T_u with another parameter that we think is a main parameter of a more significant mechanism (point 4).

(4) On the nest, each water forager downloads W_{max} quantity of water to laborer wasps while pulp foragers solicit water from laborers before going out for pulp. The water forager downloads water to 5.2 wasps on average (Karsai & Wenzel, 2000). This number is higher than the number of pulp foragers on the nest during this transfer. We did not discount that a pulp forager actually may receive water directly from the water forager, but the large number of wasps (6.4 on average; Karsai & Wenzel, 2000) visited by the pulp forager to solicit water indicated otherwise. For the sake of simplicity, we assume that the active wasps store water in a "common stomach" (see the mechanism of water exchange) and foragers download and upload water from laborers (see also point 5). We assumed that the pulp forager needs a full load of water (i.e. it solicits W_{max} quantity) to process the wood into pulp on the pulp source. Water is also necessary for builders to malaxate the pulp, thus on average $1.3 * W_{max}$ load of water (W_p) is needed for the complete processing of one pulp load (Table 1). We assume that the water soliciting time is a more significant variable than pulp downloading time for regulating behavior of pulp foragers, because it varied on a larger scale and required interaction with more individuals (see point 3; Karsai & Wenzel, 2000). Moreover, if there are fewer workers available (e.g. they are experimentally removed) then it is harder to collect the necessary water from the remaining wasps (i.e. the two mechanisms supposedly have the same effect on the decisions). Therefore, for simplicity, we combined the two serial mechanisms (pulp downloading and water soliciting) into one where the small variation in T_u was neglected, and we obtained a mechanism which is close to the one we find in water foragers.

(5) Time spent on the nest with water distribution or solicitation is a linear function of the average number of successful encounters (when water is exchanged through trophallaxis) (Fig. 3). At least one encounter is necessary to distribute or collect the water load, and the water exchange takes Td and Tk time, respectively (Fig. 3, $x = 1$). If the water forager cannot download all of its water to one wasp (because it is already partially filled), then more encounters are necessary for the complete download (the same is true for soliciting water by pulp foragers). Due to the linearity of the functions (Fig. 3) the average duration between two successful encounters is constant. This time is spent by the wasp wandering around and offering or begging for water from other individuals (unsuccessful encounters). A simple mechanism is suggested to connect the saturation level of the colony and the number of encounters, including rejected offers.

THE MECHANISM OF WATER EXCHANGE

We suppose that the number of both successful and unsuccessful encounters depends on the water saturation level of the active wasps:

$$S = \frac{W}{W_{max}}, \quad (1)$$

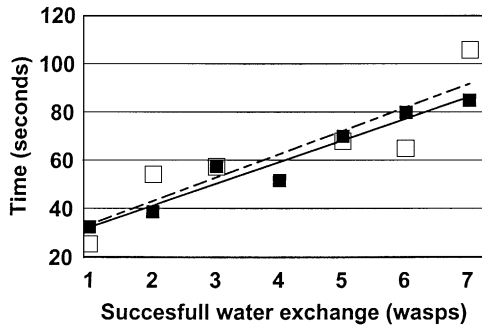


FIG. 3. Water distribution and solicitation time as a function of successful encounters. Every data point represents the average of at least two observations (Karsai & Wenzel, 2000). Only those data are used when the transfer was finished within 120 s. Black square—distribution of water by water forager; empty square—water solicitation by pulp forager. Solid line—linear regression of water distribution ($R^2 = 0.947$, $p < 0.001$, $N = 7$); dashed line—linear regression of water solicitation ($R^2 = 0.789$, $p < 0.05$, $N = 6$). Slope and intercept of these lines were used for parameter estimation of Td , Tk and Ta (see Table 1).

where W is the average water quantity in the crop of an active wasp. For simplicity, for the calculation of W , we suppose that on average the foragers store the same quantity of water as laborers. For pulp foraging, each pulp forager has to solicit W_{max} quantity of water to fill its empty crop ($W = 0$). Because laborers contain $W = S * W_{max}$ quantity of water, then the necessary number of successful encounters to gather W_{max} quantity of water is

$$Np = \frac{W_{max}}{W} = \frac{W_{max}}{S * W_{max}} = \frac{1}{S}. \quad (2)$$

For the sake of simplicity, we neglected the change of W during solicitation. We assumed that the laborers gave all of their water to the solicitor and by interaction with other laborers, they refilled themselves to the new W after the pulp forager finished collecting the water.

We suppose that between two successful encounters several wasps may refuse to give water to a solicitor, and the number of these unsuccessful encounters (Nn) is proportional to $1 - S$, i.e.

$$Nn = A * (1 - S), \quad (3)$$

where A is the maximal number of rejections for giving water. The average time between two unsuccessful encounters is ΔT , thus the maximum time between two successful encounters is $Ta = A * \Delta T$. As S increases, the number of unsuccessful encounters decreases, thus the average time spent with unsuccessful encounters will be

$$Tn = Ta * (1 - S). \quad (4)$$

Thus, the total time, which is required to fill the crop of the pulp forager with water, is

$$\begin{aligned} Tlp &= Tk + Ta * (1 - S) * \frac{1}{S} \\ &= Tk + Ta * \left(1 - \frac{1}{Np}\right) * Np \\ &= Tk + Ta * (Np - 1), \end{aligned} \quad (5)$$

where Ta can be interpreted as the slope and Tk as the intercept at $x = 1$: of the linear function of the water exchange mechanism (see Fig. 3).

The water downloading process can be treated similarly if we replace S by $1-S$. In this case,

$$\begin{aligned}
 Tlw &= Td + Ta * S * \frac{1}{1-S} \\
 &= Td + Ta * (Nw - 1). \tag{6}
 \end{aligned}$$

Using this information we can describe the change of water saturation in time as

$$\begin{aligned}
 \frac{dS}{dt} &= \frac{Rw}{Tw + Td + Ta * (Nw - 1)} \\
 &\quad - \frac{Rp * Wp}{Tp + Tu + Tk + Ta * (Np - 1)} \\
 &\quad - \frac{N}{Na} * C * S, \tag{7}
 \end{aligned}$$

where the first expression describes the water influx carried out by water foragers, the second expression shows the water consumed by pulp foraging and building, while the third expression describes the water consumed for reasons other than construction behavior. For simplicity, we assume that this water consumption (drinking, cooling and so on) is a linear function of variable C , the number of adults (N) and the saturation itself (S) (Table 1).

THE MECHANISM OF TASK CHANGE

The proportion of both forager types changes in time, and there is a dynamic interaction between laborers and foragers [Fig. 2(b); Karsai & Wenzel, 2000]. It is obvious that both internal and external factors should influence how a laborer takes up a foraging task. For simplicity, we describe this as a multiplication of a constant probability (P) and the water saturation level (S). The P (specified as Pw and Pp) may represent internal factors, e.g. as laborers age, the probability that they will forage increases. In the case of stable colony size and conditions, Pw and Pp can describe the probability of becoming a water forager or a pulp forager per laborer per time unit (Table 1). S represents the crucial external factor in this case. For example, if S is low, it stimulates the emergence of water foragers, but not of pulp foragers.

Foragers may stop foraging by reverting into a laborer or by dying (Karsai & Wenzel, 2000). For simplicity, we assume that death of the forager is the same as reversion, i.e. if colony size is constant, then death of a forager means emergence of a new laborer (therefore, we were able to unify the two phenomena). We also considered those biological results where the downloading ease or the number of encounters was considered to have regulatory effects on task change (Jeanne, 1986, 1996; Kühnholz & Seeley, 1997). Combining these, we assumed that the probability of reverting from forager to laborer is decided at the start of the next foraging cycle on the basis of the number of total encounters during water exchange (see previous section). The Weibull distribution (Weibull, 1951) was used to calculate the probability of task switching assuming that the probability of change is a smooth ($k3 = 1$, Poisson distribution) rather than a threshold-like ($k3 = 50$) function of the stimulus (Table 1).

Thus, the change of proportion of water foragers in time is

$$\begin{aligned}
 \frac{dRw}{dt} &= Rl * Pw * (1 - S) \\
 &\quad - Rw * \frac{1 - e^{(Nw * A * S / k2)^{k3}}}{Tw + Td + Ta * (Nw - 1)} \tag{8}
 \end{aligned}$$

and the same for pulp foragers is

$$\begin{aligned}
 \frac{dRp}{dt} &= Rl * Pp * S \\
 &\quad - Rp * \frac{1 - e^{(Np * A * (1-S) / k2)^{k3}}}{Tp + Tu + Tk + Ta * (Np - 1)}. \tag{9}
 \end{aligned}$$

Results

GLOBAL BEHAVIOR OF THE COLONY AND PREDICTION OF THE MODEL

Initial Conditions and the Effect of Water Consumption

The results show that the proposed regulation mechanism is robust and is able to account for several global properties of the natural system [Fig. 4(a)]. For simplicity, it was assumed that at

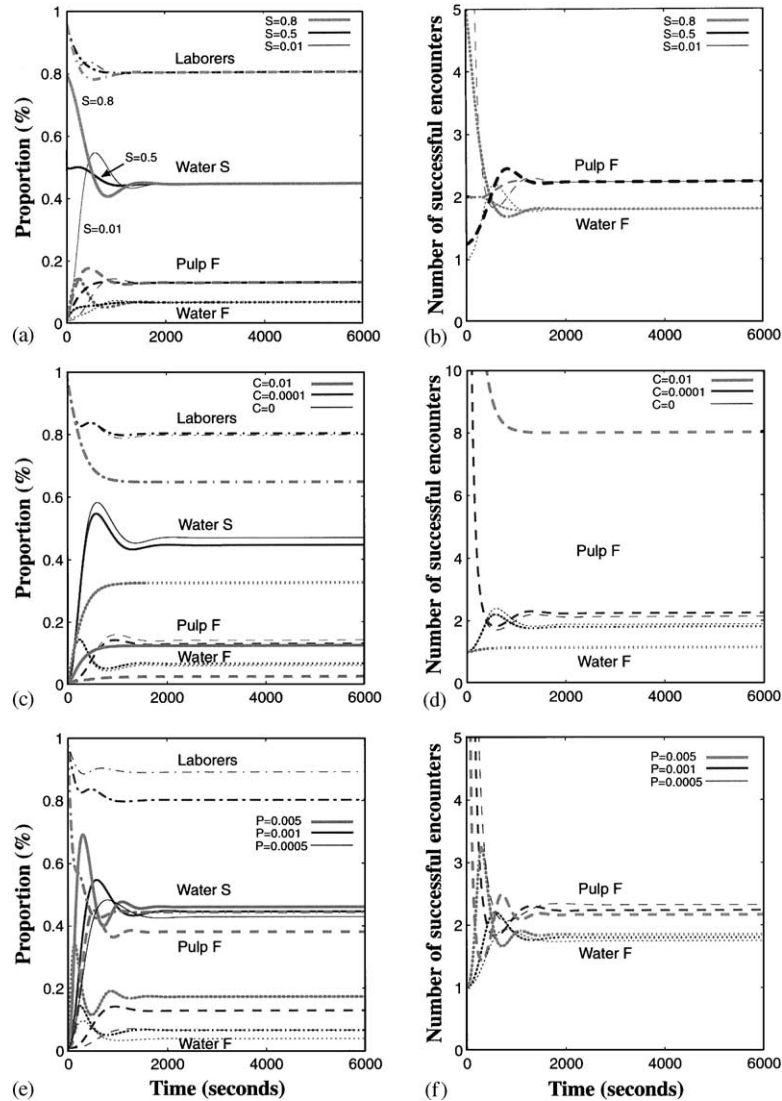


FIG. 4. Dynamics of task groups, number of encounters and water saturation level. (a and b) effect of different starting values of water saturation (S : 0.01, 0.5, 0.8); (c and d) effect of different water consumption (C : 0, 10^{-2} , 10^{-4}); (e and f) effect of the probability of becoming forager (P : 5×10^{-3} , 10^{-3} , 5×10^{-4}). Thickness of the lines corresponds to the value of the studied parameters (i.e. thicker lines represent larger value). Other parameters were set to the standard values (Table 1). Dot dash line—laborer (Laborers); dashed line—pulp forager (Pulp F); dotted line—water forager (Water F); solid line—water saturation (Water S).

the beginning of the simulations both the water content of the colony and the proportion of foragers were close to zero (Table 1). In the course of time, both forager groups emerged from the laborer wasps, and both the proportion of foragers and the water saturation level of the colony stabilized at approximately 3000 time steps. At the beginning, when the colony water saturation level was low, pulp foragers tended

to revert back to laborers, because they had to visit a large number of wasps to solicit water [Fig. 4(b)]. On the other hand, due to the ease with which water is downloaded, the number of water foragers first increased very quickly, then decreased back to about half of its maximum value and stabilized. In the quasi-stable state, both forager types encountered a moderate number of wasps (5–15 with unsuccessful

encounters) while up- or downloading water. The stabilized values of the parameters were independent of the actual starting values of the foragers and S [Fig. 4(a) and (b)].

Allocation of water to different purposes is crucial. If more water is required for cooling, drinking and for other non-building related activities (i.e. C is increased), the model predicts that the ratio of pulp foragers drops to one-fifth when consumption increases 100 times [Fig. 4(c)]. Although little water is needed for building when pulp input is so low, due to intensive water consumption the proportion of water foragers increased, the water saturation level of the colony dropped to only about one-third. This balancing behavior of the system emerges from the ease of downloading water and the difficulties of pulp foragers in soliciting water at the individual level [Fig. 4(d)] (a great number of encounters is necessary).

The Effect of Individual Flexibility and the Decision Mechanism

We assumed that the probability rate of taking over a foraging task was constant in time. Modeling different strategies of individual flexibility by taking different transitional probabilities (increase of P_w and P_p means higher probability to acquire foraging behavior) predicted that both the number of the fluctuation in the dynamics and the number of foragers increased when P_w and P_p increased, while the colony water saturation level did not change considerably [Fig. 4(e)]. This means that with more flexible behavior, the colony is able to allocate more foragers to collect materials, and therefore it is able to build relatively more material into the nest. Although the proportion of foragers increased at the expense of laborers when P_w and P_p increased, the ratio of the two forager types is balanced and the number of encounters remained at very similar values [Fig. 4(f)].

A Weibull distribution was used to describe the relation between the number of encounters and the probability that a forager has reverted to laborer. By changing the parameter k_3 , one can predict the effect of different decision mechan-

isms. If $k_3 = 1$, then the Weibull distribution is transformed into the Poisson distribution where the probability of reverting is independent of previous history and therefore increases smoothly with the number of encounters (Fig. 5). On the other hand, if k_3 is smaller or larger than the decision becomes steeper and threshold-like. Increasing k_3 not only increased the fluctuations in the system, but also the number of encounters necessary, for both the pulp forager and the water forager to become more similar [Fig. 6(a) and (b)]. The water saturation level of the colony increased slightly as k_3 increased as the consequence of the more sudden transformations of foragers to and from laborers. On the other hand, decreasing k_3 below 1 caused an increase in the probability of reverting suddenly when the number of encounters was low, with a very slight increase after that (Fig. 5). Increasing k_2 will decrease reverting, because the function reaches the same value at a larger number of encounters. This will lead to an increase in the proportion of foragers while the water saturation level increased only slightly [Fig. 6(c)].

Increasing maximal number of rejection (A) decreased the ratio of foragers, because the foragers tended to revert back to laborers due to the increased number of total encounters [Fig. 6(d)]. As a consequence of this (assuming constant C), the incoming water content

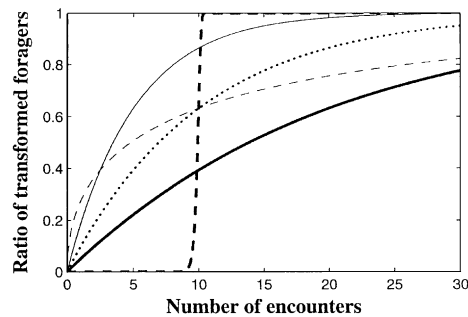


FIG. 5. Effect of the number of encounters on transformation from foragers to laborers. Different values of the parameters of Weibull distribution represent different decision mechanisms. Thickness of the lines corresponds to the value of the studied parameters (i.e. thicker lines represent larger value). Dotted line—standard parameters (Table 1); solid line—effect of change in parameter k_2 (k_2 : 5, 20); dashed line—effect of change in parameter k_3 (k_3 : 0.5, 50).

decreased and several water foragers reverted back to laborers before completing the downloading of all the water, causing a drop in the water saturation level of the colony. On the other hand, the colony allocated more foragers when the collection of a given material required more time (T_w or T_p increased), while the number of encounters and the water saturation level did not change significantly [Fig. 6(e) and (f)].

PERTURBATION OF CONSTRUCTION IN THE MODEL

Performing perturbation experiments in the model system makes it possible not only to test the robustness of the model, but in this case also provides a series of predictions which can be compared with data from field perturbation experiments (Table 2). In each case the perturbation happened after the values stabilized.

Removing water foragers decreased the number of pulp foragers slightly. Water required for

pulp foraging and building was used from the water reservoir stored in the crops of the wasps. As the number of water foragers was restored, an overcompensation occurred in the number of water foragers before stabilizing to replenish the used up water, i.e. to restore the water saturation level of the colony [Fig. 7(a), Table 2].

Removing pulp foragers resulted in decreased pulp arrivals (hence number of building acts) and increased water saturation, and this in turn decreased the number of water foragers slightly. This decreased the water saturation level, which restored the number of water foragers as well. However, these small changes in the number of water foragers were barely detectable [Fig. 7(b), Table 2].

Removing part of the laborers (decreasing the number of potential builders) increased the relative number of foragers at the time of the perturbation. After the perturbation, the number of both foragers started to drop, i.e. foragers

TABLE 2
Predictions of the model for perturbation experiments and agreement with literature data

Experiment	Parameter	Effect	Reference
Removal of water foragers	D Wf	Water arrivals D Overcompensation	1, Fig. 7(a) 1, Fig. 1, Fig. 7(a)
Removal of pulp foragers	D Pf	Pulp arrivals D Water arrivals N Pf restore slower Building acts D	1, 2, Fig. 7(b) 1, 2, Fig. 7(b) 1, 2, Fig. 7(a and b) 2, (less pulp arrives)
Removal builders	D Rl	Pulp arrivals D Building acts D	1, 2, Fig. 7(c) 1, 2, (less pulp arrives)
Addition of pulp (not wet)	$Tp = 0$	Pulp arrivals D Water solicit time I Building rate I Encounters of Pf I	1, 2, Fig. 7(d) Fig. 7(e) 1, Fig. 7(d) and text 1, Fig. 7(e)
Addition of water	$S = 0.8$ $Tw = 0$	Water arrivals D Pulp arrivals I Building acts I	1, 2, Fig. 7(f and g) 2, Fig. 7(f and g) 2, (more pulp arrives)

Note: Perturbations of the model imitated field experiments as closely as the constitution of the model allowed by modifying a single parameter (second column; for acronyms see Table 1) at 3000 steps. Effects of the perturbation and agreement with literature data are presented in the next two columns. Acronyms: D = Decrease, I = Increase, N = not changed considerably, reference 1—Jeanne (1996); 2—Karsai & Wenzel (2000). In the model the number of building acts was not explicitly followed because it was derived from the number of pulp arrivals directly, therefore in the reference section instead of a given figure we refer to the change in a corresponding variable (more or less pulp arrives).

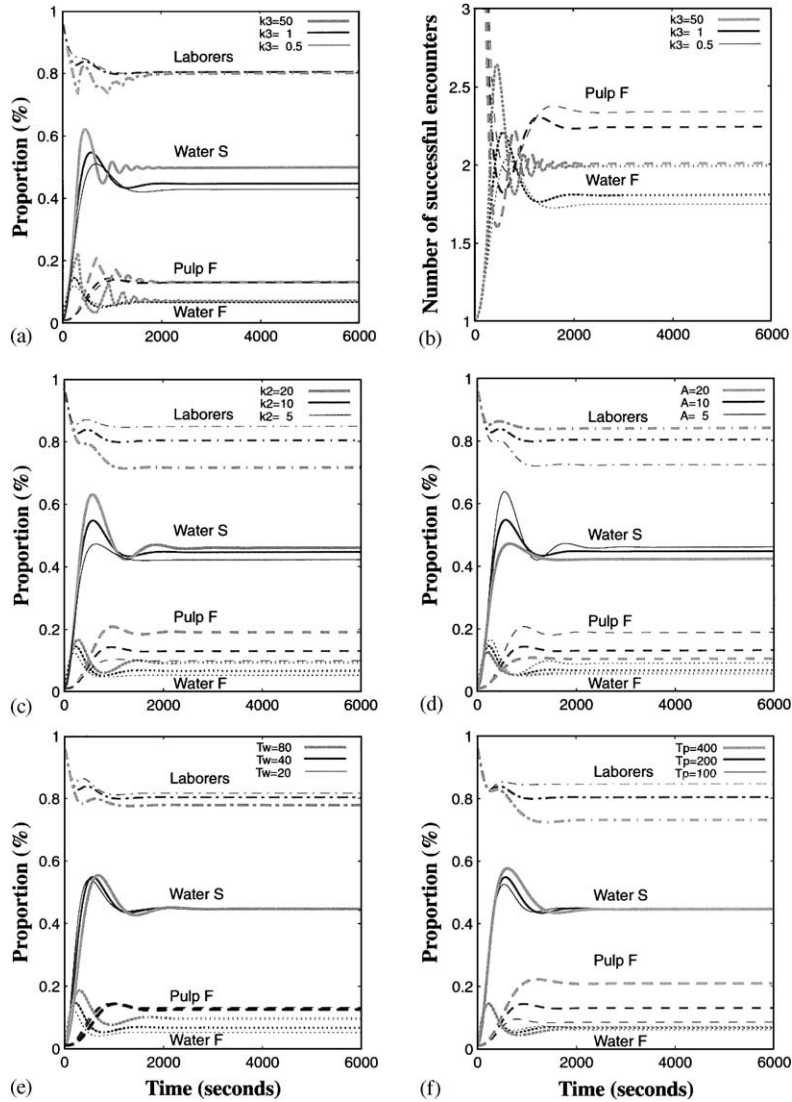


FIG. 6. Dynamics of task groups, number of encounters and water saturation level. (a and b) effect of the Weibull parameter k_3 (k_3 : 0.5, 1, 50); (c) parameter k_2 (k_2 : 5, 10, 20); (d) effect of the size of maximal number of rejections for giving water (A : 5, 10, 20); (e and f) effects of the time needed for collecting water (T_w : 20, 40, 80) and pulp (T_p : 100, 200, 400), respectively. Thickness of the lines corresponds to the value of the studied parameters (i.e. thicker lines represent larger values). Other parameters were set to the standard values (Table 1). Dot dash line—laborer (Laborers); dashed line—pulp forager (Pulp F); dotted line—water forager (Water F); solid line—water saturation (Water S).

reverted back to laborers until the ratio of the groups was restored. Because collecting and travel time for water foraging is shorter than that of pulp foraging ($T_w < T_p$), water foragers reverted back more quickly causing a drop in the water saturation level of the colony [Fig. 7(c), Table 2].

To simulate the case when pulp (dry pulp, i.e. water is needed before it is passed to the builders) availability increased, the searching

and collecting time was reduced to zero ($T_p = 0$). The number of pulp foragers dropped, because easy access to pulp decreased the water saturation of the colony [Fig. 7(d), Table 2], which made the water solicitation more difficult for the pulp foragers, who had to meet more wasps (it took more time than before the perturbation) [Fig. 7(e)]. The increase of water foragers restored the water saturation level, but the number of pulp foragers remained low,

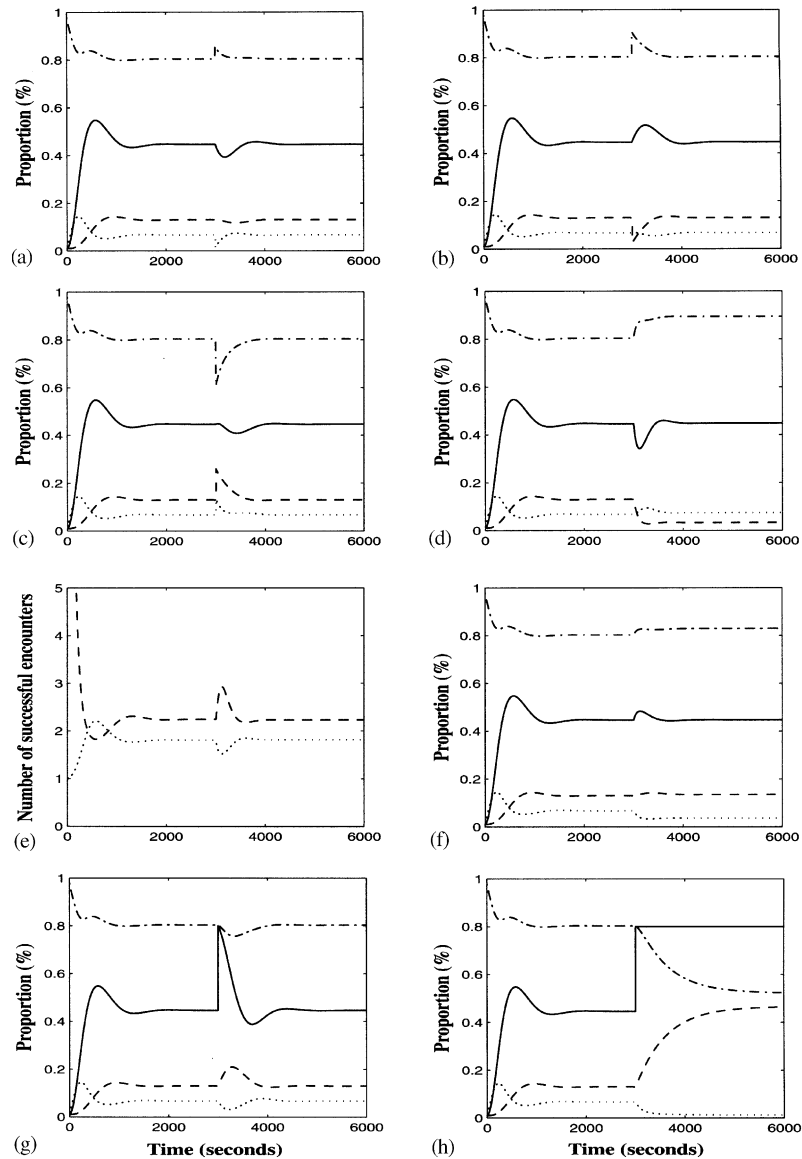


FIG. 7. Perturbation experiments and the dynamics of task groups, encounters and water saturation levels. Perturbation was made as a change in a single parameter (Table 2) after the values stabilized at 3000 time steps. Other parameters were set to the standard values (Table 1). Perturbations: (a) proportion of water foragers decreased to one-fifth; (b) proportion of pulp foragers decreased to one-fifth; (c) both the proportion of water foragers and pulp foragers are doubled to decrease the proportion of laborers by approximately 25%; (d and e) time needed for collecting pulp decreased to zero, i.e. $Tp = 0$; (f) time needed for collecting water decreased to zero, i.e. $Tw = 0$; (g) water saturation level increased to $S = 0.8$; (h) water saturation level increased and kept at $S = 0.8$. Dot dash line—laborer; dashed line—pulp forager; dotted line—water forager; solid line—water saturation.

because the pulp collection became less time consuming. After the system relaxed to the new values, the number of encounters was set back very close to the previous values, but the colony was built at a higher rate ($5.67 \cdot 10^{-4} \text{ pulps s}^{-1} > 5.04 \cdot 10^{-4} \text{ pulps s}^{-1}$), using far fewer pulp

foragers and a few more water foragers than before [Fig. 7(d) and (e), Table 2].

The effect of water addition was studied in two ways. In the first case, as in pulp foraging, we assumed that searching and collecting water cost no time ($Tw = 0$). This, in the short term,

increased the water saturation level of the colony, which made the number of water foragers drop and caused a slight increase of pulp foragers [Fig. 7(f), Table 2]. After the water saturation level rebounded, the colony allocated much fewer individuals for water foraging (reverted water foragers back to laborers) and more for pulp foraging, which finally resulted in a higher building rate and water influx ($8.28 * 10^{-4} Wmax s^{-1} > 8.05 * 10^{-4} Wmax s^{-1}$).

In a second case, we suddenly increased the water saturation level of the colony by almost 100% ($S = 0.8$). This elicited a very similar response to that seen in the first case, i.e. the number of water foragers dropped while the number of pulp foragers increased more sharply [Fig. 7(g), Table 2]. However, in this case the system rebounded to the original values, because the applied perturbation was instant. When the high water saturation level was maintained continuously, it led to a drop in water foraging close to zero and a very high level of pulp input [Fig. 7(h)].

Discussion

Our model gave good predictions for both the general responses (Karsai & Wenzel, 1998) and the results of perturbation experiments made on *Polybia* and *Metapolybia* colonies (Jeanne, 1986, 1996; Karsai & Wenzel, 2000). Good agreement was found between the current model's prediction and the field data of Jeanne (1996) in spite of the significant difference between the regulation mechanisms proposed here and by Jeanne (1986, 1996) (see Fig. 2):

(1) Instead of the chained flow of information from one task group to the next, a regulatory substance (water) regulates task allocation and nest construction (Karsai & Wenzel, 2000).

(2) Instead of pre-determined task groups, it is assumed that all workers perform every kind of activity, but with individually different frequencies (see in Karsai & Wenzel, 2000).

(3) In the current study, construction behavior is related to other colony level tasks (water used for other tasks was considered), and the mechanism of transformation between task groups are included and explained.

ALTERNATIVE REGULATOR MECHANISMS

Some of these differences in the proposed regulation of the system emerge from different views of colony and individual flexibility and of the meaning of specialization and efficiency by the authors. At a larger scale, Jeanne (1991, 1999) separated wasps into independent founders and swarm founders and examined other behavioral traits in the light of this dichotomy. At a certain scale, this approach can be straightforward (see Wenzel & Carpenter, 1994), but little is known of how other behavioral traits are distributed on the phylogenetic tree (see Hunt, 1999). It is possible [as Bourke (1999) showed for several other reproductive-related traits], that swarming habits may have emerged due to increased colony size in a manner analogous to the emergence of reduced body size (Karsai & Wenzel, 1998). Examining only the two distinct strategies (*Polistes*: small colony size, independent founding vs. *Polybia*: large colony size, swarm founding) may lead to false assumptions. We suggest that assuming differences between *Polistes* and *Polybia* building systems (namely that the latter uses integration of information about nest and brood while the former does not; see Jeanne, 1999), and linking construction behavior to reproductive strategy, is unnecessary (see also Karsai & Pénczes, 2000).

For *Polybia*, Jeanne (1986, 1996) discriminated builders, pulp and water foragers. All these can be in the idle or active state, and foragers sometimes become elites. This is clearly a simplification, which may enhance understanding of the system in a given situation, and may make experiments tractable. However, studying the behavior of individuals in detail both in *Polybia* (Jeanne, 1987) and *Metapolybia* (Karsai & Wenzel, 2000) has revealed that individuals are flexible, and allocating the wasps into groups according to their behavior preceding their capture is not reliable (Karsai & Wenzel, 2000). For balancing the construction system, the flexibility of pulp foragers seemed to be the most important element (Karsai & Wenzel, 2000), because they have direct connections with every individual and material that relates to construction, and they may

carry out every type of construction-related behavior beyond pulp foraging (Karsai & Wenzel, 2000). Using the classification system proposed by Jeanne (1986, 1996) it would be easy to conclude that a very active individual was a specialist while a less active individual with the same degree of task fidelity might easily be regarded as idle or as a generalist. A high-level specialization does not automatically mean that efficiency will increase (Ratnieks & Anderson, 1999b).

The proposed regulation mechanism is different from Jeanne's (1996) in that it does not assume the existence of pre-determined worker groups. There is only one category called laborers that provide the active labor force of the colony. If any of them takes up a behavior that relates to construction, it can be followed and registered as an individual that carries out a given work. In this manner, one may call it "builder" between the time when the wasp accepted pulp and built the pulp into the nest, but it will become a general laborer again (with a unique proficiency and attraction set, see supposed genetic components in O'Donnell, 1996, 1998), when the actual behavior is finished. The wasp does not become idle (off mode), but instead takes over another task including other active, non-construction related ones or resting (i.e. the general activity level decreases in this case, but not to zero and resting may have important functions). By regarding foragers in the same manner we may build up a tractable experimental and theoretical system without pre-determined worker group categories (Karsai & Wenzel, 2000). By *not* assuming pre-determined worker groups we were able to build a model that not only deals with material and information flow between task groups but also proposes a mechanism for task allocation. This approach also made it possible to study the effect of degree of specialization of the individuals. Changing the value of our P_w and P_p parameters, we were able to show how the same mechanism generated different colony level outcomes as a function of individual flexibility. Our model predicted that larger individual flexibility enabled faster construction via the allocation of more foragers for both materials.

THE CUES FOR REGULATION

For the *Polybia* system, Jeanne (1996, p. 474) proposed that "...the three tasks are kept in balance and queuing delays are kept to a minimum (Jeanne, 1986)." However, he only showed that certain handling time becomes *shorter* in larger colonies. In the strict sense, to minimize waiting time would mean to give up task partitioning (Ratnieks & Anderson, 1999b). Queuing delay is not necessarily a cue that workers may rely on to estimate relative work capacities, but rather a consequence of optimal information acquisition in the case of a task partitioned system (Ratnieks & Anderson, 1999a; Hart & Ratnieks, 2001).

Lindauer (1954) suggested that water collectors in bee colonies acquire information about their colony's need for more water by noting how easily they can unload their water inside the hive. Kühnholz & Seeley (1997) provided experimental support for this hypothesis. They suggested three possibilities for how a water collector may sense the ease of unloading: initial search time, total search time and delivery time. All variables changed, but what changed most strongly was the number of unloading rejections. Jeanne (1996) showed that in *Polybia*, the addition of supplemental pulp increased rejected pulp offers. Kühnholz & Seeley (1997) did not conclude causation from the correlation: they claimed instead that we do not know precisely which variable(s) of the unloading experience is (are) actually noted by the water collectors in forming an overall sense of the ease of unloading. The utility of an indicator variable depends not only on the quality of the information it gives (they found that unloading rejection varied more strongly), but also on the precision with which it can be understood. The perception of duration of events (such as search times) is a well-known phenomenon for honeybees, but the perception of the number of events (such as unloading rejections) is not (von Frisch, 1967, p. 102). Our model predicted that increasing the number of rejections decreased the ratio of foragers and hence the material flow. On the other hand, the colony allocated more foragers, when the collection of a given material required more time. Both of these processes ensure a

steady construction with different rates in a changing environment.

Insect societies show considerable time lags and overcompensation in their response to change of demands or to perturbations. Although Jeanne (1996) speculated as to why this should be adaptive, there was no explanation of how these time lags and overcompensation emerged, i.e. what the mechanism is beyond the individual interactions. Our aim was to provide a mechanism which retains the importance of individual interactions, but where these interactions are governed by a substance (i.e. by water that is itself also a building material). Water saturation level in the colony not only regulates construction behavior and task allocation (the number of individuals that carry out different construction related behaviors), but it also links construction behavior to other colony level operations (e.g. thermoregulation). In our model system both time lags and overcompensations emerged from the elementary mechanisms, when we assumed that the water is stored in the "common stomach" of the colony.

WATER SATURATION AS REGULATOR

In a preliminary study, Jeanne (1987) postulated that construction is driven by the supply of water brought in by water foragers, because removed "elite" water foragers were not replaced within an hour. He also said: "What determines the rate of flow of water into the system is not understood." (Jeanne, 1987 p. 241). His view only stressed the importance of water input and not the state of the water content (i.e. what we call water saturation level). Based on more study, Jeanne (1996) finally rejected his early idea. Instead, he proposed that the builders are the driving force behind construction behavior. Jeanne (1996) assumed that it is necessary to perceive nest damage directly, i.e. stimulation of construction should be manifested as a contact cue for the builders. However, there is a simpler alternative. We do not need to assume that removing the outer envelope affects a special group. In fact, we do not know which groups are affected, what cues the wasps use to start building and how the wasps perceive nest damage. If the envelope is not complete or is

removed, then the microenvironment of the colony might be very different (cells are exposed to light, air is moving near the comb, temperature and humidity could differ, and so on). This information may be available for all members of the colony without directly investigating the place of actual construction. It would seem best not to invoke any special unsupported assumption. Our assumption is very simple and trivial: the colony as a whole transforms itself into a different state where it *may* allocate more effort to construction than otherwise (see constrains from adaptive demography in Wilson, 1968; Herbers, 1980). *How* this regulation and this allocation can happen is a different question, but we propose that it does not require a demand-driven system through direct examination of the construction site by the builders. In *Metapolybia* the number of potential building positions was much greater than the number of places occupied by the builders (I. Karsai, pers. obs.). In the spatial restriction hypothesis proposed by Jeanne (1996), it is impossible to explain how and why the wasps will start constructing something new (no free construction site), and why the intensity of the construction does not decrease as a function of the size of the buildable surface (or we have to assume that building and nest repairing are very different phenomena). Jeanne's schema is dependent on the "spatial restriction" assumption, because this is the moderator of his demand-driven runaway system. However, there is no support for this assumption. That is why we neither invoked the self-regulation of the builders nor the assumption that the builders set the pace of the construction operation. We propose instead that the colony allocates effort to construction behavior considering restrictions that stem from colony demography and from various other demands (e.g. thermoregulation), therefore construction rates vary largely even if the "damage" has the same extent (Jeanne, 1996; Karsai & Wenzel, 2000).

As Robinson (1992) asserted "A major gap in our understanding of the regulation of division of labor is how workers acquire information on colony requirements." He suggested that information can be obtained either by sampling (see for example Lumsden & Hölldobler, 1983) or via

perception of signals and cues, where stimuli they encounter during the performance of a task may influence the likelihood of performing a given task including switching to another one [see for example Seeley (1989) for foraging or Karsai (1999) for construction behavior]. Why do some individuals take up the risky foraging task and what is the ratio of workforce that the colony allocates for the forager task? Reeve & Gamboa (1987) showed that in *Polistes*, dominance interactions induced foraging. Kiechle (1961) tested Lindauer's (1954) hypothesis on bees: the colony foragers are stimulated to collect water by becoming thirsty. Kühnholz & Seeley (1997) proved that the colony adaptively adjusts its water collection. Thus, the general question of adaptive control in colonies of social insects is this: how does the colony make adjustments for proper functioning in response to both internal changes and external contingencies? In the current model we assumed that both internal (such as age of the wasp or the effect of dominance behavior) and external (such as the water saturation level) factors affect task change. Our simple model predicted that the system is fairly resistant to perturbations. However, it is not the building rate that is balanced (it varies) but instead the water saturation level, which connects together several groups of behavior. Neither this property nor the final value of the water saturation level is programmed directly into the model, rather it is an emergent property of the system. The exact value of the water saturation in this balanced situation depends on several parameters, but its self-regulation allows a steady building rate, considering the other demands. A pure demand-driven system would quickly cause a runaway, where construction and foraging taking over all the work force of the colony. We suggest that the negative feedback of the system is ensured by a multipurpose substance (water) instead of spatial restrictions coming from the accessibility of buildable positions (contra Jeanne, 1996).

Cassil & Tschinkel (1999) found that task selection by workers of the fire ant *Solenopsis invicta* depends on crop fullness. They speculated that division of labor in *S. invicta* depends on worker age and size and is fine-tuned "by ever-changing state of their crop volume and crop

content" (Cassil & Tschinkel, 1999, p. 309). Cassil & Tschinkel (1999) were interested in the problem of task selection concerning feeding behavior, and they found that the food itself has a very important role in the regulation. The building behavior of social wasps shows a similar system, where the building material (water) stored in the crop of individuals (i.e. the water saturation level if we describe this at the colony level) is able to regulate both the building process and task allocation. It is known that several ant species do not use pheromones to organize and regulate their construction behavior, but instead the interaction with other colony members and different building materials provides sufficient information to build the nest (see for example Franks & Deneubourg, 1997). Although Ishay & Perna (1979) suggested the existence of building pheromones in wasps (*Vespa orientalis* and *Polistes foederatus*), such pheromones were neither confirmed nor identified later. Simple rules of thumb, individual interactions, the building material itself and self-organization processes are able to provide regulation mechanisms for such a complex pattern as construction and task allocation of social wasps.

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