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Original Article

Regulation of task partitioning by a "common stomach": a model of nest construction in social wasps

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Metapolybia wasps construct their nests on flat surfaces using plant materials, which they process into paper. For processing the pulp wasps need water, which is collected by water foragers, and it is transferred to pulp foragers indirectly via a "common stomach." The common stomach is formed by generalist wasps that can engage in water exchange and can store water in their crops. Our goal is to provide an alternative model for regulating task partitioning in construction behavior, focusing on worker connectivity instead of using threshold curves to model mechanisms of colony-level regulation. We propose that the existence of an information center and of a network of worker interactions, which establish sets of positive and negative feedbacks, allow collective regulation of colony-wide behaviors. Using a Stock and Flow modeling framework, we illustrate that the common stomach could serve both as a temporal storage for water and also as a source of information about the colony's current demands related to nest construction tasks. Our model predicts that assessing colony needs via individual interactions with the common stomach leads to a robust regulation of task partitioning in construction behavior. Using perturbation experiments in our simulations, we show that this emergent task allocation is able to dynamically adapt to perturbations of the environment and to changes in colony-level demands or population structure. Our model closely mimics and predicts the behavior of *Metapolybia* wasps, demonstrating that the regulation mechanism based on worker connectivity through a common stomach is a plausible hypothesis for the organization of collective behavior. *Key words:* common stomach, regulation of behavior, social crop, social wasp, system dynamic model. *[Behav Ecol 22:819–830 (2011)]*

INTRODUCTION

Insect societies function as superorganisms (Holldobler and Wilson 2008) in which interindividual conflict for reproductive privilege is largely reduced, and the worker caste is selected to maximize colony efficiency (Ratnieks and Helantera 2009). Division of nonreproductive tasks among workers (polyethism) is a key adaptation promoting the evolutionary and ecological success of eusocial insects (Wilson 1990). Division of labor is one of the most widely studied aspects of colony behavior in such insect societies. Many of these studies are concerned with the integration of worker behavior into colony-level task organization and with the question of how regulation of division of labor may contribute to colony efficiency (Oster and Wilson 1979; Plowrigth RC and Plowright CMS 1988; Jeanson et al. 2007). Because colonies and their environments are dynamic in nature, tasks need to change over time, and the division of labor needs to accommodate to altered levels of demand. To meet new labor demands, efficient (re)allocation of individuals to different tasks is required via continuous dynamic adjustments in response to these changes of demand. Workers that are already active at a given task can adjust their rate of performance. New workers can also be recruited to perform a task and to abandon other tasks (Oster and Wilson 1979; Seeley 1989). Colony-level flexibility in response to external changes and internal perturbation are essential feature of division of labor (Calabi 1988; Robinson 1992).

The relationship between castes and tasks needing to be performed has been central to our understanding of the organization of work in insect societies for almost a century. This concept has been the subject of some criticism in recent decades: One critique suggested that temporal castes are too inflexible to allow a colony to rapidly reallocate labor in response to changing conditions (Wilson 1983). Conversely, others emphasized that task switching is so prevalent that the reorganization of labor in social insects is likely more complex than simply activating unemployed specialized workers to meet emergencies (Karsai and Wenzel 1998; Johnson 2002, 2003). It seems that worker behavior is not "fixed" according to worker age or size, and tasks can be allocated according to colony needs (Wilson 1984; McDonald and Topoff 1985; Robinson 1992; Beshers and Traniello 1994; Brown and Traniello 1998; Gordon and Mehdiabadi 1999; Seid and Traniello 2006), even if flexibility in task allocation has limits (Brown and Traniello 1998; Johnson 2002, 2005). It seems reasonable to assume that adaptive division of labor must also include hypotheses on worker behavioral flexibility.

The behavioral flexibility in wasp societies correlates with body size, colony size, productivity, and the ways individuals interact (Karsai and Wenzel 1998). O'Donnell (2006) and O'Donnell and Bulova (2007) propose that interactions among workers (termed "worker connectivity") often play

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important roles in structuring division of labor. For example, biting is a form of worker connectivity that seems to be an important mechanism of communication between *Polybia* workers. It leads to the activation of foragers (O'Donnell 2001, 2003, 2006). However, beyond simple activation, the task partitioning needs to be regulated and readjusted to respond to dynamic changes.

Relying on shared and connected information can be beneficial for faster information transfer for more flexible and faster task changes and for providing more reliable and efficient information transfer among individuals (O'Donnell and Bulova 2007). Besides the well known connection networks, such as pheromones and dances, honeybee and ant workers are also connected through a wide variety of direct and indirect communication networks to regulate or fine tune their division of labor (Dornhaus 2009). For example, in *Solenopsis invicta* ants, the division of labor depends on worker size and age and is fine tuned by the states of their crop volume and content (Cassill and Tschinkel 1999). In honeybees, food reserves not only ensure homeostasis of the colony but also regulate division of labor (Schmickl and Crailsheim 2004). In social wasps, we found that construction behavior is regulated by indirect worker connectivity via the temporally stored water in the crop of the insects (Karsai and Wenzel 2000; Karsai and Balazsi 2002; Karsai and Runciman 2009).

Models are excellent tools for deciphering probable mechanisms of task regulation and division of labor. Traditionally models of division of labor incorporate both variations in task performance among workers and individual worker flexibility (Beshers and Fewell 2001). We think that worker connectivity should be added to this list of modeling requirements, as we assert that without incorporating these interaction mechanisms, such a model would miss an essential component. Different models on division of labor emphasize these issues differently (see detailed review of models in Beshers and Fewell 2001). The group of "response threshold models" assumes that workers vary intrinsically in task preference (Robinson and Page 1989). Other models emphasize the interactions between intrinsic processes and effects of other workers: such as the social inhibition models (Naug and Gadagkar 1999; Beshers et al. 2001) and the self-reinforcement models (Deneubourg et al. 1987; Spencer et al. 1998). The "forage for work" models (Tofts and Franks 1992; Tofts 1993; Franks and Tofts 1994) and the network models (Gordon et al. 1992; Pacala et al. 1996) assume no intrinsic differences among workers. Although spatiotemporal effects on task opportunity are important in the first group of models, changes in task allocation result from simple direct interactions among workers in the second model.

It is especially challenging to incorporate environmental variability, efficiency, age polyethism, and individual flexibility into these models (Wakano et al. 1998). Bonabeau et al. (1996, 1998) constructed an individual-based model for *Pheidole* ants using data of Wilson (1984, 1985) that predicted that task selection based on behavioral thresholds resulted in similar patterns observed on real colonies. This model was later extended by Deneubourg et al. (1987); Plowright RC and Plowright CMS (1988); Theraulaz et al. (1991, 1998); and Gautrais et al. (2002) who added positive feedback mechanisms to these thresholds to model emergent specialization as an individual runaway dynamic process. These studies were reanalyzed by Merkle and Middendorf (2004) who showed that some of the results of these models originated from specific parameterizations and from specific initial starting conditions, thus the reported findings of threshold-adaptation mechanisms are not necessarily emergent properties of threshold-adaptation mechanisms. Considering these findings, Schmickl and Crailsheim (2008a, 2008b), Thenius et al. (2008) as well as Schmickl et al. (2010) constructed individual-based models of task allocation for 3 task cohorts of honeybee workers (nectar foragers, nectar storers, and brood nurses) to compare the colony-level efficiency of several types of task regulation: fixed threshold, adapting thresholds, and random thresholds. In a recent paper, Schmickl and Crailsheim (2011) pointed out that threshold-reinforcement mechanisms led to a reduced working efficiency of the simulated colonies. From these current studies, it can be concluded that plausible work distributions may emerge within such collective systems without implementing nonlinear abandonment and recruitment mechanisms, without implementing mechanisms based on behavioral thresholds, and without exploiting morphological heterogeneity among workers:

For example, *Metapolybia* and *Polybia* wasps exhibit neither morphological differences nor high degrees of temporal polyethism, but their workers exhibit flexible and adaptive task specialization in which distinct subsets of complex tasks are finely partitioned between cooperating teams of nest mates (Jeanne 1996; Karsai and Wenzel 2000; Karsai and Balazsi 2002). Therefore, we based our model on a mechanism that is different from the ones described above. Instead of using a threshold model, we focused on worker connectivity, which uses simple cues (Lloyd 1983) like local water availability to regulate division of labor dynamically according to the current balance of supply and demand. A similar concept of colony-level regulation in honeybees called "information center strategy" was presented by Seeley (1985, 1998). He showed that it is a network of worker interactions that establish sets of positive and negative feedbacks based on modulation of worker behavior. In short, the existence of "information centers" allows both collective information processing and the homeostatic balancing of colony-wide behaviors. On the basis of our field studies (Karsai and Wenzel 2000) and a previous model (Karsai and Balazsi 2002), we propose that, assuming no intrinsic differences among workers, division of labor can emerge and be maintained via individual interaction of the workers through the "common stomach." The common stomach is a platform of worker connectivity where pairs of individuals exchange water (direct interaction), and the water is temporarily stored in the crops of the insects, which together comprise the common stomach or "social crop" of the colony. We assume that the key role of the common stomach is to provide indirect interactions between the water providers and users, and this, in turn, regulates the construction behavior.

In this paper, we use a top-down model to describe the regulation of task partitioning in these wasp societies. Allocation of the workforce into 4 linked task groups ensures steady construction as an emergent phenomenon. The common stomach as a communication platform in worker connectivity serves both as a temporal storage for one of the building materials (water) and also as an information source (information center) about the colony needs that relate to nest construction. We will also show that this system is able to dynamically adapt to perturbations of the environment and to changes in colony-level demands or population structure.

The current model is much more realistic and predictive than our previously published incipient model (Karsai and Balazsi 2002) that is based on 3 differential equations only. The current model is based on a Stock and Flow modeling framework (Forrester 1961) that follows the flow quantities of building material and of wasps in different task groups quantitatively. Although in the previous model, the task group "builders" were pooled with the generalist wasps, in the current model, nest builders are represented as a distinct group. This allows us to incorporate more feedback mechanisms into the system and also allows for constructing a more detailed model. Pooled stimulus functions of the preliminary model were also dissected into simpler subcomponents resulting in a larger, but less complex network of (mostly linear) relationships and feedbacks. With the current model, we are able to implement new experiments (addition of pulp, removing builders), which are then compared with the result of field experiments (Jeanne 1996; Karsai and Wenzel 2000).

In the following section, we describe our model of construction behavior of *Metapolybia* colonies. Our goal is to predict general patterns of division of labor, carry out experimental treatments on the model colonies, and compare these predictions to field data. In addition, we analyze the sensitivity of our model to key parameters and also predict global fitness of the modeled colony in terms of construction efficiency. These measurements allow us also to interpret the impact of environmental fluctuations and of sudden changes in colony structure onto the colony's global fitness. This is achieved by our model without assuming any individual adaptation (like adapting behavioral thresholds) and without assuming any initial individual differences between workers.

MATERIALS AND METHODS

Description of the model

Description of the colony

Our field study (Karsai and Wenzel 2000) and literature data (Jeanne 1996) were used to parameterize the model (Table 1). The colony of *Metapolybia mesoamericana* we used as our focus species consisted of $N = 107$ individuals and only 34 wasps from these were engaged in any form of the construction behavior (Karsai and Wenzel 2000). The construction of the nest requires pulp and builders; the collection of pulp requires water and pulp foragers. Water foragers provide water for builders and for pulp foragers.

Based on our observations, we assume that the wasps that take part in construction belong to one of the following groups (see Figure 1):

Inactive workers (IW): these wasps are generalists and can occasionally change into specialists.

Water foragers (WF): specialists that deliver water to the nest.

Pulp foragers (PF): specialists who take water from the colony's common stomach to forage for pulp and which afterward deliver new pulp to the nest.

Nest builders (NB): specialists who build the pulp into the nest.

Model assumptions

For simplicity, we assume that every individual has the same propensity to perform any type of behavior. Experience, age, genetic differences, and other preconditions are not incorporated into our model. We are aware that these are important preconditions, especially for species that form larger colonies (O'Donnell 1998; Karsai and Wenzel 2000). *Metapolybia* and several other wasp genera (the focus of our model) generally establish small- and medium-sized colonies, where worker flexibility is prominently present (Karsai and Wenzel 1998). We assume in our model that the decision-making regarding tasks is dependent on only the interaction of the focal worker with other individuals. We also assume that the insects do not have any global information about the distribution of labor in the colony. These modeling assumptions make our model significantly different from other models that are published on the topic of division of labor in social insects (Beshers and Fewell 2001).

Rules of task switching

Details and the accurate function for task switching are still not completely understood for swarm-founding social wasps. However, several studies (Jeanne 1996; Karsai and Wenzel 1998, 2000) showed that the foragers are prone to retain their task if unloading their material was easy after the previous working trip and if the preparation for leaving the nest again for the same job required only a short time and few interactions. If it took a long time to accomplish a foraging cycle (due to large number of interactions), it was highly probable that this wasp would stop foraging for that resource again. Also, if the preparation for the collection trip took a long time, the wasp would be more eager to quit that job. Our model is based on mechanisms that exploit 4 omnipresent cues—common stomach, unloading rate, water collection rate, and pulp availability—which are easy to "read" for every potential wasp worker. The aim of our model is to show that by correlating their behavior to the encountered levels (durations) of these cues, the wasps are able to assess how optimal their current duties fit to the current colony needs.

Table 1
Parameters of the model

Constant	Value	Unit	Description	Source
τ_w	70	Seconds	Duration of the water forager's cycle	1
τ_p	200	Seconds	Duration of the pulp forager's cycle	2
τ_b	130	Seconds	Duration of builder's cycle	1
τ_h	10	Seconds	Time needed to transfer the pulp load to builders	1, 2
Ω	1	Cropload/wasp	Water collected by a water forager per trip	1
Φ	1	Cropload/wasp	Water needed for the pulp forager to collect 1 pulp load	Assumption
Λ	0.0375	Cropload/wasp	Water used by one builder per construction cycle	1
E	1	Cropload/wasp	Maximum crop volume of wasps	Assumption
α_w	0.002	1/second	Maximum recruitment rate for water foragers	Assumption
α_p	0.001	1/second	Maximum recruitment rate for pulp foragers	Assumption
α_b	0.03	1/second	Maximum recruitment rate for nest builders	Assumption
β_w	1	Dimensionless	Maximum fraction of water foragers that abandon their task per trip	Assumption
β_p	1	Dimensionless	Maximum fraction of pulp foragers that abandon their task per trip	Assumption
β_b	1	Dimensionless	Maximum fraction of nest builders that abandon their task per building cycle	Assumption
H	1/8	Pulploads/wasp	Amount of pulp load acquired by one builder from one pulp load per nest building cycle	1
Σ	1	Pulpload/wasp	Amount of pulp collected by a pulp forager per trip	1

Reference in source column: 1: Karsai and Wenzel 2000; 2: Jeanne 1986. Some values were slightly changed for the model due to rounding. If there were several values available in literature, a value that corresponds to the majority of sources was chosen. The tag "assumption" indicates that parameter's actual values were not estimated directly from real colonies but are set to scale the model and balance the other parameters.

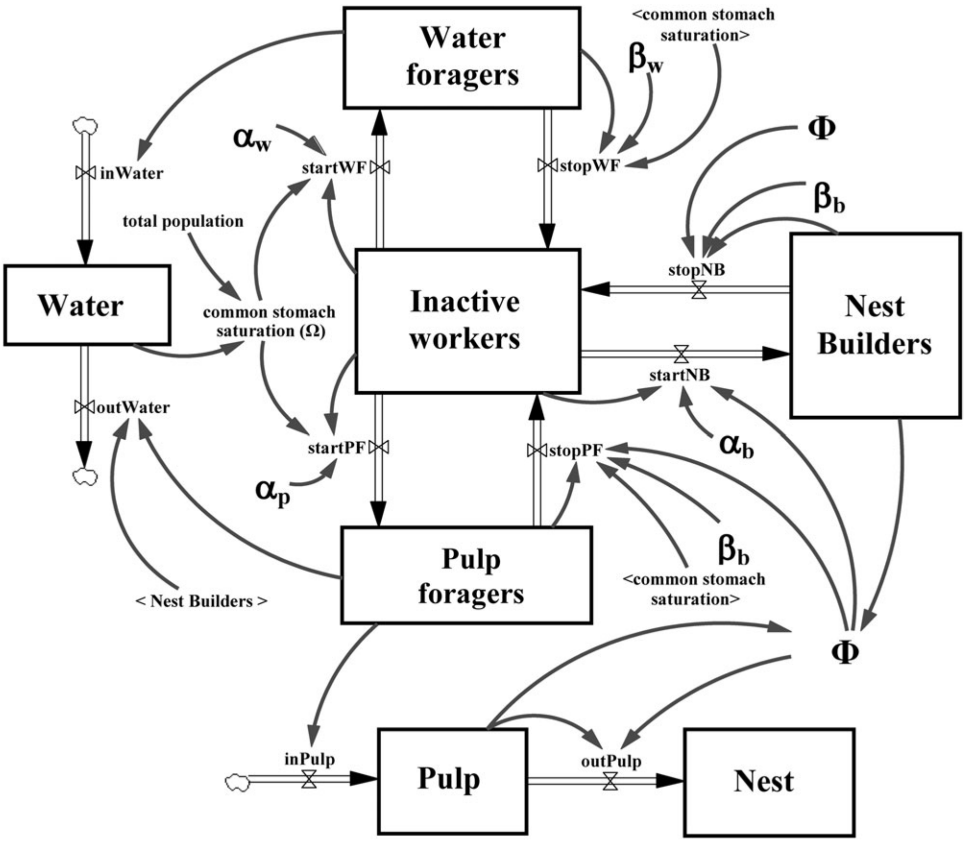

Figure 1
The system dynamics of the task partitioning of the building behavior. The model is depicted as a Stock and Flow diagram. Rectangular components indicate stocks of quantities, which can accumulate material or task associated workers over time. Double-lined arrows with valves indicate flows of quantities between stocks, single-lined arrows between components, and variables indicate dependencies. Cloud-like symbols indicate sinks and sources, this is where quantities are allowed to enter or leave the modeled system (model boundaries). To avoid crossings of arrows, so-called shadow variables (indicated by "< >"-type brackets) can represent model components at distant places in the diagram, something that is often called to be an "alias." To simplify the diagram, constants and unit integrity variables used in the model are not shown but are explicitly listed in Table 1 and are used in our equations.

For the sake of simplicity, we assume that there is no individual variation either in load size or duration of activities. These parameters are set to be close to the average value measured in natural colonies (see Table 1). We assume that all foraging trips are successful, and all foragers return with the same size of load. We further assume that all collected loads will be processed by the colony.

Common stomach
Water is not only a building material in the wasp colony, but it also provides an indirect source of important information about the colony's status. This is achieved in the form of a social crop or common stomach (Karsai and Wenzel 2000), which we think acts as a global information center system in the wasp society. This common stomach is formed because water has to be temporarily stored in the crops of the active members of the wasp society. In contrast to honeybees, which can simply store water, nectar, and pollen in their wax combs, wasps are unable to deposit water droplets in their paper-like nest cells because they would evaporate or would disintegrate the nest. To compensate for this inability, wasps have developed a special treatment for the water flows in their colony: Water foragers unload water to wasps that sit around the nest entrance, and pulp foragers beg for water from these wasps. Thus, this indirect water transfer between these 2 forager groups is the dominant type of interaction on the nests. For simplicity, in this model, we neglected the rare water-forager-to-pulp-forager water transfer and the water exchange between water-retaining wasps. For simplicity, we assumed that the mean saturation (i.e., the average crop filling) of the common stomach is the average value of water that the wasps participating in the construction (IW, NB, PF, and WF) store in their crop. This amount of water is accessible for nest construction and for the water provisioning of pulp foragers. The quantities of water that is used for other purposes such as drinking and cooling are not considered in this study.

Unloading of pulp
In our model, pulp foragers and nest builders are also coupled by a regulation mechanism that we modeled by introducing the unloading rate of pulp. Incoming pulp increases the number of nest builders because one pulp load is received and processed by 8 wasps that are recruited from the inactive worker group for one working cycle (Karsai and Wenzel 2000). However, such an increase in the number of nest builders consequently decreases the number of inactive workers that are available to receive pulp from the pulp forager. This, in turn, makes the pulp unloading for the pulp forager more difficult and more time consuming, which decreases the consecutive pulp unloading rate, which in turn decreases the further recruitment rate of nest builders. In contrast to this situation, low pulp input favors the reversion of builders into inactive workers. This, in turn, increases the recruitment of new pulp foragers. This combination of a positive and a negative feedback loop mimics the regulation we observed in real colonies (Karsai and Wenzel 2000) and is expected to be one of the important homeostatic control loops of the wasp society.

Derivation of the model's structure

Based on the assumptions mentioned above, we define a model that describes the dynamics of the 4 worker groups "G_I" (inactive wasps), "G_W" (water foragers), "G_P" (pulp foragers), and "G_B" (builders). In addition, our model should predict the dynamics of the 3 resources that are important for a wasp colony: "W" (water), "P_P" (pulp), and "P_N" (nest material). The water saturation of the common stomach (Ω) is also an important variable in our model. In contrast to a previous work (Karsai and Balazsi 2002), we explicitly model the quantities of building materials here. Furthermore, in the current model, worker group sizes are described by quantities instead of fractions of the total population. To accomplish this, we take the approach of "system dynamics" (Forrester 1961) and use the methods of Stock and Flow modeling. The resulting flows of materials and the rates at which workers join or abandon task-related groups are depicted in Figure 1.

In the following, we describe the dynamics of the 7 stocks in the model (Figure 1). The dynamics of the collective water reserve in the colony are described by Equation 1,

$$\frac{\mathrm{d}W}{\mathrm{d}t} = \omega\frac{1}{\tau_\mathrm{w}}G_\mathrm{W} - \varphi\frac{1}{\tau_\mathrm{p}}G_\mathrm{P} - \lambda\frac{1}{\tau_\mathrm{b}}G_\mathrm{B}, \tag{1}$$

where ω represents the water volume fed into the system by a single water forager after one trip. The constant τ_w represents the duration of a water forager's trip. The constant φ represents the amount of water used per second by each active pulp forager. The constant τ_p represents the duration of a pulp forager's trip. The constant λ represents the volume of water a builder loads per building cycle. The constant τ_b represents the duration of a builder's nest building cycle.

Knowing the total population of the colony, which is modeled by

$$N = G_\mathrm{I} + G_\mathrm{W} + G_\mathrm{P} + G_\mathrm{B}, \tag{2}$$

We can calculate the dimensionless average saturation of the common stomach Ω by

$$\Omega = \frac{W}{\varepsilon N}, \tag{3}$$

where ε is the maximum cropload a wasp can fill with water (i.e., the volume of the average wasp's crop).

The next step is to model the dynamics of the water foragers, which we express by the following equation

$$\frac{\mathrm{d}G_\mathrm{W}}{\mathrm{d}t} = \alpha_\mathrm{w}G_\mathrm{I}(1-\Omega) - \frac{\beta_\mathrm{w}}{\tau_\mathrm{w}}G_\mathrm{W}\Omega, \tag{4}$$

where α_w represents the recruitment rate (per second) of water foragers, and the constant β_w represents the maximum fraction of water foragers that give up their task after a completed foraging trip.

In a next modeling step, we have to model the dynamics of the pulp foragers. In principle, this is similar to the case of the water foragers, but the pulp foragers depend on 2 constraints that have to be satisfied: To leave the nest for pulp collection, these wasps first need to fill their crop with a full load of water ($\varphi = 1$ cropload/wasp). In addition, they need 8 nest builder wasps to take over their single pulp load for nest building, thus the pulp load taken up by 1 builder is $\eta = 1$ pulp load/8 wasps. We assume that the act of handing over 1 pulp load takes a period of $\tau_\mathrm{h} = 10$ s, thus a fraction of $1/\tau_\mathrm{h}$ of the pulp is on average available for unloading. Before we can model the dynamics of the pulp foraging group, we have to model how many pulp foragers can be unloaded by the current number of nest builders, which we do by

$$\Phi = \min\begin{bmatrix}\frac{G_B\eta\tau_h}{\tau_b P_P}\\ 1\end{bmatrix} \tag{5}$$

A value of $\Phi = 1$ of this dimensionless unloading efficiency index means that all collected pulp can be unloaded by the nest builders, whereas a value of $\Phi = 0$ means that no pulp can be unloaded at all. Based on this unloading efficiency rate, we are now able to model the dynamics of the pulp foraging group

$$\frac{\mathrm{d}G_\mathrm{P}}{\mathrm{d}t} = \alpha_\mathrm{p}G_\mathrm{I}\Omega - \frac{\beta_\mathrm{p}}{\tau_\mathrm{p}}G_\mathrm{P}(1-\Phi)\left(1-\Omega\right), \tag{6}$$

where α_p represents the recruitment rate (per second) of pulp foragers, and the constant β_p represents the maximum fraction of pulp foragers that give up their task after a completed foraging trip. Each pulp forager brings a full pulp load ($\sigma = 1$ pulp load/wasp). We assume that the act of handing over one pulp load takes a period of $\tau_\mathrm{h} = 10$ s.

Based on this, we can now model the dynamics of the pulp that is kept in the system by

$$\frac{\mathrm{d}P_\mathrm{P}}{\mathrm{d}t} = \frac{\sigma}{\tau_\mathrm{p}}G_\mathrm{P} - \frac{1}{\tau_\mathrm{h}}P_\mathrm{P}\Phi. \tag{7}$$

Because we have modeled the pulp unloading now, we can model the dynamics of the nest structure that is constructed by the unloaded pulp as

$$\frac{\mathrm{d}P_\mathrm{N}}{\mathrm{d}t} = \frac{1}{\tau_\mathrm{h}}P_\mathrm{P}\Phi. \tag{8}$$

The dynamics of the group of building wasps are now described by the following equation

$$\frac{\mathrm{d}G_\mathrm{B}}{\mathrm{d}t} = \min\begin{bmatrix}\frac{1}{\eta\tau_\mathrm{h}}P_\mathrm{P}\\ \\ \alpha_\mathrm{b}G_\mathrm{I}\end{bmatrix}(1-\Phi) - \beta_\mathrm{b}G_\mathrm{B}\Phi, \tag{9}$$

where α_b represents the recruitment rate (per second) of builders, and the constant β_b represents the maximum fraction of nest builders that give up their task after a completed nest building cycle. The recruitment for pulp foragers is, on the one hand, limited by the currently recruitable number of inactive workers, as is expressed by $\alpha_\mathrm{b}G_\mathrm{I}(1-\Phi)$. On the other hand, we assume that the colony will not recruit more wasps than needed to process the current pulp unloading demand, which is modeled by the term $\frac{1}{\eta\tau_\mathrm{h}}P_\mathrm{P}(1-\Phi)$.

Finally, we can calculate the number of inactive wasps as

$$\begin{aligned}\frac{\mathrm{d}G_\mathrm{I}}{\mathrm{d}t} = {} & \left(\frac{\beta_\mathrm{w}}{\tau_\mathrm{w}}G_\mathrm{W} - \alpha_\mathrm{p}G_\mathrm{I}\right)\Omega \\ & - \left(\alpha_\mathrm{w}G_\mathrm{I} - \frac{\beta_\mathrm{p}}{\tau_\mathrm{p}}G_\mathrm{P}(1-\Phi)\right)(1-\Omega) \\ & + \beta_\mathrm{b}G_\mathrm{B}\Phi - \min\begin{bmatrix}\frac{1}{\eta\tau_\mathrm{h}}P_\mathrm{P}\\ \\ \alpha_\mathrm{b}G_\mathrm{I}\end{bmatrix}(1-\Phi),\end{aligned} \tag{10}$$

which contains all the terms on the right hand side (RHS) of Equations 4, 6, and 9 with reversed signs. For the perturbation experiments, we carry out in this paper, it is necessary to calculate the number of inactive wasps with all terms on the RHS of Equation 10, instead of keeping the total population size constant (like "$N = 34$ wasps") and then just subtracting the recruited workers from this constant population. Such a procedure would not work in many of our simulation experiments shown in this article, where we remove or add wasps to specific task groups, because the colony size changes in these cases.

To allow us to make assessments of the efficiency of the whole system, we have already introduced Equation 8, which is used to accumulate all unloaded pulp that was used by the nest builders to construct the nest. The rate of growth of the nest (actually the RHS of Equation 8) is a good measure of the current nest building activity at any point in time. To generate a summarizing measure of efficiency of a whole run, we calculate the average nest building activity over time by the following equation

$$\xi = \frac{P_{\mathrm{N}}}{t}, \tag{11}$$

where t represents the amount of time that has already passed in a simulation run.

Starting conditions, simulation settings, and parameterization

We start our simulation runs with starting conditions that are similar to the colony we observed while the wasps constructed their nests: $\{G_{\mathrm{I}}, G_{\mathrm{W}}, G_{\mathrm{P}}, G_{\mathrm{B}}\} = \{15, 3, 3, 13\}$ wasps. Therefore, the initial total population size of the colony is set to 34 wasps as described in Karsai and Wenzel (2000). The resource levels are set to $W = 17$ croploads and $\{P_{\mathrm{P}}, P_{\mathrm{N}}\} = \{0.02, 0\}$ pulp loads. Our simulation runs are performed for 10 000 time steps where one time step (Δt) in our simulation corresponds to 1 s of real time in our parameterization, thus representing 2.78 h of real time. We use a fourth-order Runge–Kutta method for numerical simulation. For all simulations of our model, we use VensimTM 5.4 DSS (www.Vensim.com).

RESULTS

Normal run

Our model generated a mix of task groups that were similar to our observed colonies of *Metapolyia* wasps (Karsai and Wenzel 2000). The colonies operated close to 1.7 water foragers and 3.7 pulp foragers, 19.3 builders and 9.3 inactive workers (Figure 2). After the initiation period, the system stabilized quickly, and the common stomach converged to an equilibrium level of 0.43 cropload/wasp average fullness and to a building efficiency of 0.019.

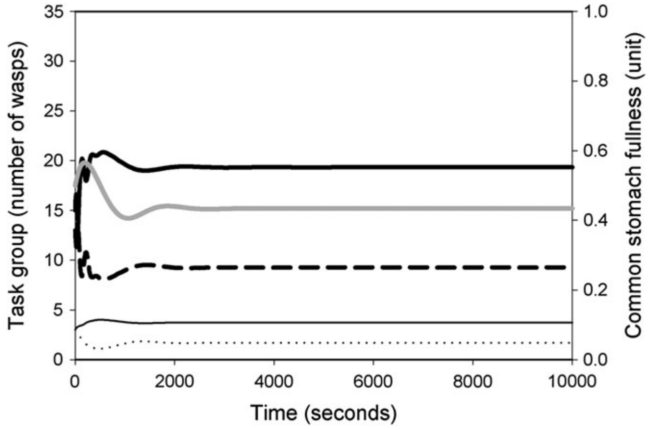

Figure 2
Normal run of the model; both the task groups and the common stomach are relaxed after the initial fluctuations. Dotted thin line: water foragers; solid thin line: pulp foragers; solid thick line: nest builders; broken thick line: inactive wasps; and gray solid thick line: common stomach fullness (secondary y axis).

Noise and periodicity perturbation

Stability analysis revealed that our model is very robust: Neither applying white noise nor strong periodicity resulted in unexpected divergences from the normal run or revealed that the model is sensitive to the used parameters (Figure 3). Applying periodicity to the recruitment of water foragers affected the number of water foragers, the common stomach, and, to a smaller extent, the number of inactive workers and builders but had no significant effect on the pulp foragers (Figure 3a). Even when the periodicity was longer, the effect was very similar (Figure 3b). Noise applied to the common stomach resulted in no discernible effect of the task group numbers, even in case of large noise levels (Figure 3c,d).

Comparisons with real colonies: perturbation experiments

Performing perturbation experiments on the model system makes it possible not only to test the robustness of the model, as we did in the previous section, but also to make a series of predictions that can be compared with the results of perturbation experiments that were carried out in the field on natural colonies (Jeanne 1996; Karsai and Wenzel 2000). The model system was run until it stabilized, and then, at 5000 time steps, one component of the model was suddenly increased or decreased by our simulation settings. We observed the reaction of the system qualitatively and compared our simulation results with empiric experiments published on natural wasp colonies (Figure 4; Table 2). In the natural system, every addition or removal of wasps or material takes time. Thus, we performed the perturbation experiments in a way that these perturbations were not all applied at once. Instead, colony variables were modulated throughout a plausible time window (several minutes) with plausible rates. For example, we assumed during a certain period of time that 25% of all wasps, which return from a water foraging trip are successfully captured by a (simulated) experimenter. Whenever we removed wasps or material, the removed quantities were not returned to the system after the perturbation's time window was over, so the colony had to find a new permanent equilibrium. If we removed wasps, the water that was in their crops was removed with them and was also removed from the water balance. If we added wasps to the colony, we assumed that they entered the system with an empty crop. Perturbation experiments lasted for 10 000 s, which corresponds to 2.77 h. We applied the perturbations always at the half-time of the runs, to allow the system to settle at an equilibrium value before the perturbation and to give enough time to reach a new equilibrium afterward. For detailed results of the 6 perturbation experiments we performed, see the detailed legends of Figure 4.

Both addition of water and addition of pulp increased the number of nest builders via different mechanisms (Figure 4a,b). Addition of water increased the water content in the common stomach, and this in turn increased the number of pulp foragers, which transported a larger amount of pulp into the nest, which was then processed by more builders. On the other hand, adding pulp recruited a large number of builders, and this in turn decreased the size of all other task groups and the water content in the common stomach. Removing foragers decreased nest construction as the number of nest builders was decreased due to the lowered material input (Figure 4c,d). Removing water foragers reduced the water content in the common stomach, and this caused a drop in the number of pulp foragers and builders. Removing pulp foragers decreased the amount of consumed water, therefore the stored water in the common stomach increased. This in turn decreased the number of water foragers. Also the number of builders dropped considerably

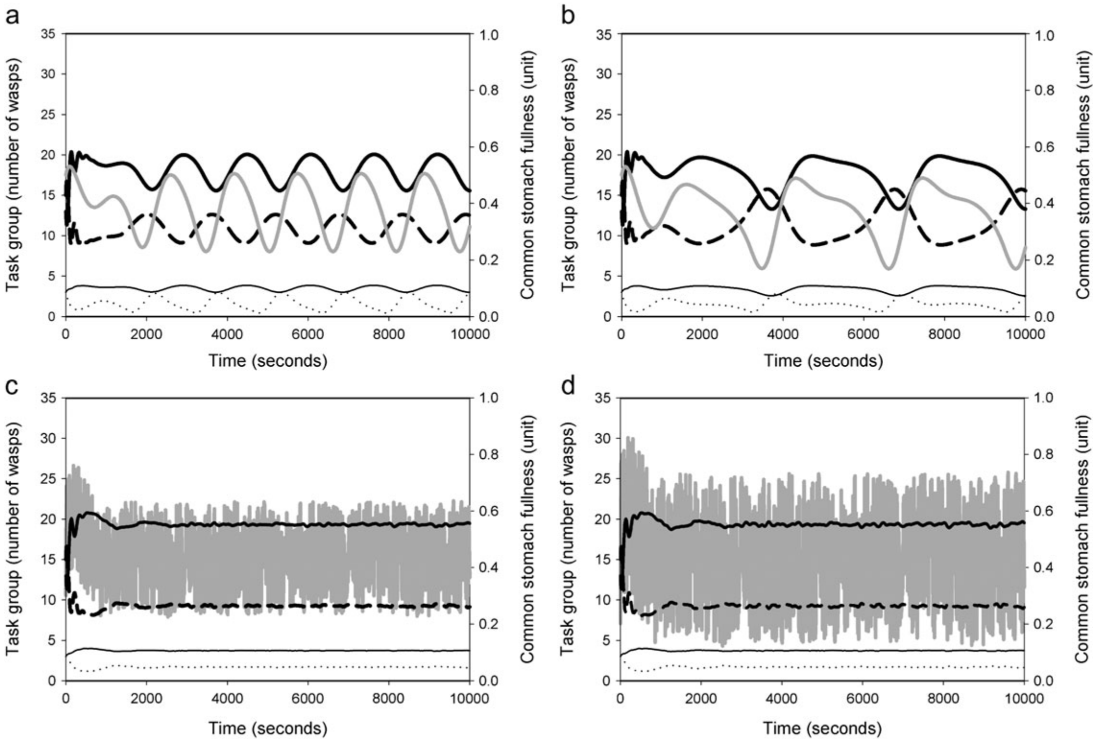

Figure 3
Testing the sensitivity of the model; periodicity was implemented using a sine function applied to the recruitment of water foragers. (a) Period length of sine function: 500 steps. (b) Period length of sine function: 1000 steps. Uniformly generated random noise was applied with ±0.2 (c) and ±0.3 (d) levels to the common stomach. Dotted thin line: water foragers; solid thin line: pulp foragers; solid thick line: nest builders; broken thick line: inactive wasps; and gray solid thick line: common stomach fullness (secondary *y* axis).

because of the decrease in the pulp input. Removing builders (Figure 4e) caused all task groups to decrease, and the water content in the common stomach increased. Adding inactive workers to the colony resulted in just the opposite reaction, that is, all task groups increased in number, and the water content of the common stomach decreased and then rebounded (Figure 4f). The last 2 experiments showed that the system is able to rebalance itself after loss or gain of considerable numbers of individuals. The predictions of our model agree with results obtained from natural wasp colonies with 2 exceptions (see "a" and "b" marks in Table 2). Removing builders and pulp foragers both resulted in a drop in water foragers in the model, but this was not or not clearly demonstrated in natural colonies.

Building efficiency

The global task for the colony is to organize their division of labor in nest construction efficiently, considering a given colony population structure and environmental conditions. We expressed this building efficiency by the rate of nest material accumulation (Equation 11, model variable: ξ). To investigate how the simulated perturbations affected colony efficiency, we analyzed the dynamics of ξ for all simulation experiments we performed (Figure 5).

Adding inactive workers resulted in a great increase in efficiency because these extra wasps began to participate in the construction behavior (Figure 5). Addition of pulp or water had an immediate positive effect on the predicted nest building efficiency. After the extra material is spent by workers, the predicted efficiency stabilized again. Removal of members from specific task groups had a clear negative effect on the nest building efficiency. The general reason for this is that removal of any type of foragers leads to a decrease of the colony size. As the colony autoregulates its task equilibria, this ultimately leads to a lowered number of nest builders, therefore the building efficiency decreases. Removal of builders directly decreases the number of wasps that construct the nest, causing a strong drop in the building efficiency.

Sensitivity analysis

Most of the parameters that we used in our model are based on empiric observations of wasps made by the authors personally or reported in literature (Table 1). However, the recruitment and abandonment rates we used in our model are calculated from the observed shifts of task performance reported in Karsai and Wenzel (1998, 2000) in a way that we assume that they hold for a common stomach concentration of $\Omega = 0.5$ cropload/wasp. Such assumptions, as well as all other task switching rates, are empirically not easily testable. This might cause a significant level of uncertainty in parameter estimations. To expose this issue explicitly, an additional set of sensitivity analyses were performed on the model that used variations of the default parameter set (Table 1). We performed 1000 runs of simulation in which initial values of the parameters $\{\alpha_w, \alpha_p, \alpha_b, \beta_w, \beta_p, \beta_b\}$ were sampled randomly with the Latin-Hypercube sampling method. Parameters were varied uniformly within a range of ±50% around the default values given in Table 1.

To minimize the number of figures that we needed to illustrate these results, we designed a special perturbation scenario for the simulated colony. Each simulation run lasted for 20 000 time steps (real time 5.55 h), and every 2500 time steps, one of the perturbations shown in Figure 5 was performed. As we

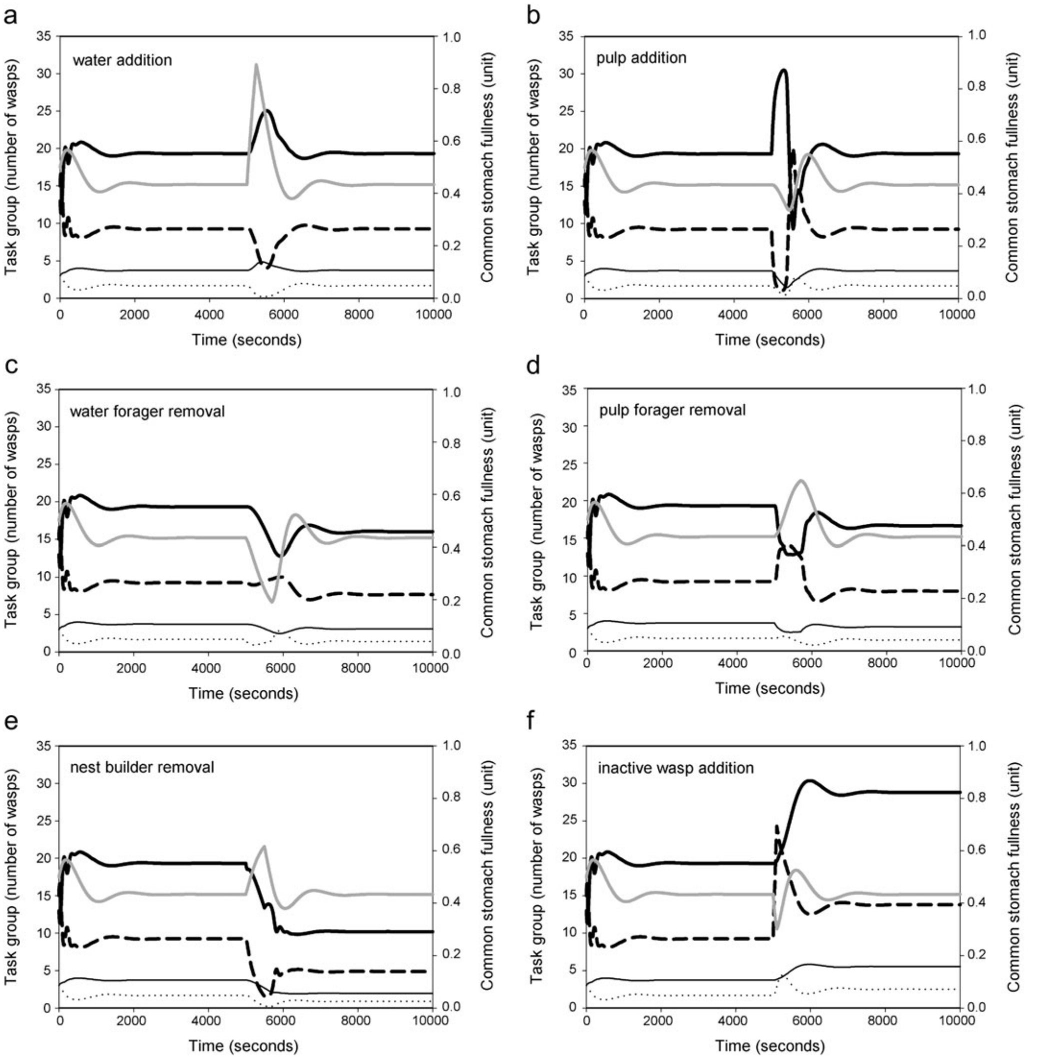

Figure 4

Perturbation experiments and the dynamics of task groups and the fullness of the common stomach. Perturbations were carried out at $t = 5000$. (a) For 250 s, we simulated an additional water input, which was equivalent to the water collected in this time period by 5 average water foragers. (b) For 250 s, we simulated an additional pulp input, which was equivalent to the pulp collected in this time period by 5 average pulp foragers. (c) For 700 s, we simulated that 25% of all returning water foragers were captured and removed from the system before they could unload themselves. (d) For 1800 s, we simulated that 50% of all returning pulp foragers were captured and removed from the system before they could unload themselves. (e) For 500 s, we simulated that 25% of all abandoning nest builders were captured and removed from the system. (f) For 100 s, inactive wasps were added at a rate of 1 wasp per 6 s. Dotted thin line: water foragers; solid thin line: pulp foragers; solid thick line: nest builders; broken thick line: inactive wasps; and gray solid thick line: common stomach fullness (secondary *y* axis).

varied the parameter values (α, β) intensively, we realized that the perturbation in which we suddenly added water to the common stomach generated unrealistic values in some runs, where the sampling algorithm picked extreme parameter settings. For example, some parameter settings can lead to a high equilibrium value of the common stomach saturation (Ω). The quick addition of a large amount of water (such as a load of 5 water foragers) can "overfill" this highly saturated common stomach. To prevent our analysis from generating such "artifacts" that may emerge from a combination of extreme parameter combinations and strong disturbances of the system, we added the water load of 2.5 water foragers instead of 5 water foragers in the water addition perturbation. All other perturbations were performed identical to those depicted in Figure 5. In our sensitivity runs, removed wasps were reintroduced to the colony as inactive wasps, otherwise the repeated disturbances would have shrunk the colony significantly.

Our model reacts in a very insensitive way to all tested parameters (Figure 6). The equilibrium levels of materials (water, pulp, and common stomach saturation) are more sensitive to the tested parameter variations than the pattern of worker recruitment. Our analyses also show that variation in the undisturbed periods (undisturbed equilibrium) is higher than during the perturbation phases, that is, those periods of time when the system is changing to reach a new equilibrium again. This clearly shows that the feedbacks that we modeled govern the behavior of the system in a counter-compensating way. This "driving force" of the feedbacks is strong enough to minimize the effects of different levels of recruitment rates and abandonment rates.

DISCUSSION

Our model provides an alternative mechanism to the threshold models in explaining how regulation and readjustments of

Table 2

Comparison of the model predictions with the result of experiments in real colonies

Manipulation	Studied behavior	Model prediction	Field observation
Add water	Pulp foraging	Increase	2
	Water foraging	Decrease	1, 2
	Nest construction	Increase	2
Add pulp	Pulp foraging	Decrease	1
	Nest construction	Increase	1
Remove WF	Water foraging	Decrease	1
		(Overcompensation of WF later)	1
Remove PF	Pulp foraging	Decrease	1, 2
	Water foraging	Decrease[a]	1, 2
	Nest construction	Decrease	2
Remove Builders	Pulp foraging	Decrease	1, 2
	Water foraging	Decrease[b]	2
	Nest construction	Decrease	1, 2

References show agreement with field studies: 1: Jeanne 1996; 2: Karsai and Wenzel 2000.

[a] Model prediction is in agreement with field studies except field data is mixed (non conclusive): in the field both no change and decrease in water foraging was detected.

[b] Model prediction is in agreement with field studies except: nonsignificant change in water foraging was observed on the field. See discussion for explanation.

workforce are possible in decentralized insect societies. The key result of our study is that our model predicts plausible patterns of work allocation without implementing any nonlinear abandonment/recruitment terms. Our model, similar to the published network models (Gordon et al. 1992; Pacala et al. 1996), assumes no initial intrinsic differences among the workers and emphasizes the importance of individual interactions, but it is unique in that these interactions happen via the common stomach, which is both an information center and a storage/buffer for water. Our simulations' results fit closely to empirical results of perturbation experiments and observations made on *Polybia* and *Metapolybia* colonies (Jeanne 1986, 1996; Karsai and Wenzel 2000). In general, these colonies steadily carry out construction work of their paper-made nests when environmental factors are steady (Karsai and Wenzel 2000). We observed very few and small divergences between the predictions of our model and empirical field data (see Table 2). Observing in detail how the modeled feedbacks caused this deviation from empirical data, we found the following causations: Removing builders or pulp foragers from the colony both resulted in a drop in water foragers in the model because the total number of wasps and, henceforth, the number of wasps where from water foragers can be recruited is also decreased. Furthermore, the colony needed less water because many water consumers were removed. One of the strengths of the Stock and Flow modeling technique used in this paper is that all quantities are precisely tracked, and "conservation of mass" is guaranteed. Our previous simpler model (Karsai and Balazsi 2002) worked with ratios of task groups, so the model was less sensitive to the effect of removing individuals than the more realistic current model. However, such a clear effect on the decrease in water foraging is not demonstrated in natural colonies (Jeanne 1996; Karsai and Wenzel 2000). It is possible that those natural colonies consumed extra water for cooling the nests or for other non-construction related activities, and this concealed the drop in water usage due to the removal of water users.

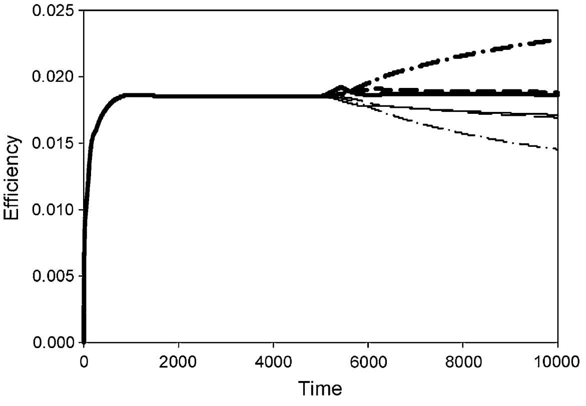

Figure 5
Efficiency of nest building. After running the simulations with the basic parameters, perturbations were made at $t = 5000$ s (see Figure 4). Adding components: thick solid line: add pulp; thick broken line: add water; thick dot dash line: add wasp. Removing components: thin solid line: remove pulp forager; thin broken line: remove water forager; and thin dot dash line: remove builders.

When wasps use water for other purposes than construction (such as cooling the nest), the speed of construction can slow down considerably, even if water foraging increases. We modeled this aspect of colony behavior in a previously published article (Karsai and Balazsi 2002). In the study presented here, we assumed that water is only consumed for nest construction. We think that this simplification was necessary to describe the main mechanism of task allocation more clearly. The experiments that implemented noise and periodic perturbations in the system are to be interpreted as follows: These additional system components summarize the net effects of all external factors on the water inflow and storage, thus these experiments test the model's stability against these factors. As we discovered, the colony is able to buffer these external variations; therefore, we can conclude that this simplification did not change the predictive value and the robustness of our model.

It is also noteworthy that the detection of a drop in the number of water foragers (low numbers naturally) can be difficult in case of field studies. The number of literature-reported field experiments focused on this aspect of construction behavior is low in number, and it is even sometimes contradictory (Jeanne 1996). We think that the current model actually has a correct prediction and that water foraging is actually decreasing when water users are removed from the nest. More field experiments are needed to reach a better understanding on the effects of different perturbations on water foraging and usage. Field experiments need to focus on time periods when the most water is used for construction, and the study needs to be well planned to able to detect significant differences between small values.

Wasps show quick reactions to a variety of perturbations. This underlines the importance of flexibility and adaptivity of workers within these societies. This flexibility correlates with other life-history parameters, such as colony size, body size, and nesting habits (Karsai and Wenzel 1998). The colonies that we used as the focus of our model are of medium size, and individual workers are not strongly fixed in a task. In contrast, they can change their behavioral profile quickly (Karsai and Wenzel 2000). Based on these studies, we assumed for our model that every worker wasp is identical to the others and that every wasp has the same propensity to change its working profile in the same way. It is possible that learning abilities, tempo, and similar properties are varying among individuals, but the model we presented is based on mean field estimations, and it is not an individual-based model.

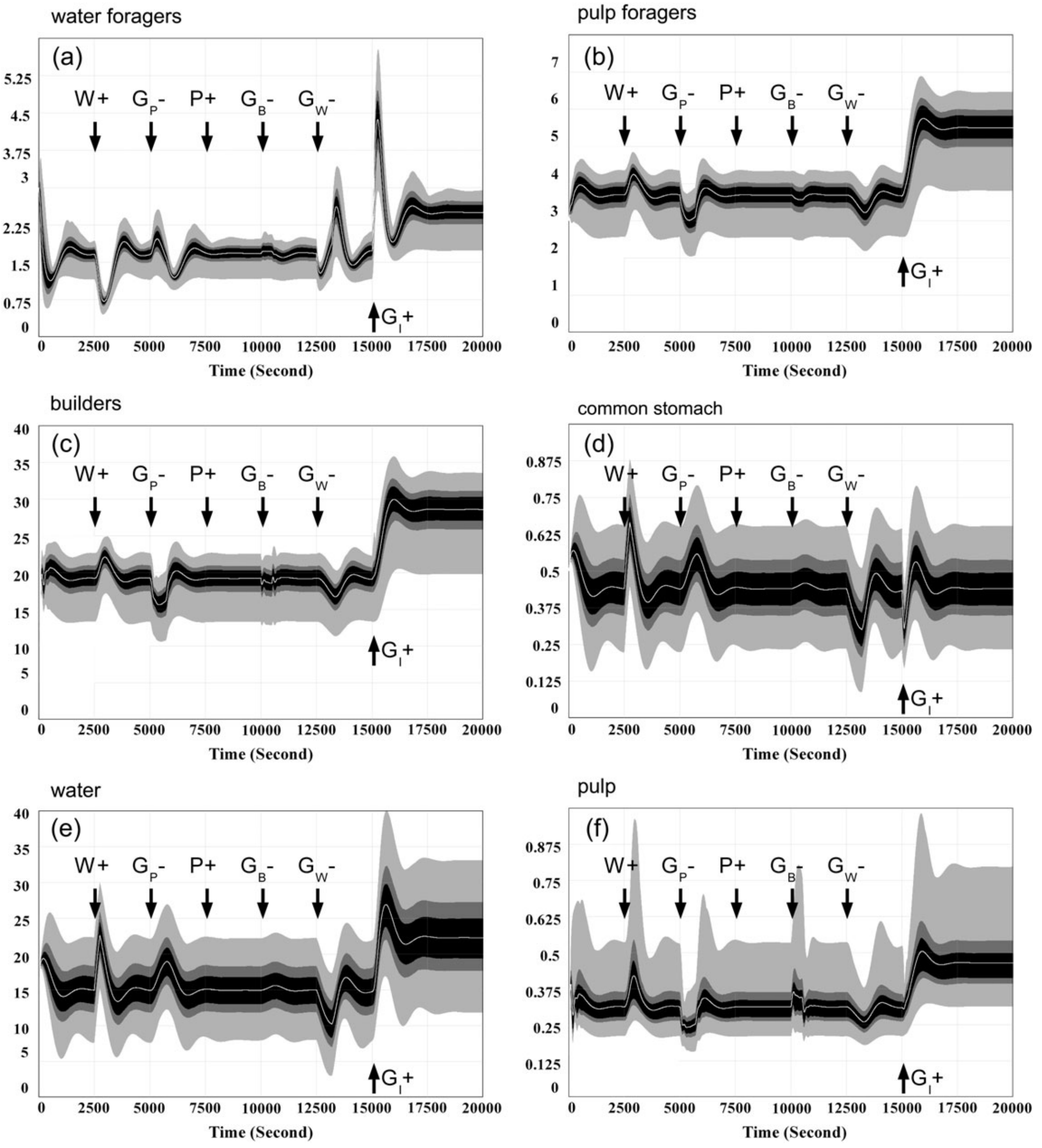

Figure 6
Sensitivity analysis of our model. We performed 1000 runs with varying combinations of the recruitment and abandonment rates of foragers and nest builders. Six consecutive perturbations were performed within each run: $W+$: water addition; $P+$: pulp addition; $G_{\mathrm{P}}-$: Removal of pulp foragers; $G_{\mathrm{w}}-$: removal of water foragers; $G_{\mathrm{B}}-$: removal of nest builders; and $G_{\mathrm{I}}+$: Addition of inactive wasps. Bright gray area: 100% of simulation results fall into and between these regions; dark gray area: 75% of simulation results; black area: 50% of simulation results; and white line: mean result.

We are also aware that more and more evidence about genetic (O'Donnell 1996, 1998; Keller 2009), physiological, and other aspects could be taken into account (O'Donnell and Jeanne 1992; Page and Erber 2002). In our model, we did not include age-related factors or other propensities that change in the long-term because we focused on short-term responses of the colonies only. We presented in this paper division of labor as an emergent property of the society (Beshers and Fewell 2001; Gordon 2003), where individual differences of workers are not needed to predict dynamic division of labor.

Division of labor in these wasp societies seems to tend toward a combination of workforce where most of the colony is only sitting on the nest and not foraging (see also Karsai and Runciman 2009). Wasps that process materials (foragers and builders) are visually active. Other wasps which do not seem to engage in work actively may have an important role in the colony: These wasps store water and provide a receptive partner for foraging wasps, which load or unload water at these common stomach wasps. For simplicity, we assumed in our model that all wasps participating in the construction take part in storing water. Thus, the common stomach is formed by all wasps that store some amounts of water in their crops. In nature, a certain fraction of water might be inaccessible for foragers in some periods. For example, water in the crops of builders is "locked," whereas these wasps are on their construction trip in the nest. In our model, these particularities are omitted to allow the model to be simple and robust. These kinds of details could be implemented more easily in an agent-based model system where each individual is treated as an agent with its own rules and properties.

Applying strong random noise to the common stomach showed that the system is not sensitive to such short-term disturbances. One of the main reasons for this is the fact that the common stomach plays a role as a strong buffer for the whole water provisioning system. The wasp society is able to cope with perturbations profoundly because the sudden changes are affecting the common stomach first. Over time, these variations of water availability are dispersed through the colony at a slow pace (diffusion-like process), giving the colony enough time to develop countermeasures for the disturbance such as intensifying the recruitment of foragers. The larger the colony size is, the more efficient this buffer system seems to work (Karsai and Wenzel 1998; Karsai and Runciman 2009).

Certain handling time, which is the time it takes to load or unload materials, tends to become shorter in larger colonies (Jeanne 1996; Karsai and Wenzel 2000). In part, this is the consequence of the fact that finding partners is easier in larger colonies (Karsai and Runciman 2009). We included this important fact in our current model in 2 ways: On the one hand, the relationship between pulp foragers and available builders is controlled by the rate of pulp unloading. On the other hand, foragers and inactive workers are coupled indirectly through the common stomach. The available water in the common stomach affects the recruitment and abandonment rates of foragers. In nature, this can be observed as the effects of queuing delays, which increase for pulp foragers in the case of water shortages. However, the existence of these delays in nature is not only the consequence of a suboptimal workforce mix but also a natural consequence of optimal information acquisition in task partitioned systems (Ratnieks and Anderson 1999; Hart and Ratnieks 2001).

A study on the properties of the common stomach itself was performed on a simple and abstract system (Karsai and Runciman 2009). It showed that the existence of the common stomach, that by definition requires additional water transfers and henceforth causes additional delays, is beneficial for most colonies except if the density of the wasps is very low (hard to find partners) or very high (easy to find a partner for direct transmission). We suspect that the size of the interaction platform in wasp nests is a consequence of evolutionary pressures that favor mechanisms that allows a steady construction by using only a small number of foragers. In addition, such a system is found to be highly adaptive to perturbations. The modeled colony reacts in ways that still retain a high number of inactive workers and builders in the nest and recruits only a small proportion of the workforce for additional foraging. This has 2 positive consequences for such a colony: Large numbers of inactive workers on the nest provide secondary functions for the society, as they can defend and patrol the nest while they simultaneously hold water in their crops. Keeping the number of foragers low by using them efficiently is also beneficial to the colony, as foraging is in general a dangerous task for all social insects (Sakagami and Fukuda 1968). Using a common stomach instead of using a direct water transfer system from water foragers to pulp foragers minimizes searching times at the expense of additional nest-bound workers (Karsai and Runciman 2009). As a consequence of the almost omnipresent and fast water availability, only a few foragers are required to fulfill the colony's demand for material by performing the risky trips. These individuals will be highly efficient due to the experience they have gained over their frequent trips (Jeanne 1986).

The common stomach, or social crop, was found to be an efficient self-organizing mechanism for regulation of work in insect societies of ants (Cassill and Tschinkel 1999) and bees (Schmickl and Crailsheim 2004), as well. We propose that via communicating through an information center and using a network of worker interactions that establish sets of positive and negative feedbacks, wasps' societies are able to achieve collective information processing and regulate their colony-level behavior.

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