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Regulation of task differentiation in wasp societies: A bottom-up model of the "common stomach"

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A B S T R A C T

Metapolybia wasps live in small societies (around one hundred adults) and rear their young in nests they construct on flat surfaces from plant materials. For processing nest paper, they must gather plant materials and process it into pulp with water. The water is collected by water foragers and is transferred to pulp foragers indirectly via a "common stomach." The common stomach, or social crop, is formed by generalist wasps called laborers. These wasps can engage in water exchange, store water in their crops, and may become specialist foragers or builders. We provide an alternative model for regulating task partitioning in construction behavior by using an agent based modeling framework parameterized by our field observations. 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. By 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. The robustness of our model stems from the fact that the common stomach is both a strong buffer and a source of several feedback mechanisms that affect the individual wasps. We show that both the efficiency and the task fidelity of these colonies are dependent upon colony size. We also demonstrate that the emergence of specialist wasps (individuals with high task fidelity) does not require any special initial conditions or reinforcement at the individual level, but it is rather a consequence of colony-level workflow stability. Our model closely mimics the behavior of *Metapolybia* wasps, demonstrating that a regulation mechanism based on simple pair-wise interactions through a common stomach is a plausible hypothesis for the organization of collective behavior.

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1. Introduction

Insect societies can be conceived as superorganisms in which inter-individual conflict for reproductive privilege is largely reduced and the worker caste is selected to maximize colony efficiency (Robinson, 1992; Holldobler and Wilson, 2008; Ratnieks and Helantera, 2009). Division of nonreproductive tasks among workers (polyethism) is a key adaptation promoting the ecological and evolutionary success of insect societies (Wilson, 1990). Studies on division of labor are often concerned with the integration of individual 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, 1978; Plowright and Plowright, 1988; Jeanson et al., 2007). These societies typically develop into parallel processing systems where the colony performs all of its operations concurrently instead of

sequentially (Oster and Wilson, 1978; Karsai and Wenzel, 1998; Anderson and Franks, 2001), and where frequent adjustment of the worker force undertaking different tasks is required (Oster and Wilson, 1978; Robinson, 1992; Seeley, 1995; Gordon, 1996; Ratnieks and Anderson, 1999).

Insect societies appear to be remarkably robust. Division of labor and task allocation is often organized in more or less the same way regardless of the society's nestmate relatedness (Korb and Heinze, 2004). Recently we have increasing evidence that although genetic, physiological and other aspects must be taken into account (O'Donnell, 1996; Page and Erber, 2002; Keller, 2009), and mechanistic and evolutionary explanations should be studied together (Franks et al., 2009; Burd and Howard, 2008; Sumpter, 2010), division of labor is an emergent property of the society (Beshers and Fewell, 2001; Gordon, 2003; Detrain and Deneubourg, 2006) and can be considered as a model system for collective decision making (Pratt, 2009). A social insect colony operates without any central control so a worker cannot assess directly the needs of the colony. Each worker uses simple local information and rules to operate and thus cannot compare its

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experience to that of its nestmates. Such limitations of the individual contrast with the diversity of colony level responses that efficiently track environmental opportunities and challenges (Detrain and Deneubourg, 2002, 2006; Theraulaz et al., 2003).

Although the caste concept in division of labor has been fundamental to our understanding of the organization of work in insect societies, the concept has been subject to debate. One approach suggested that temporal castes are too inflexible to permit a colony to swiftly reallocate labor in response to changing conditions (Wilson, 1983), while others stressed that task switching is so prevalent that reorganization of labor in social insects is likely more complex than simply activating specialized but idle workers to meet emergencies (Karsai and Wenzel, 1998; Johnson, 2002, 2003, 2009). Thus, models of division of labor must incorporate both variation in task performance among workers and individual worker flexibility (Beshers and Fewell, 2001; Fewell et al., 2009). Different models on division of labor emphasize these two points differently (see detailed review of models in Beshers and Fewell, 2001, and Franks et al., 2009). The response threshold model assumes that workers vary intrinsically in task propensity (Robinson and Page, 1989). Other models, such as the social inhibition models (Beshers et al., 2001; Naug and Gadagkar, 1999) and the self-reinforcement models (Denebourg et al., 1987; Spencer et al., 1998), emphasize the interactions between intrinsic processes and effects of other individuals. On the other hand, the forage for work models (Tofts, and Franks, 1992; Tofts1993; Franks and Tofts, 1994) and the network models (Gordon et al., 1992; Pacala et al., 1996) assume no intrinsic differences among workers. Johnson (2009) used identical response threshold coupled with random walk to model task allocation in honey bees. While the locational effects on task opportunity is important in the forage for work models, in the network model change in task allocation results from simple, direct interactions between individuals.

Because colonies and their environments are dynamic in nature, the labor requirements of the colony change over time, and the division of labor must accommodate these new demands. Colony level flexibility commonly stems from behavioral variability and flexibility at the individual level (Karsai and Wenzel, 1998; Nicolis et al., 2008) which in turn can cause observable differences at the colony level (Gordon et al., 2011). To make these colony level adjustments happen, the colony must possess information about the colony needs and the changes in the environment and the behavior of some of the individuals needs to be altered. Seeley (1985, 1998) presented a colony level regulation mechanism based on "information center strategy" where the network of worker interactions, which establish a set of feedback mechanisms, is based on the modulation of worker behavior. These information centers allow collective information processing and organizing colony level behaviors. A dependence on connected and shared information can be beneficial for more rapid information transfer, for more flexible and faster task change and for providing more efficient and reliable information transfer among individuals (O'Donnell, 2006; O'Donnell and Bulova, 2007).

On the basis of our field study (Karsai and Wenzel, 2000) and our previous Ordinary Differential Equation (ODE) top-down models (Karsai and Balazsi, 2002; Karsai and Schmickl, 2011), we propose a new bottom-up model. We will demonstrate that division of labor emerges from the interaction of workers. These interactions are direct at the individual level, because pairs of individuals exchange materials. At collective level the "common stomach" (or social crop) is used as a platform of worker connectivity, an information center and for water storage. Construction behavior of wasps is used as our model system because the behavior of individuals and the flow of building materials (water and pulp) can be easily monitored and manipulated in

nature (Jeanne, 1996; Karsai and Wenzel, 2000). The nest construction involves three tasks: nest building (which requires pulp), wood-pulp foraging (which uses water and provides pulp), and water foraging (which provides water for the colony). Generally, different individuals show different task fidelity and activity level while the colony level building proceeds at a steady rate (Karsai and Wenzel, 2000).

The current model is very different in scope and structure from our previously published models (Karsai and Balazsi, 2002; Karsai and Schmickl, 2011). These models were top-down models using differential equations and the framework of system dynamics. These models focused on describing the flow of building materials and of wasps in different task groups in the colony. Our current model is individual based, where each individual has an internal state and the fate of the individual can be followed in time. Individual based modeling has become a widely used tool for describing complex systems made out of autonomous entities (DeAngelis and Mooij, 2005; Grimm et al., 2006). This approach allowed us to ask new questions (e.g., about task fidelity) and carry out new experiments (such as studying the effects on colony size) that we could not do with our top-down models. We compare the predictions of our model to field data where possible. In fact, we carry out perturbation experiments to mimic closely the field studies of Jeanne (1996) and Karsai and Wenzel (2000) to test especially the following hypotheses:

(a) A balanced division of labor emerges without assuming initial individual differences and adaptation (like adapting behavioral threshold).
(b) Task fidelity emerges without intrinsic differences among workers and individual adaptations.
(c) Task fidelity and the stability depend on the colony size: larger colonies have more efficient and stable performance with more "specialists".
(d) This system is resilient against perturbations and react as we observed in natural colonies.

2. The model

2.1. Purpose

The purpose of the model is to understand how flexible task partitioning and fidelity emerges and is maintained in swarm founding wasp societies. An agent based model using a cellular automata approach was developed to model the nest construction behavior of the wasps. Nest-building requires wood pulp and builders. For the pulp collection the colony needs water and pulp foragers; for the water the colony needs water foragers. Our goal is to present a bottom-up model of the division of labor in social wasp colonies based on interactions between individual wasps. Exchange and storage of water through a "common stomach" is used as an information center and in turn regulates the work and leads to complex colony-level patterns. We seek robust performance and high predictive power as well as good agreement with the observed data of *Metapolybia* and *Polybia* wasp societies (Jeanne, 1996; Karsai and Wenzel, 2000). The model is described using the Overview, Design concepts and Details (ODD) protocol advocated by Grimm et al. (2006).

2.2. State variables and scales

The model comprises the following hierarchical levels: individuals, interaction platform, building site, and environment. The first two are modeled explicitly while the last two are modeled abstractly (the wasps at the building site or collection sites are

simply spending time away from the interaction platform). The colony consists of N individuals from which only a small set of individuals are active in construction (N_a). In swarm founding wasp societies most individuals do not participate in construction related activities. Young wasps generally sit motionless almost all day on a hidden part of the comb without interacting with others or performing any activities (Karsai and Wenzel, 2000). Other individuals focus on different tasks such as larva tending that do not affect construction behavior. Since this model focuses on construction behavior, our modeled wasp population is comprised of only those active individuals that interact with others and take part in the construction activities. We also assumed that during the modeled time scale (1 day), reallocation of workforce of the active population (N_a) was the only way to adapt to the short term changes and demands. The assumption that there is no substantial recruitment from the passive population in the short term is well supported by field observations (Karsai and Wenzel, 2000).

The individuals are characterized by the state variables: identity number, internal state (water stored in stomach and the number of unsuccessful interactions) and task assignment. In the model every active wasp is represented by an agent and each agent is defined by its behaviors and parameters (Table 1). In nature, active wasps (N_a) carry out all kinds of activities, but with different intensities and sometimes with some specialization (Karsai and Wenzel, 2000). In our model these intensities and specializations emerge from the interactions among the active wasps.

The model is both spatially explicit (all agents have a definite location) and mobile (agents move throughout the environment). The characteristics of each of these agents are tracked through time and the state of the model can be defined by the location and interactions of each agent in the environment. The interaction platform is an $L_x \times L_y$ (15×15) cell lattice (torus) where the wasps search for interactions. The natural wasp nests provide such a platform of interaction on the lower part of the envelope that covers the combs. The wasps land on this area—or move here immediately after landing—and search for other wasps to interact with. Wasps ready for work are also waiting and patrolling in this area seeking a job. Wasps that are building or collecting material are absent from the interaction platform for a given length of time (Table 1).

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 values measured in natural colonies (Jeanne, 1986; Karsai and Wenzel, 2000). We assume that all foraging trips are successful and all foragers return with the same sized pulp and water load. All water loads will be processed, but part of the pulp load can be discarded if there are not enough laborers on the nest to accept and process it (Karsai and Wenzel, 2000). The number of wasps belonging to different task groups, the fullness of the common stomach and the efficiency of construction are followed as colony-level descriptors (Table 1).

To scale the model in time realistically we assumed that the wasp walks around 10 s before it attempts an interaction (Karsai and Wenzel, 2000). Because of the size of the platform of interaction and the speed of the wasp we assumed that at the end of the 10th second the wasp may be at any position of the platform. If more than one wasp lands on the same position at the end of the 10th second, then these wasps will choose again a random position for landing (this eliminates any possible bias from the order of landing). Although our solution seems artificial, this is close to what happens in natural colonies (Karsai and Wenzel, 2000) and the simplification allows us to disregard the individual walking patterns and use an approach based on density instead. This means that each time step is a "snapshot" of the system at that moment where wasps appear on the active platform in a random position and then try to initiate an interaction in their local neighborhood. Because we used 10 s as our time unit, we rounded and scaled all time parameters accordingly (Table 1). We intend to model a short term behavior of the society, therefore our simulation period lasts 8 h 20 min (3000 time steps). This covers well the length of daily building activity of these wasps in nature.

2.3. Process overview and scheduling

At each discrete time step, a given list of actions is performed in sequential order. This consists of landing on the interaction platform, attempting an interaction, exchanging material, doing task related work, and changing tasks. In each turn, every individual (activated in a dynamically randomized order) carries out one action or decision relevant for the given individual depending on its internal state and the current job cycle of the wasp (Fig. 1).

Table 1
Parameters of the model. In each time related parameter 10 s was converted into 1 time step in the "used" column. References: 1: Karsai and Wenzel (2000); 2: Jeanne (1986); 3: Karsai and Balazsi (2002).

Description	Acronym	Estimated	Used	Reference
Number of active wasps	N_a	34	30	[1]
Time between two successful encounters (s)	Te	9.74, 9.02	1	[1,3]
Length of activity/day (s)	T	28,800 (8 h)	3000	Pers. obs.
Time for collecting water (s)	Tw	41.3	4	[2]
Time for collecting pulp (s)	Tp	219	20	[2]
Time for pulp processing and building (s)	Tb	131.5	13	[1]
Maximum units of water stored by a wasp	W	5.2	6	[1]
No. of wasp process a single pulp load	P	7.9	8	[1]
Consumption of water/wasp/time	Wd	0.0000781	0.001	[1]
Neighborhood radius?	R			
Number of laborer	L			Measured
Number of builder	Lb			Measured
Number of pulp forager	PF			Measured
Number of water forager	WF			Measured
Status of the common stomach	S			Measured
Efficiency of construction	E			Measured
Fidelity of water forager	Fw			Measured
Fidelity of pulp forager	Fp			Measured
Water level of a wasp	Wl			Measured
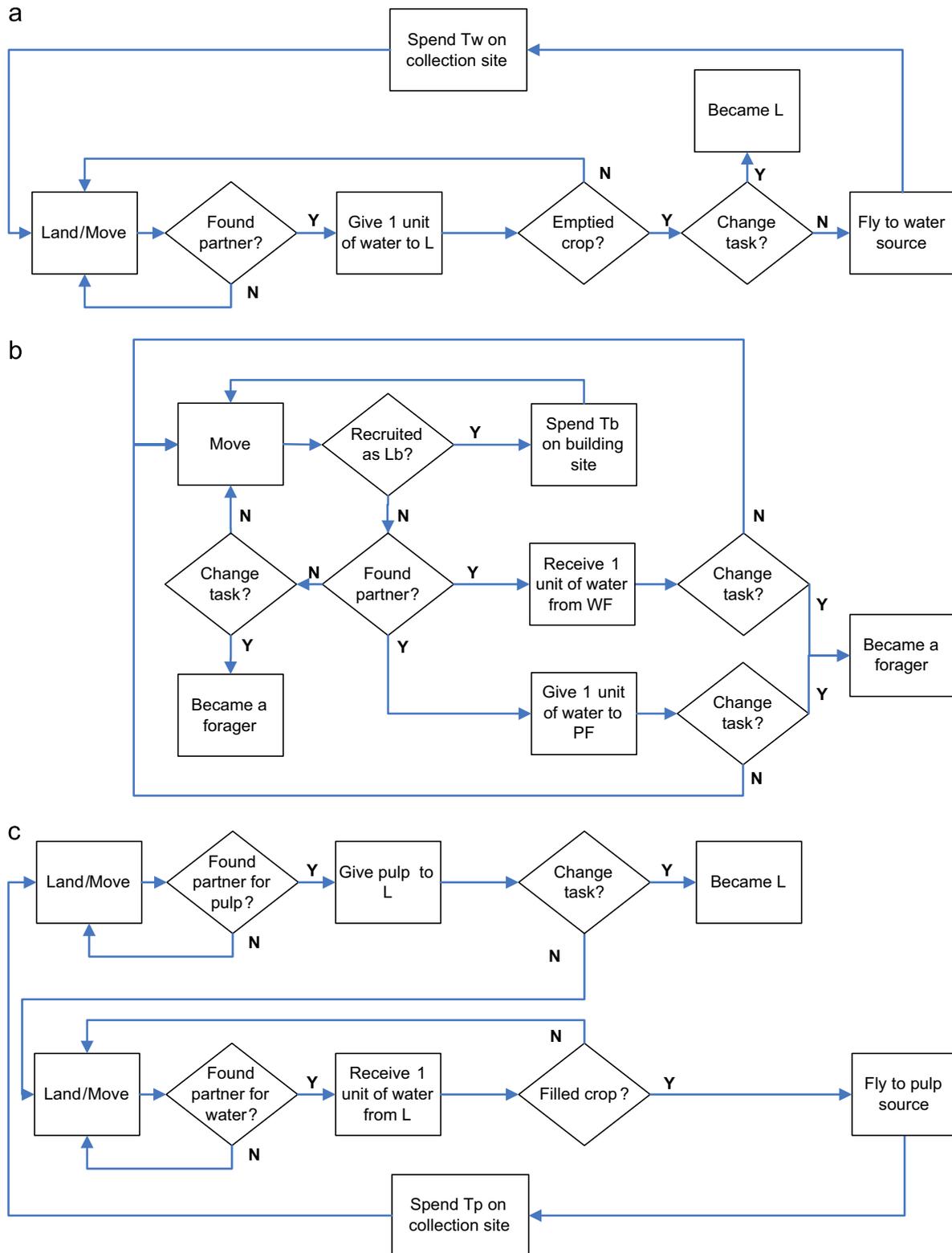
Fig. 1. Process overview of the model. Each task group has a working cycle that includes landing/moving decisions and actions. Actions taking more than one turn are indicated by a *T* parameter. Water forager (a) and pulp forager (c) can change to laborer. Laborer (b) can accept pulp and turn to builder, receive and give water, and can change to forager.

2.4. Design concepts

2.4.1. Emergence

Division of labor emerges from the behavior of the individuals and their interactions. All individuals start with the same parameters and task type, but the interactions of the individuals and simple rules leads to diversification and the emergence of foragers. Task fidelity, another emergent property of the system this paper focuses on, emerges automatically as a consequence of the underlying feedback mechanisms of the system. We also

show that the system has an emergent adaptability, which largely stems from the buffering effect of the common stomach, which is in turn, another emergent entity in this system.

2.4.2. Adaptation and fitness

Adaptation and fitness-seeking is not explicitly included in this mechanistic model. The only exception is in the decision rule of a laborer when it decides on whether it will become a pulp or a water forager. This decision is based on how much water the individual is already holding in its crop. Colony-level efficiency is measured as an indicator of how well the colony performs in the construction activities, but this measure has no effect on the individual behavior.

2.4.3. Sensing

Individuals are assumed to know their own internal state (water content, number of unsuccessful interactions performed and task group) and they behave accordingly. Each individual has an action radius in which they can sense the presence and task type of other individuals. Sensing of the presence of pulp ready for construction is considered globally available perception.

2.4.4. Interactions

Interactions between individuals are modeled in great detail (see Section 2.7). Interactions are pair-wise contacts between a laborer and a forager. Indirect interactions among foragers happen through the emergent common stomach.

2.4.5. Stochasticity

Random numbers were generated using the "Mersenne Twister" algorithm (Matsumoto and Nishimura, 1998). Stochastic events are landing and partner choice. Task change is interpreted as a probability drawn from the Weibull cumulative distribution (see details in Section 2.7).

2.4.6. Collectives

Individuals are grouped and followed according to their task group. However, these collectives are emergent in nature, because at the beginning all individuals belong to the laborer task group and changing tasks stems from interacting with other individuals.

2.4.7. Observation

In order to show the behavior of the system and analyze the results of the model, a simulation was written using the C# programming language. A graphical output was used for inspecting and testing the model step by step. The following were monitored and saved into a file for further data processing: number of wasps belonging to different task groups, fullness of the common stomach, building efficiency, used and discarded pulp and task fidelity. To compare the predictions of different runs SPSS statistical package (version 17, nonparametric statistics) was used.

2.5. Initialization

Each run was initialized in the same way (except when noted otherwise), using the same parameters depicted in Table 1. At time zero every wasp belonged to the task group laborer and had no water in their crop, consequently the common stomach was empty. This onset imitated the start of the day of natural colonies, when all wasps are on the nest and water collected in the previous day is used up. Parameters such as time lengths, consumption rates and material units (Table 1) were estimated from field studies (Jeanne, 1986; Karsai and Wenzel, 2000). The sequence of random numbers is itself randomized at the start of

each simulation so that replicate simulations using the same set of parameters will produce different predictions. All simulations were repeated 100 times in order to consider the variability between outputs for the same set of parameters and the same initial conditions.

2.6. Input

There were two types of simulation protocols developed to imitate the field experiments or to carry out specific experiments with the model system. In a series of experiments, the effect of a single parameter was used to decipher the colony-level consequence of that change. In these cases the baseline parameters were used, but a single parameter was decreased or increased at the start of the simulation. These changes are explicitly explained in the Section 3. Another set of experiments, called perturbation experiments, were run differently. These runs were started using the baseline parameters and ran for 1500 time steps. In this stage the colony was in dynamic equilibrium. We then performed a special experiment such as removing wasps from a given task group or adding material into the system (the exact nature of the perturbation is in the Section 3). After the onset of the perturbation the system was run to 3000 time steps allowing us to assess the effect of these perturbations.

2.7. Submodels

2.7.1. The tasks for construction

Every active wasp has a task (also a recognizable state), however this is not predetermined, but the result of dynamic interactions (Fig. 1). At the start of the simulations each wasp starts as an available laborer (L). Laborers move on the interaction platform and can interact with foragers. Their crops form the common stomach. Therefore they have the ability to accept, give, or store water via interactions and can convert to foragers or to temporal builders (Lb).

Water foraging: Water is transported to the nest by water foragers (WF). The water forager leaves the interaction platform with an empty crop and spends Tw time away while collecting W quantity of water. This water is distributed by WF to L wasp only (see water exchange mechanism later). Our field studies (Karsai and Wenzel, 2000) showed that the incoming water is stored in the "common stomach" of L wasps and the foragers upload and download water from the laborers. The WF attempts to give water away until its crop becomes empty, then decides if it will continue to work as WF or change into L (see task change mechanism later).

Pulp foraging: Pulp is transported to the nest by pulp foragers (PF). The PF wasps need water to scrap and process the pulp of woody material, therefore they solicit water from the "common stomach" via begging L wasps for water. When the PF has collected enough water for pulp collecting (for simplicity we assume that $Wp=W$), the wasp spends Tp time away from the interaction platform while it collects pulp. When the PF arrives to the interaction platform it carries P quantity of pulp and it has lost all of its water ($W=0$). Our observations showed that the pulp forager generally gave the whole pulp load to the first free laborer (Karsai and Wenzel, 2000) it met. In our model, PF wander on the interaction platform until it finds a free L wasp within the R interaction radius and then gives the whole load to this laborer for further distribution. For simplicity we neglect the rare occasions when more than one wasp accepts the load from the PF (Karsai and Wenzel, 2000). In the next step, the pulp forager decides whether it wants to carry on as a pulp forager (in which case it will start to beg for water again) or change into laborer (in which case it remains on the nest with an empty crop).

Building: The laborer who accepts the pulp load offers part of the load to other laborers and the pulp is separated into units. *P* number of *L* wasp became *Lb* wasps and process the pulp further and built it into a nest. If there is not *P* number of free *L* wasp on the interaction platform then the excess part of the pulp is discarded (Karsai and Wenzel, 2000). Processing and building take time (*Tb*) and the wasp also use up the water it holds in its own crop. During this time the laborer is not available to interact with the foragers. After finishing the building, the builder Lb becomes an available laborer (*L*) again with an empty crop and it can interact with the foragers or become a forager itself. Because the processing and building time (*Tb*) is relatively long and the pulp is very attractive for the wasps we assumed that *L* wasp will find the pulp carrier wasps and accept one unit of pulp even if they are not within the action radius in a given time step. Simplifying the system into having global information in this aspect imitated the observed real colonies well (Karsai and Wenzel, 2000). Construction does not happen on the interaction platform, therefore its size will not change during the simulation.

2.7.2. Interactions

In our model all interactions occur between one Forager and one Laborer, that is, there is neither laborer–laborer nor forager–forager interaction. Furthermore, all interactions are pair-wise interactions, i.e., one forager will interact with only one laborer in the same time step. While these seem to be strong simplifications, our field study shows that most interactions on the interaction platforms are in fact pair-wise forager–laborer interactions (Karsai and Wenzel, 2000). The interactions of agents are strictly local. This locality is defined by a parameter called neighborhood (*R*) that is defined as a Moore neighborhood with radius *R*. A wasp only has access to its own internal information and limited information about a local *partner* wasp in its neighborhood. For example, a Forager can make a "request" to wasps that occupy a cell in the neighborhood. The given "partner" grants or denies this request based on its own internal information. At no time does any wasp have access to the internal information of another wasp. However, a wasp can identify the current job (*L*, *PF* or *WF*) of other wasps in its nest. If there is no appropriate partner, or the interaction fails the wasp will move again for 10 s and initiate the next interaction at the next time step.

Foragers control the interactions in the system. Laborers simply wait to be contacted, but Foragers must actively search for Laborers with which to interact. To do this each Forager must search each cell in its neighborhood *R* and determine if there are any Laborers available. If there are multiple Laborers available, then one will be uniformly, randomly selected. Because of this random selection, we must be careful not to introduce bias with the selection order. This is handled similarly to the landing method discussed above. Each Forager that has landed on the nest searches its neighborhood and selects its partner. After each Forager has selected a partner, we check if multiple Foragers have selected the same Laborer. If so, we randomly select which Forager interacts with that partner. The unsuccessful Foragers then have no partner with which to interact in this time step.

Water exchange: Water exchange is the most important and frequent interaction in our model. The water is not only a building material, but the main regulator of the system (Karsai and Wenzel, 2000; Karsai and Balazsi, 2002). The water is stored in the crop of laborer wasps and these crops form a common stomach for the colony to download and upload water. For simplicity we assumed that every wasp can store maximum *W* quantity of water. If the laborer interacts with a water forager and its crop is not full, it will accept one unit of water. After the water exchange the pair breaks and both participants move on the interaction platform. The *PF* and *L* interactions operate the same

way, except the laborer gives 1 unit of water to the pulp forager, if its crop is not empty. For the sake of simplicity we did not assume a special resistance function for the water exchange, i.e., we assumed that water transfer is independent of the internal state of the laborer wasp, as long as this wasp is able to be a partner of a given forager. Our observations shows that normally both the *WF* and the *PF* visit about 5–6 wasps to empty or fill their water reservoir before flying out to collect.

Water is also used for other activities like cooling the nest and drinking. Implementing the *Wd* parameter as a leak of the common stomach we are able to simulate different environments where other activities compete for water with the construction behavior. For simplicity, we assume that each laborer loses 1 unit of water from its crop by *Wd* probability at every time step.

2.7.3. Changing of tasks

In this model we assumed that all N_a wasps have the same abilities and potential and each wasp is able to perform any kind of construction related behavior. Our study targets mainly small and medium sized colonies where this flexibility is strongly present in nature (Karsai and Wenzel, 1998, 2000). We assume in this model that the job each wasp takes ultimately depends on its interaction with other wasps. We also assume that the wasps have no global information about the distribution of labor in the colony and there is no central control for division of labor. At the beginning of the simulation each wasp start as an *L* wasp with empty crop (*W*=0), and they may change tasks depending on the interactions they will experience.

Details and the accurate function for task switching of natural colonies are unknown. However, several studies (Jeanne, 1996; Karsai and Wenzel, 1998, 2000) showed that the foragers tend to retain their task if downloading their material is easy and preparation for leaving the nest again requires only a short time and few interactions. If it takes a long time and many interactions to download the material or prepare for the collection trip, it is highly probable that the wasp will stop foraging. The laborer wasp can turn into a forager based on its internal state, probabilistically described by a Weibull cumulative distribution function, a function commonly used in problems related to aging and stress (Weibull, 1951):

$$F(x; \alpha, \beta) = 1 - e^{-(x/\beta)^{\alpha}}$$

This function describes that as the number of unsuccessful interactions increases (*x*), the probability to stay in the same task decreases. The basic parameters we used for the Weibull function ($\alpha=5$, $\beta=20$) provided a function which emulated the behavior of foragers we observed in nature. In ideal condition each forager in general contacts 5–6 wasps before they fly out again (Karsai and Wenzel, 2000), therefore for our normal runs we opted for a function that does not provide significant abandonment of the given job if the number of contacts was fewer than 15 and the wasp will change jobs with increasing probability as the number of contacts increases beyond that. In our model the parameters of the function will not change and are not different among the individuals.

The independent variable of the probabilistic function is the number of non-contributing interactions. This is a counter that increases by one if the laborer wasp had no interaction involving water or pulp exchange and did not participate in building. If there is a meaningful interaction, this counter drops back to zero. In every time step the value of Weibull function is calculated and gives the probability of changing to a forager task in that time step. The wasp also knows how much water is in its stomach. If the wasp decides to become a forager from a laborer then its internal water level determines whether it becomes a pulp forager (*W* > 3) or waterforager (*W* < 3) (randomly if *W*=3).

Foragers can revert into laborers easily if the foraged material is not readily accepted by the colony. When the water forager returns from the water source it tries to give away the water load. If there are not enough free workers or their crops are already full of water, it takes longer to find receptive laborers and unload the water load. In this case the water forager have difficulty to finish its job and this indicates that the system has a surplus of water foragers, so the water forager should revert to laborer with higher probability. This probability is a (Weibull) function of the number of interactions required to unload the water. The same function with the same parameters is used as for the task switching of the laborer, but with the significant difference that the counter of non-contributing interactions will not drop to zero when a successful transfer is made, but continue to count until all water is downloaded (until the job cycle is done). This way the counter measures how successfully (or quickly) the given job was accomplished and in turn, this information is used to establish the probability of reverting to laborer or the continuation of the work as water forager. Reverting from a pulp forager to a laborer is very similar to the mechanism described above for the water foragers, but the number of interactions has two terms: (a) the ease of giving away the pulp and (b) the number of wasps begged to receive W quantity of water. If the sum of these interactions is large, then the forager reverts to laborer with higher probability.

2.7.4. Monitored values

The number of wasps belonging to different work groups (WF; PF; L and Lb) was followed and other colony-level values were calculated (Table 1). When a given forager completes the foraging cycle, it needs to decide whether it stays a forager or not. The length of the consecutive "stay as forager" decisions (L) and the number of occasions being forager (i) are measured. The colonial level fidelity for the pulp forager (Fp) and water forager (Fw) is calculated as follows:

$$Fp = \frac{\sum_0^i Lp}{i}, \quad Fw = \frac{\sum_0^i Lw}{i}$$

During each run, the maximum length of being continuously a pulp forager (Lp) and water forager (Lw) is recorded. The mean and standard deviations of these values are taken across parallel runs of the simulation. If the value is large, it indicates that there are specialized foragers in the colony. If the value is smaller, it indicates that foragers are frequently reverting to laborers and thus there is little specialization.

The average quantity of water in the crop of non-constructing laborers ($L-Lb$) represents the status or fullness of the common stomach (S).

$$S = \frac{\sum_{i=0}^{L-Lb} wi}{L-Lb}$$

where wi is the quantity of water in a crop of the ith wasp. This value can change between zero and W, where W is the maximum units of water stored by a wasp.

The efficiency (E) of the construction behavior is assessed by the amount of pulp built into the nest ($P_u - P_d$) and is measured by

$$E = \frac{P_u - P_d}{N_a/T}$$

where P_u is the amount of pulp that has been delivered to the interaction platform, P_d is the amount of pulp discarded because of lack of free laborers on the nest; N_a is the number of active wasps and T is the number of time steps since the simulation started.

3. Results

3.1. Normal run, the effect of starting conditions and action radius

We started our colonies from a state when each wasp was a laborer with an empty stomach. Soon after, some laborers converted to water forager and began to fill the common stomach with water (Fig. 2a). As the common stomach was filling up, it became harder to download the water for the water foragers and the excess water foragers started to revert back to laborers, while pulp foragers began to emerge from some of the laborers. The pulp foragers used water from the common stomach and carried pulp to the nest. If too much pulp arrived, then most laborers would be occupied with building which made downloading pulp or gathering water take longer for the pulp foragers. Therefore these excess pulp foragers reverted back to laborers. During the first 500 time steps the system was fluctuating extensively, but later this fluctuation decreased as the common stomach provided an efficient buffer and the efficiency of the construction is maximized (Figs. 2b and 3). On average, the water level of the common stomach stabilized slightly below half-full. The numbers of wasps belonging to different tasks stabilized and the colony is using less than 15 percent of the individuals as foragers, one-third of the wasps as builders and about half of the colony serve as available laborers (Fig. 3). This emergent mix of the different task groups provided steady progress during the day (there was no shortage of available laborers to interact with) and minimal amount of discarded pulp.

The system was very robust and the main dynamics seemed to be independent of the initial water level of the common stomach after 1000 time steps (Fig. 4a). When the starting value is close to
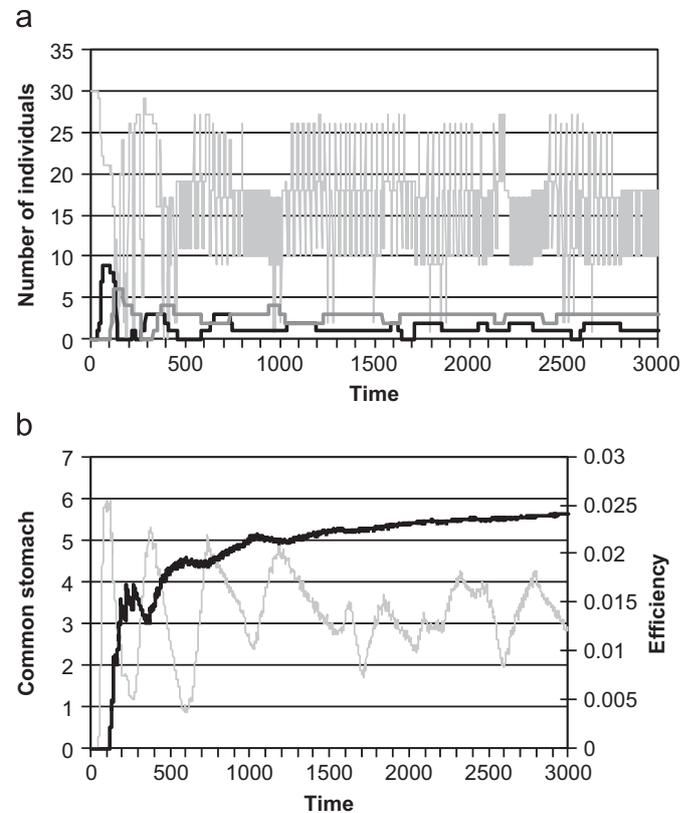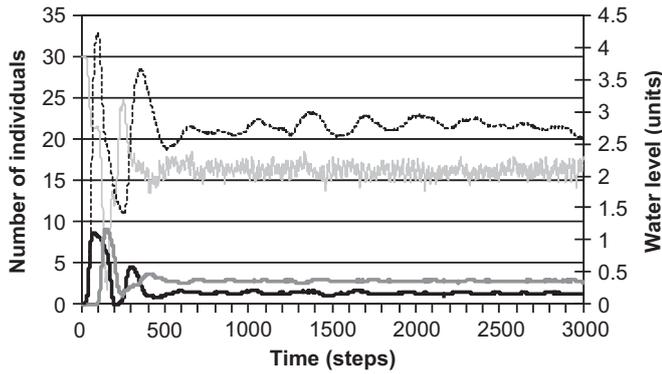

Fig. 2. A single simulation with basic parameters (Table 1): (a) dynamics of task distribution; thick black line: water forager; thick gray line: pulp forager; thin gray line: available laborers; (b) the efficiency (black thick line) and the amount of water in the common stomach (thin gray line).

Fig. 3. Average value of 100 simulations with the basic parameters (Table 1). Thick black line: water forager; thick gray line: pulp forager; thin gray line: available laborers; broken black line: water level in the common stomach (secondary Y-axis).

the relaxed value, the system did not fluctuate so much, and this significantly increase the building efficiency (Table 2). The task fidelity of both the water foragers and the pulp foragers were not different, with the exception of a marginally significant case for the pulp foragers (Table 2: Fp (3–6): $p = 0.048$). This indicates that task specialization happened after the system stabilized. These results were reinforced by the effect of the initial task distribution of the colony that provided a similar picture. Independently of the initial setup all colonies reached the same equilibrium size (Fig. 4b and c). Colonies started without any foragers were significantly less efficient than those who had some, but having many foragers did not provide a better result than having only very few (Table 2). There was no significant difference among the groups in the fidelity values (Kruskal–Wallis test, $p > 0.05$), indicating that most specialized individuals emerged after the colony stabilized.

Surprisingly, the dynamics of the system were fairly robust with regard to the size of action radius of the wasp. If the wasp is able to contact only adjacent neighbors ($R = 1$) then the water level of the common stomach stabilizes at a slightly lower value even though the number of water foragers is higher, because in this case it is more frequent that in a given time step the wasps have no other wasp available for interaction (Fig. 5). While the effect of the action radius size is moderate on the dynamics of the colony, it has a significant effect (Kruskal–Wallis test $p < 0.05$) on the efficiency (Fig. 5b) and the task fidelity (Fig. 5c). Both efficiency and task fidelity increase with the action radius. although the difference is not significant between action radius 3 and 4 or 4 and 5. While strictly local contacts were the less efficient way to construct the nest, and the foragers more commonly reverted to laborers, the loss of the efficiency is moderate and beyond $R > 3$ there is no significant gain in efficiency (Fig. 5b) or in fidelity (Fig. 5c). A larger radius made it highly probable that the forager found an appropriate partner, therefore their job was carried out faster which in turn ensured they retained their job with higher probability. These results indicated that the nest building mechanism does not require global information and local information with $R > 2$ can provide very efficient performance.

3.2. Internal and external factors

The decision of the wasps on task change or retention depends ultimately on the water usage, the interaction with the common stomach (external factors), and a decision function (internal factor). Modifying the parameters of the Weibull function allowed us to model different decision mechanisms (Fig. 6). Changing the
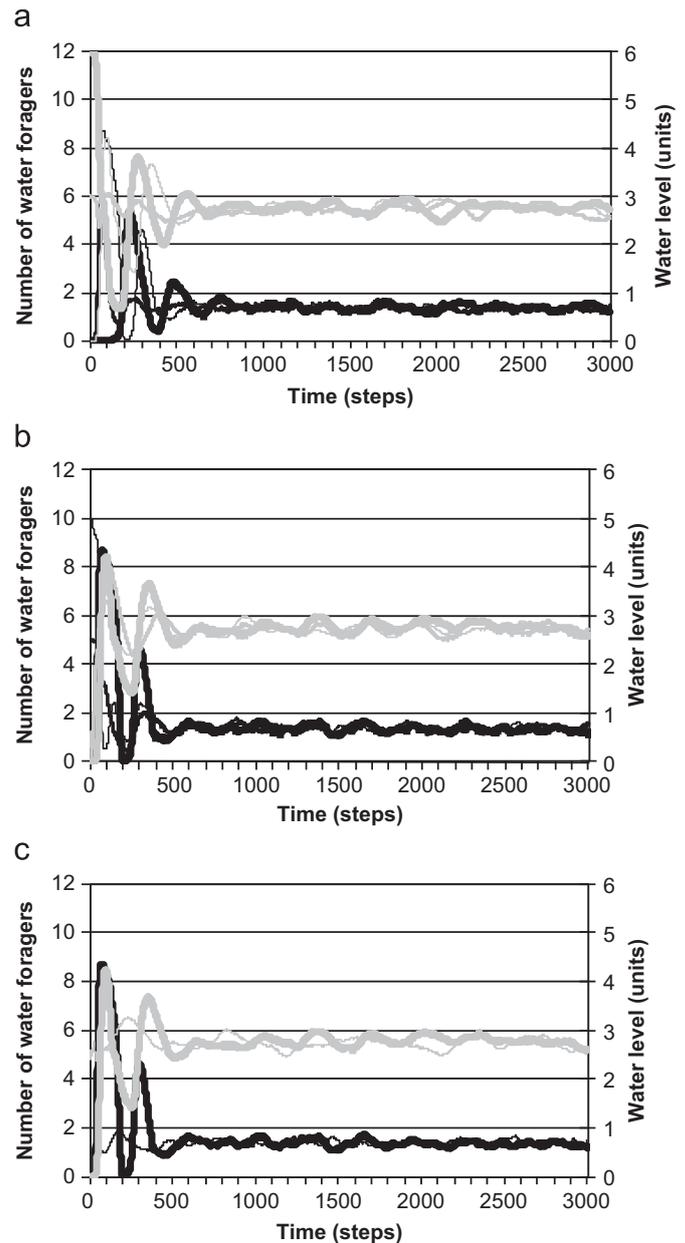

Fig. 4. The effect of initial parameters: (a) the effect of initial water level of the common stomach; thicker lines mean higher initial values (0, 3, 6); (b) and (c) the effect of initial colony composition; thicker lines mean higher number of laborers in the initial composition: thin solid line: $10L + 10WF + 10PF$; medium solid line: $20L + 5WF + 5PF$; thick line: $30L$; (c) thin solid line: $36L + 1WF + 3PF$ with $W = 3$; thick line: $30L$ with $W = 0$. Number of water foragers (black lines) and the water level of the common stomach (gray lines). Average values calculated from 100 parallel runs.

value of alpha can provide decision functions of a different nature. As alpha increases the decision function will approach a 0–1 step function, while decreasing alpha will result in a speedier abandonment as the probability of staying in the job is dropping very quickly. The latter case emulates well those colonies where all worker wasps work as jack of all trades, while the former is close to the more rigid task changing strategies of very large societies (Karsai and Wenzel, 1998). Task fidelity depends greatly on the value of alpha, because higher alpha makes task change less common (Fig. 6c). When alpha is low, the water level of the common stomach is lower and the number of both forager types are higher compared to the basic runs (Fig. 6a). Lower alpha also increased the efficiency of the colony (Fig. 6b), but 16 percent of

Table 2
Efficiency (*E*) and fidelity values (*Fw*: water forager fidelity; *Fp*: pulp forager fidelity) of different runs (average values $\pm$ std. dev. of 100 runs). Column value shows the value of the parameter for the given experiment. Other parameters were set to the standard set (Table 1). Column Comp shows the experiment that was tested against the experiment listed in the Value columns, if the Kruskal–Wallis test were significant. Mann–Whitney *U* tests ($N=200$); *p* values: NS: $p > 0.05$; *$0.05 > p > 0.01$; **$p < 0.01$; no sign: the Kruskal–Wallis test is not significant. Experiments: Initial *WL*: The water level of the wasp is set to this value at the start of the simulation.

Experiment	Value	Comp	E	Fw	Fp
Initial *WL*	**0**	3	0.0233 ± 0.0012**	71.97 ± 27.47 NS	53.36 ± 16.38 NS
	3	6	0.0240 ± 0.0012**	74.34 ± 30.12 NS	50.36 ± 17.90*
	6	0	0.0235 ± 0.0012 NS	66.34 ± 23.66 NS	48.59 ± 14.80 NS
Initial task	**1: L10W10P10**	2	0.0240 ± 0.0011 NS	70.72 ± 28.07	50.45 ± 16.85
	2: L20W5P5	3	0.0240 ± 0.0010**	74.01 ± 26.43	50.58 ± 16.15
	3: L30W0P0	1	0.0233 ± 0.0012**	71.97 ± 27.47	53.36 ± 16.38
	4: L26W1P1	3	0.0243 ± 0.0012**	78.35 ± 28.17	55.23 ± 19.58
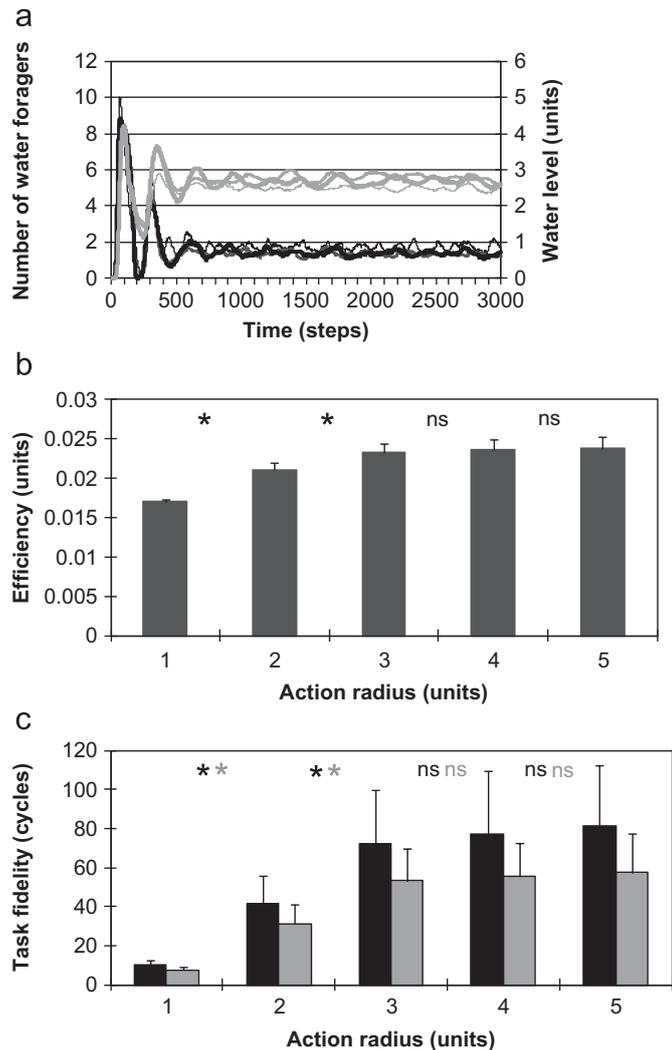
Fig. 5. The effect of action radius on: (a) the number of water foragers (black lines) and the water level of the common stomach (gray lines). Thicker lines mean higher value in action radius ($R=1$, 3 and 5); (b) colony-level efficiency; (c) task fidelity of water foragers (black columns) and pulp foragers (gray columns). Average values and standard deviations were calculated from 100 parallel runs. Significance level: *$p < 0.05$; ns: $p > 0.05$ based on Mann–Whitney *U*-test.

the colonies failed to build (every wasp became a forager). Five percent of failure happened in cases when the alpha was very high as well. While these failures stem from our model system and the assumptions we used (all wasps start as empty laborer), these results indicate clearly that the decision function evolved to work in concert with other life history parameters of the species and the colony size (Karsai and Wenzel, 1998).

By modifying the beta parameter we could model how quickly the wasps reacted to the unsuccessful contacts using the same "type" of decision curve. Decreasing beta made the wasp abandon their current task easier and this resulted in a lowered task fidelity (Fig. 6f). While higher beta increased task fidelity, the efficiency is significantly smaller (Fig. 6e). There is no significant difference between the efficiency of colonies that used beta 10 and 20, but nine percent of colonies that used the smaller beta failed to build. Colonies with larger beta tend to fluctuate more at the beginning of the simulation, but the number of foragers and the average water level seems to be robust to changes in beta in the examined range (Fig. 6d).

Besides nest building, water is also used for reasons such as cooling the nest and drinking. Several of these activities dependent upon external environmental factors and different activities may compete for the available water. We modeled the connection of construction behavior to other water consumptions via changing the value of the *Wd* parameter (Fig. 7). Moderate (10 times) changes in water consumptions seem to have no effect on the colony dynamics, but when the water loss is hundred times higher than normally (the nest needs cooling for example) the water level of the common stomach drops even though the number of water foragers increased several fold (Fig. 7a). The water foragers are not only more numerous, but also have significantly higher level of job fidelity (Fig. 7c). The job fidelity of the pulp foragers did not show significant difference among colonies with different *Wd* values (Kruskal–Wallis test, $p > 0.05$). As expected, the colony efficiency increases when less water is used for purposes other than construction (Fig. 7b).

3.3. Colony size and perturbations

In our model we assumed that the number of active wasps increases linearly with colony size. The number of active wasps (N_a) determines the maximum density of wasps on the interaction platform since the size of the platform is constant. The density of wasps affects the number of interactions. When $N_a=10$, 28 percent of the colonies failed to build the nest. This indicated that the building rules we used do not work well in very small colonies and this agrees with what we find in nature (Karsai and Wenzel, 1998; Forsyth, 1978). After 1000 time steps larger colonies tends to fluctuate less (Fig. 8a) and they use more foragers with higher fidelity values (Fig. 8a and c) providing more efficient construction (Fig. 8b).

Performing different perturbation experiments in the model system makes it possible not only to test the robustness of the model, but also provides predictions, which can be compared with data from field perturbation experiments. Removing all
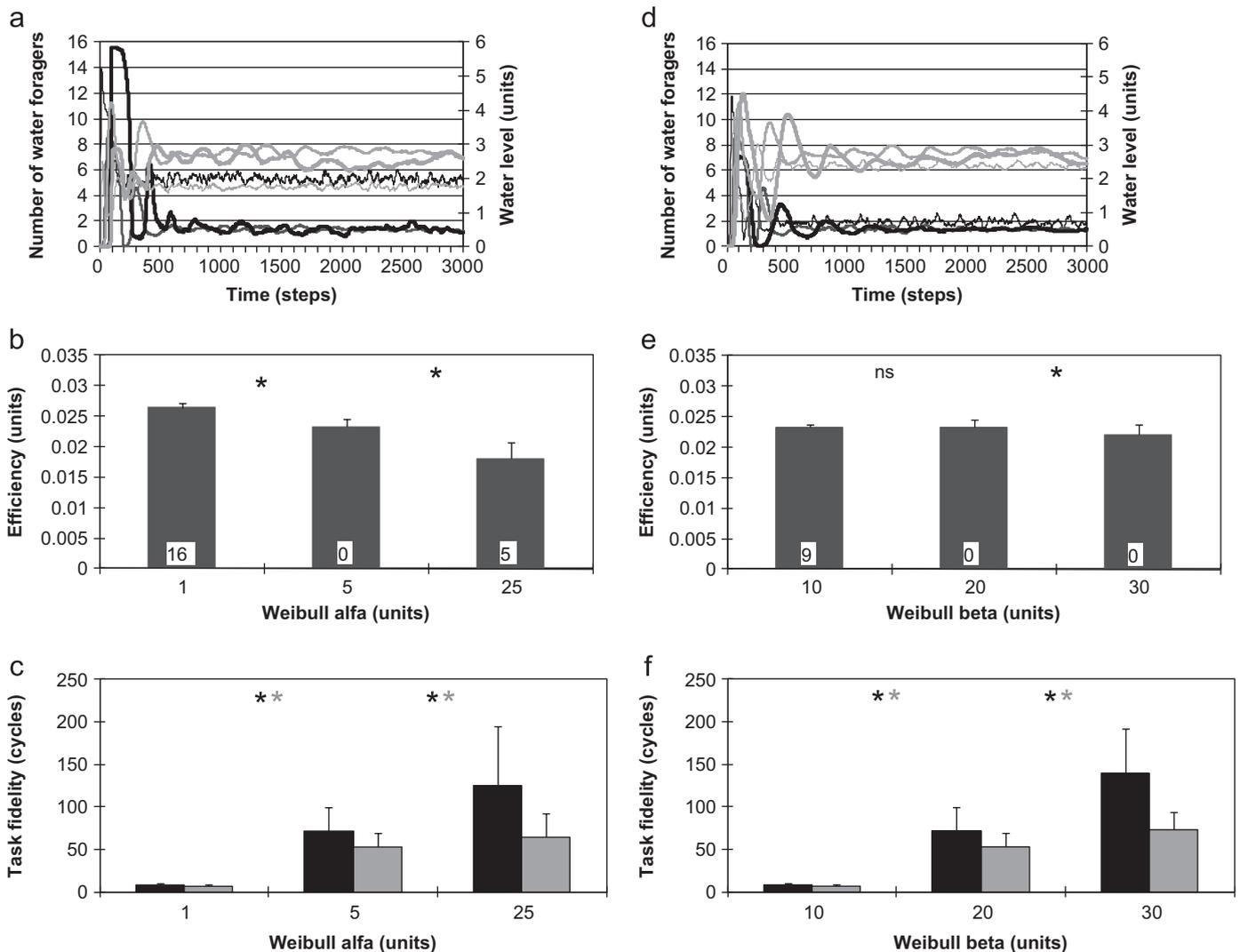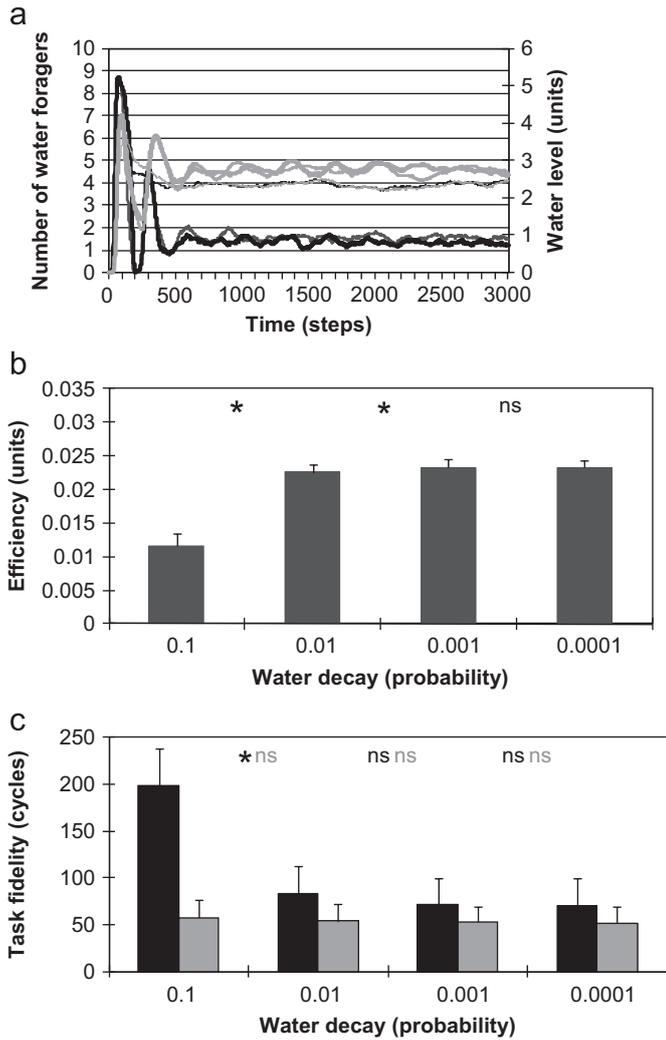
Fig. 6. The effect of Weibull alpha (a)–(c) and Weibull beta (d)–(f) on colony-level performance: (a) and (d) the number of water foragers (black lines) and the water level of the common stomach (gray lines). Thicker lines mean higher value in the parameters (a) Weibull beta=20, Weibull alpha=1, 5, 25; (d) Weibull alpha=5, Weibull beta=10, 20, 30, (b) and (e) colony-level efficiency. Numbers inside the columns indicate the number of failed colonies, (c) and (f) task fidelity of water foragers (black columns) and pulp foragers (gray columns). Average values and standard deviations were calculated from 100 parallel runs (failed colonies were not considered). Significance level: *$p < 0.05$; ns: $p > 0.05$ based on Mann–Whitney U-test.

water foragers resulted in a quick decrease in the water level of the common stomach and in turn the number of pulp foragers decreased. Due to the water shortage, more water foragers were recruited and the system rebounded to its original state within 400 time steps (Fig. 9a). Removing pulp foragers (water users) resulted in an increased water level in the common stomach, which in turn elicited a fast recruiting of pulp foragers and, consequently, the number of water foragers increased as well causing the water level in the common stomach to stay high for 100 time steps. Available workers for construction and interaction became the bottleneck, therefore the foragers reverted to laborers and the system relaxed after few oscillations to the original values (Fig. 9b). Building efficiency significantly decreased when pulp foragers were removed, but removal of water foragers had no effect on the overall efficiency (Fig. 9c). The task fidelity significantly decreased in the perturbed colonies except in the case of the water foragers' task fidelity when pulp foragers were removed (Fig. 9d).

By changing the time interval required to accomplish a task we were able to simulate scenarios where water or pulp were easily ready near the nest site or when building requires more time than

usual. Decreasing time needed to retrieve water ($Tw=1$: simulating an experiment when water is available near the nest) caused a small drop in the number of water foragers, less fluctuation in the water level of the common stomach, and slightly increased the number of pulp foragers (Fig. 10a). Shortening the pulp collecting time ($Tp=1$: simulating a case when a pulp load is provided at the nest to the pulp forager) caused a dramatic drop in the number of pulp foragers and a slight increase in water foragers, while the water level of the common stomach rebounded to the same value (Fig. 10b). When building took longer than usual ($Tb=26$), the number of pulp foragers dropped, the water level of the common stomach increased slightly while the number of water foragers stayed about the same (Fig. 10c). Increasing the time needed to complete a single building cycle resulted in a significant decreased colony efficiency (Fig. 10e) and task fidelity of the foragers (Fig. 10f). Decreasing the time of collecting pulp increased the colony efficiency and also the task fidelity of the decreased number of pulp foragers, while the task fidelity of the water foragers did not differ from the normal run. Decreasing the water foraging time did not change significantly either the colony efficiency or the task fidelity of the foragers (Fig. 10e and f).
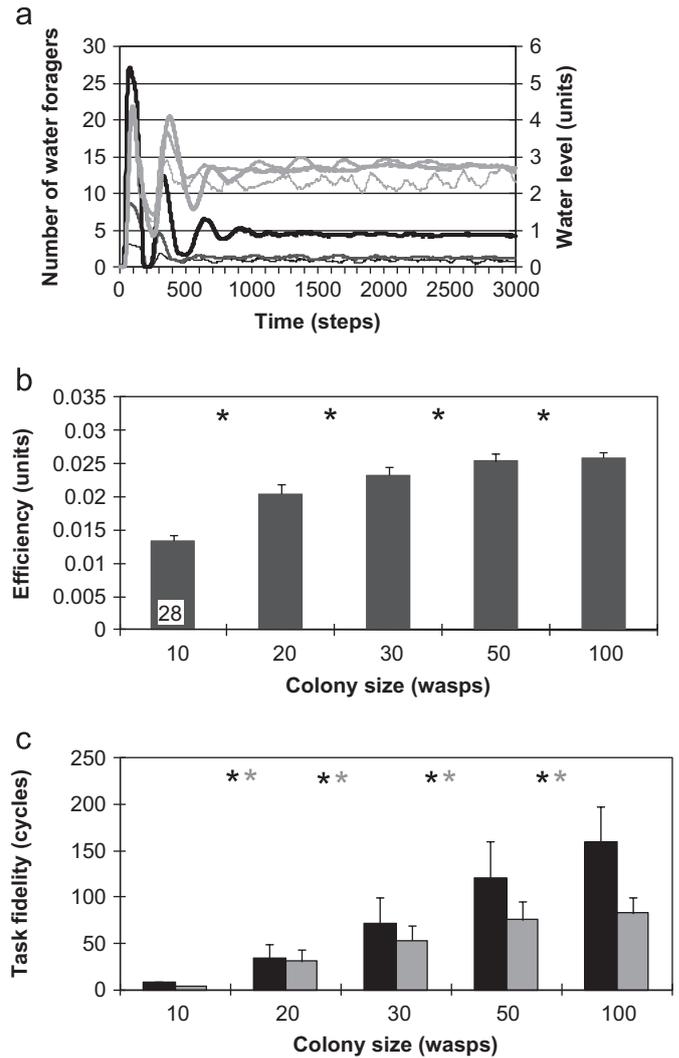
Fig. 7. The effect of water loss (likelihood that a laborer loses 1 unit of water during a time step) on colony-level performance: (a) the number of water foragers (black lines) and the water level of the common stomach (gray lines). Thicker lines mean higher value in the parameters ($Wd=0.1$, 0.01 and 0.001), (b) colony-level efficiency, (c) task fidelity of water foragers (black columns) and pulp foragers (gray columns). Average values and standard deviations were calculated from 100 parallel runs. Significance level: *$p < 0.05$; ns: $p > 0.05$ based on Mann–Whitney U-test.

Fig. 8. The effect of colony size on colony-level performance: (a) the number of water foragers (black lines) and the water level of the common stomach (gray lines). Thicker lines mean higher value in the parameters ($N_a=10$, 30 and 100), (b) colony-level efficiency. Numbers inside the columns indicate the number of failed colonies, (c) task fidelity of water foragers (black columns) and pulp foragers (gray columns). Average values and standard deviations were calculated from 100 parallel runs (failed colonies were not considered). Significance level: *$p < 0.05$; ns: $p > 0.05$ based on Mann–Whitney U-test.

However, when we simulated an experiment where water was applied directly to the surface of the interaction platform (laborers obtain water from the droplets directly, not from the water foragers; and we assumed that all free laborers filled up its crop completely) this decreased the fidelity of the foragers (Fig. 10f), because this perturbation resulted in a strong change in the dynamics (Fig. 10d). The number of water foragers dropped close to zero and stayed there for about 100 time steps, while the number of pulp foragers increased. These in turn led to a quick decrease of the water level of the common stomach followed by the drop in the numbers of pulp foragers and new recruitments of water foragers. The system rebounded after a few damped oscillations and the perturbation did not change the efficiency of the colony significantly (Fig. 10e).

4. Discussion

Our model gave good predictions for both the general responses (Karsai and Wenzel, 1998) and the results of

perturbation experiments that have been done on *Polybia* and *Metapolybia* colonies (Jeanne, 1986, 1996; Karsai and Wenzel, 2000). The current agent based model also showed major agreement with the predictions of our preliminary ODE model (Karsai and Balazsi, 2002) and system dynamic model (Karsai and Schmickl, 2011), in spite of having a different modeling design and structure. Our model provides an alternative mechanism to the threshold models (see Schmickl and Crailsheim, 2011 for a current overview and analyses) and to the chained information flow hypothesis suggested by Jeanne (1996) for the wasps. Our approach shows some similarity to the network models (Gordon et al., 1992; Pacala et al., 1996) in assuming no initial intrinsic differences among the workers and emphasizing the importance of individual interactions, but it is unique as these interactions happen indirectly via the "common stomach" that is both an information center and a storage/buffer for water. We showed that this system is resilient to perturbations and can react quickly to environmental changes. We also showed that the emergence of specialists (wasps with high task fidelity) does not require any
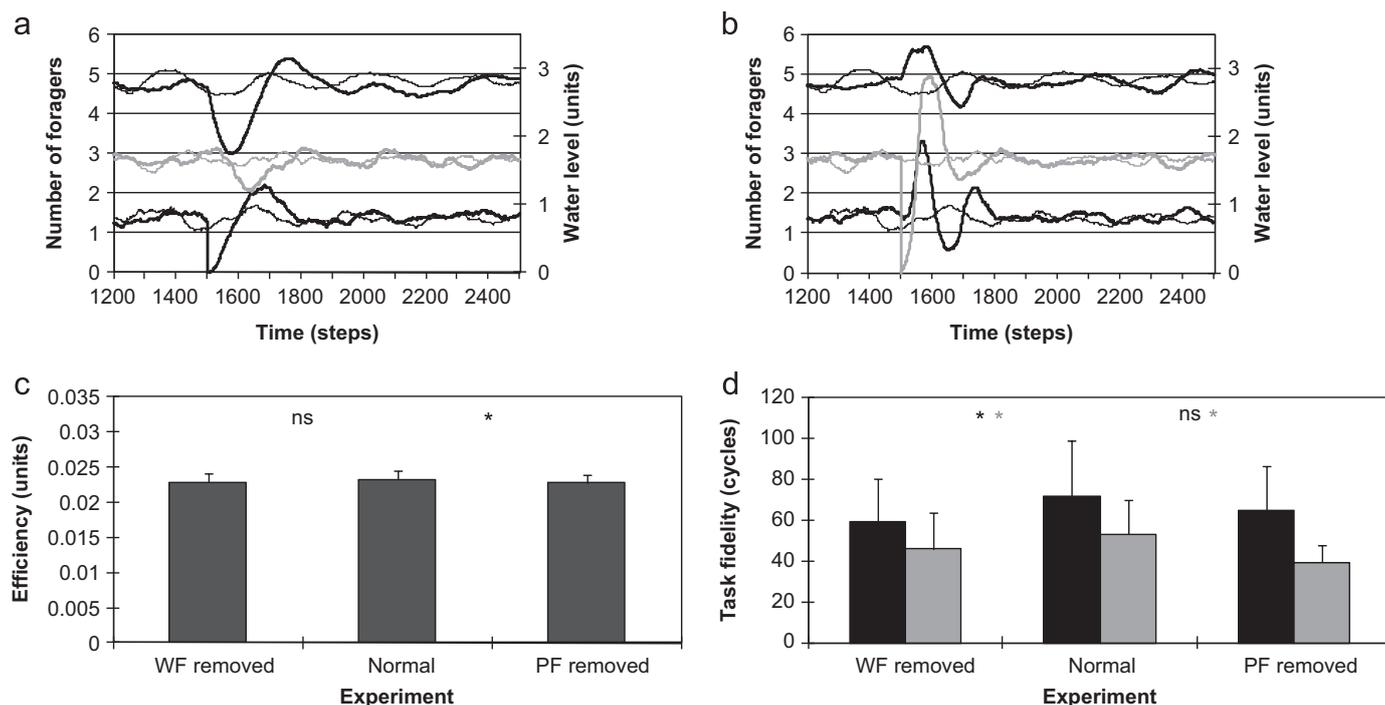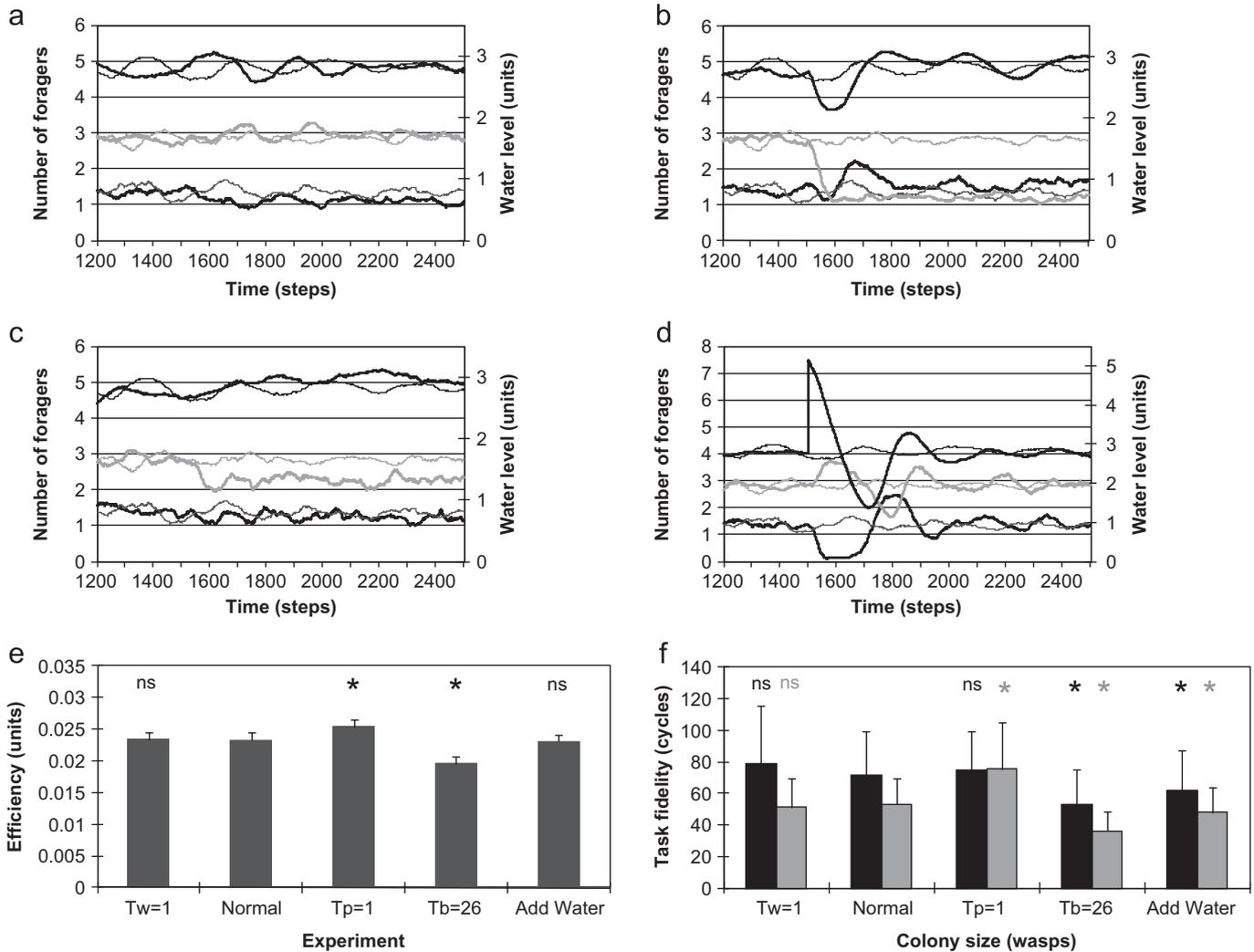
Fig. 9. The effect of colony forager removal on colony-level performance: (a) and (b) average colony dynamics without (thin lines) and with (thick lines) perturbation. (a) Removing all water foragers; (b) removing all pulp foragers at time 1500. Lower black lines: water foragers; gray lines: pulp foragers; upper black lines: water level of the common stomach; (c) colony-level efficiency; and (d) task fidelity of water foragers (black columns) and pulp foragers (gray columns). Average values and standard deviations were calculated from 100 parallel runs. Significance level: $*p < 0.05$; ns: $p > 0.05$ based on Mann–Whitney U-test.

special initial condition or reinforcement at individual level rather it is a consequence of workflow stability stemming from the buffering and information properties of the common stomach and the colony size.

For this model we had minimal assumptions about the individual wasps. We did not consider inherent individual differences, e.g., the effect of age, experience, behavioral syndromes and other properties that we know exist in wasps (O'Donnell and Jeanne, 1990; Karsai and Wenzel, 2000), but they were not necessary to model this system effectively. The mechanisms by which different tasks are allocated among workers of social insects remain poorly known (Gordon, 1996; O'Donnell and Jeanne, 1990; Holldobler and Wilson, 2008), and we still need more study to understand the interplay of mechanisms and adaptive benefits of division of labor in social insects (Dornhaus, 2008; Sumpter, 2010). For example, many theoretical and empirical studies have generated considerable debate about whether the commonly observed correlation of task performance with age should be interpreted as being caused by age of the individual or whether a similar pattern can be generated by other factors independent of age (Franks and Tofts, 1994; Robinson et al., 1994; Franks et al., 1997; Robson and Beshers, 1997; Traniello and Rosengaus, 1997). One of main arguments against age as a causative factor has been that a division of labor generated by age will tend to be inflexible (Tofts and Franks, 1992; Bourke and Franks, 1995). However, Naug and Gadagkar (1999) demonstrated that a flexible age polyethism can emerge in a colony in which the individuals show an age-dependent increase in the levels of activator and inhibitor and the inhibitor is exchanged across individuals in a random fashion (Huang and Robinson, 1992). They showed that a relative age-based division of labor can overcome the problem of inflexibility. Different factors independent of age can generate the observed pattern of correlation of task performance with age. Relative or physiological age can also generate a flexible division of labor that is regulated by a

decentralized mechanism, social interactions and realistic physiological processes (Naug and Gadagkar, 1999). The social (inter-individual) interactions themselves appear to be a possible mechanism by which wasps can assess their relative age in the colony (Naug and Gadagkar, 1998). While our model stresses the flexibility of task switching, which is prevalent in many wasp species (Karsai and Wenzel, 1998, 2000), our model is not excluding that the mechanism we describe would also work in the presence of age polyethism. In this case, for example, some (older) individuals have larger propensity to become a forager than we assumed in our current model. We intended to describe a short term (1 day) behavior of the colony and with minimal assumptions about why a given wasp becomes a forager. Our model rather focuses on how individual interactions are able to balance the workforce without invoking other factors such as genetic dispositions, memory, and experience that are linked generally to a longer time frame.

In wasp societies interactions among workers (called worker connectivity) often play important roles in structuring division of labor (O'Donnell, 2006). Bruyndonckx et al. (2006) provided experimental evidence that dominant–subordinate interactions among the workers may have been co-opted to help workers to self-regulate each other's foraging (Premnath et al., 1995). In other words, dominant–subordinate interactions exhibited by workers can be interpreted as a system of signals informing the extranidal workers, for example, of the hunger levels of the colony's adult and larvae (Gadagkar, 2001; Premnath et al., 1995). O'Donnell (1998a, b, 2001, 2003) found that dominance/biting interactions play an important role in regulating worker foraging in different species. The use of a common stomach or social crop as a way of indirect interaction and information center has been found in ants and bees. Cassill and Tschinkel (1999) found that the division of labor in *S. invicta* ants depends on worker age and size and is fine tuned by ever-changing states of their crop volume and content. Food reserves maintained by

Fig. 10. The effect of different perturbation experiments on colony-level performance. Perturbations were carried out at time 1500; $Tw=1$: time needed for water collection is decreased to 1 time step; $Tp=1$: time needed for pulp collection is decreased to 1 time step; $Tb=26$: time needed for construction is doubled; add water: the crops of all laborer was completely filled ($Wl=6$) at time step 1500. Average colony dynamics without (thin lines) and with (thick lines) perturbation (a) $Tw=1$, (b) $TP=1$, (c) $Tb=26$ and (d) water addition. Lower black lines: water foragers; gray lines: pulp foragers; upper black lines: water level of the common stomach, (e) colony-level efficiency and (f) task fidelity of water foragers (black columns) and pulp foragers (gray columns). Average values and standard deviations were calculated from 100 parallel runs. Significance level: $^*p < 0.05$; ns: $p > 0.05$ based on Mann–Whitney U-test.

honey bee colonies not only ensure homeostasis, but also regulate division of labor in honeybees (Schmickl and Crailsheim, 2004). In another paper we demonstrated that the use of a common stomach can be more efficient in regulating behavior than a regulation based on direct interactions in larger colonies even given the extra interactions involved in indirect communication (Karsai and Runciman, 2009).

It is noteworthy that our model failed to work with some combinations of parameters. These were the cases when colony size was very small and when the job change function described overtly flexible or very unflexible probability functions. In insect societies change in colony size is associated with remarkable and wide-ranging changes in the organization and operation of the colonies (Karsai and Wenzel, 1998; Bourke, 1999; Anderson and McShea, 2001). In this model we wanted to imitate closely the real colonies of mature swarm founding Metapolybia wasps. The parameter range where our model stopped working does not occur in these wasp societies, namely the colony size is always larger and the job change is neither overtly flexible nor rigid (Karsai and Wenzel, 1998, 2000). Small societies of independent founders (non swarm founding wasps) use a different method of

constructing their nest than we described here. They start their colony cycle with one or few wasps and a single individual is able to carry out the entire building sequence (Karsai and Theraulaz, 1995). There is no common stomach, pulp sharing or specialist foragers. Our goals did not include incorporating the construction behavior of these societies, thus our model failed when the parameters were out of the range of the swarm founding societies. This actually agrees with the natural patterns: there is no transition between the two construction strategies. Wasps either found their colonies in swarms or independently (one or very few individuals) and build their nest accordingly (Jeanne, 1999).

Wasps belonging to independent founders can be considered jack-of-all-trades individuals. Swarm founding wasps are also flexible, but instead of substantial individual flexibility we can observe flexibility at colony-level (Karsai and Wenzel, 1998). In our model, each wasp belonged to one of the task groups. For simplicity we assumed that each wasps belonging to a task group behaved exactly the same way. The differences among individuals of the same task group were only those parameters that affect their decision to stay or not stay in the given job (water content

and the number of consecutive unsuccessful interactions). This simplification allowed us to focus on the colony level responses. We suspect that there are several colony-level adaptations (not modeled here) that also play role in the success of these societies. For example we suspect the size of the interaction platform in wasp nests is a consequence of evolutionary pressures that favor mechanisms that allow steady construction by using only a small number of foragers and maximize the number of interactions. The interaction platform where the wasps are interacting is not a definite structure. The laborer wasps can simply set their density around the nest entrance in a way which provides a easily accessible common stomach for the foragers.

The model also mimicked very well the usual workforce mixture found in natural colonies, namely there are only a few foragers and most of the wasps are laborers sitting and waiting on the nest. The laborers will process incoming materials and the decreased efficiency of collecting material (small number of foragers) could increase the ability to handle the material when it arrives to the nest—a strategy found in the task partitioning of leaf cutter ants (Burd and Howard, 2008). The workforce distribution was not coded in our model, but emerged automatically as a consequence of the individual interactions and feedback mechanisms. The workforce distribution with a strong preference toward laborer wasps has two further positive consequences for such a colony: Large numbers of "inactive workers" on the nest are providing useful secondary functions for the colony. They can defend and patrol the nest while they simultaneously hold water in their crops and wait for the foragers to arrive. Keeping the number of foragers low is also beneficial to the colony, as foraging is in general a dangerous task for all social insects (Sakagami and Fukuda, 1968; Ishay et al., 1967). Thus efficient and specialized low number of foragers will minimize the loss of workforce. These individuals will be highly efficient due to the experience they have gained over their frequent trips (Jeanne, 1986). Using a common stomach instead of a direct water transfer system from water foragers to pulp foragers minimizes searching times at the expense of additional nest-bound workers.

At colony-level the simulated wasp society showed qualitatively similar reactions to different perturbation experiments that were carried out in natural colonies (Jeanne, 1996; Karsai and Wenzel, 2000). Removal of foragers decreased the construction, but in different ways. Removing water foragers decreased the fullness of the common stomach and thus decreased the pulp foraging. On the other hand, removing pulp foragers increased the fullness of the common stomach and quickened the recruitment of new pulp foragers which in turn increased the number of water foragers temporarily. In both cases the colony recruited the missing foragers and the colony settled at a new equilibrium. The water forager removal had a less drastic effect (there was no significant decrease in efficiency) on the colony, due to the buffering effect of the common stomach and shorter collection time we suggest. This is also supported by the water addition experiments, which were carried out in both natural and simulated colonies (Jeanne, 1996; Karsai and Wenzel, 2000). When water was applied to the surface of the nest, the laborers quickly absorbed this water and the water foragers quickly converted to laborers since there was no need to collect water. The common stomach filled up which made it possible to recruit as many pulp foragers as could be processed by the builders. On the other hand, building decreased or ceased entirely when water was needed for other activities such as cooling the nest (Karsai and Wenzel, 2000). Changing the availability of pulp or changing the time needed to accomplish a given task also showed similar patterns to those described in natural colonies (Jeanne, 1996; Karsai and Wenzel, 2000).

Perturbations naturally decreased task fidelity, since quick and drastic readjustment of the task force was needed. However,

when steady construction was ensured (no external perturbations) foragers with high task fidelity emerged. Gautrais et al. (2002) described the increase of differentiation and the occurrence of elitism with colony size in a threshold reinforcement model system. The high job fidelity in our model emerged even though there was no intrinsic propensity, threshold adaptation, memory, learning or similar reinforcement that drove an individual to keep a given job. The only parameter which affected the probability of keeping the job is the low number of unsuccessful interactions, which remains low only if the given wasp finds eager partners quickly. As colony size increases the job fidelity of the foragers increases even though there is no encoded mechanism or reward function that keeps the individual at the same job. Through the common stomach the system simply balances itself into an equilibrium where no changes are needed for steady construction. Jeanne (1986, 1996) proposed that foragers are in an off/on mode depending on the needs of the colony and genetic (O'Donnell, 1996, 1998b; Keller, 2009), and other differences (Page and Erber, 2002; O'Donnell and Jeanne, 1992) may exist among individuals that affect the fidelity towards a given task. These contingencies might play important roles, however, we suggest that the basic pattern described by Karsai and Wenzel (1998) of increasing task fidelity as a function of colony size will emerge through simple decision mechanisms via individual interactions without any individual level adaptation.

In our model with increasing colony size the efficiency of the construction also increased. While the increase was significant at higher colony sizes, the absolute value of the increase was small even when the number of wasps were doubled or tripled. It has been a more or less concealed but strong assumption in the literature that the ecological success of social insects stems from division of labor, just as the increase in productivity achieved in human societies (see more in Dornhaus, 2008). Dornhaus (2008) showed that individual efficiency is not changing with colony size and more specialized workers can actually be less efficient than other workers. She argued that in ants without morphologically differentiated workers (as in the wasps studied here), worker allocation to tasks is unrelated to their ability to perform them as an individual. Our approach supports this finding. No specific allocation mechanism is needed to assign specific individuals to carry out specific tasks. The inherent behavioral flexibility of wasp individuals ensures that the wasp can respond to colony needs by interacting with the information center called the common stomach, which is also an important buffer. Sudden changes in material input or work allocation affect the common stomach first. These changes are translated to the water content of the common stomach and over time, these variations are dispersed through the colony at a slow pace (a diffusion-like process), giving the colony enough time to develop counter measures for the disturbance such as intensifying the recruitment of foragers. The larger the colony size, the more efficient this buffer system seems to work (Karsai and Wenzel, 1998; Karsai and Runciman, 2009).

By using the common stomach to regulate their collective construction, swarm founding wasp colonies are successful and efficient without sophisticated individual adaptation and allocation mechanisms. Instead of individual adaptations, parallel processing, paired with task partitioning, is ubiquitous in socially organized entities when the given task is partitioned into subtasks that are connected strongly and sequentially. One of the simplest examples of this arrangement is the bucket brigade, where the material (water) is passed from the collector to the user via transporters (Anderson et al., 2002). Task partitioning (along with related task allocation and switching mechanisms) is, for example, a long standing challenge in computational distributed systems (Bannister and Trivedi, 1983), and swarm robotics (Gerkey and Mataric, 2004). Task partitioning and task allocation

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in distributed computational systems is often based on global all-to-all communication, or it happens in less variable environments with stable swarm size (Gerkey and Mataric, 2004). Hence, we conclude that the ability of wasp societies to evolve task partitioning, organize themselves to perform dynamics task switching, and absorb external perturbation by using distributed self-organizing systems could provide new insights into the regulation mechanisms of both natural and artificial systems.

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