THE EFFECTIVENESS OF THE “COMMON STOMACH” IN THE REGULATION OF BEHAVIOR OF THE SWARM.

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Abstract. Wasp nests are the center of social life and inter-individual interactions for wasp societies, therefore building and maintaining these nests are crucial for the colony. This requires building materials, pulp and water foragers, builders and also an organization of workforce for effective construction. Inspired by the construction behavior of social wasps, an agent based model is presented. Our goal is not to model the exact behavior of wasp societies, but rather to investigate in a more abstract way some of the features of the common stomach. The central hypothesis of this study is that the societies developed a social crop or common stomach which stores water and provides a mechanism for worker connectivity, which in turn regulates building. We show that via the common stomach usage, larger colonies enjoy the benefit of having highly effective foragers, while most of the swarm stays on the nest and only a few engage in highly risky foraging trips. We also demonstrate how colony efficiency changes as a function of colony size and the constitution of the labor distribution, as well as how indirect interactions increase efficiency.

1 Introduction

In social insects, colony-level complexity emerges from simple individual-level behaviors and interactions. 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 [6]. Emergent global properties such as colony size, degree of division of labor (which can be viewed as a consequence of life history traits), may influence individual-level behaviors themselves. Division of labor is one of the most widely studied aspects of colony behavior in insect societies. These studies are commonly 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. However, because colonies and their environments are dynamic in nature, the labor requirements of the colony may change over time, and the division of labor must accommodate to new demands. To meet new labor demands, efficient allocation of individuals to different tasks is required via continuous dynamic adjustments in response to these changes. Colony-level flexibility in response to external changes and internal perturbation is an essential feature of division of labor [2,14]. Colony size seems to correlate with variables on productivity, body size, behavioral flexibility and colony organization. Parallel processing by specialists in large colonies provides flexible and efficient colony-level functioning, while the individual behavioral flexibility of jack-of-all trades workers ensures success of small and early societies [8].

Theoretical and empirical findings on a diverse array of social insect taxa show that interactions among workers (called worker connectivity) often play important roles in structuring division of labor [11]. O’Donnell and Bulova [12] propose several advantages of relying on shared and connected information rather than on the individual agent’s own assessment: 1. Connectivity can allow the sharing of information among more workers, and across greater distances, than direct perception of task stimuli. 2. Connectivity may function to push workers into undesirable tasks, or to overcome task inertia. 3. There is a possibility that “catalytic individuals” with better or more information can propagates the information through the connected colony faster. The possible mechanisms of worker connectivity range from simple encounters with nestmates [4, 13] to specialized communicative displays [17].

Cassill and Tschinkel [3] 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 honey bee colonies not only ensure homeostasis, but also regulate division of labor in honeybees [16] . In social wasps, the

regulation of construction behavior is based on the ability of the colony to store water temporally in the crop of the insects. Using this water both as a building material and as a regulator of construction related activities [9, 10] seems to be a key element in work force allocation. These studies suggested that indirect interactions among workers (worker connectivity) paired with the use of “common stomach” (or social crop) is a very effective way to regulate division of labor.
In this paper our goal is not to model the exact behavior of wasp societies, but rather to investigate in a more abstract way some of the feature of the common stomach. While our model is inspired by the colony regulation of social wasps, the presented model is minimalistic and focuses on the function of the common stomach. Especially, we will investigate that how colony efficiency changes as the function of colony size and the constitution of the task force.

2 The model

The multi-agent simulation is written in Java and simulates the construction behavior of a swarm. Nest-building requires pulp and builders. For the pulp collection the colony needs water and pulp foragers and for the water the colony needs water foragers. For simplicity, we assumed that each agent belongs to a given task group and this will not change during the simulation. Collection of pulp and water happens outside the nest at the pulp and water source respectively (Figure 1). The time required for collecting these materials is parameterized with Tw (water) and Tp (pulp) collecting time, while the given wasp is outside the nest for collecting material. We assumed that there is no any variation in collection times or the amount of water and pulp collected. Construction of the nest is simplified into a sink. Namely, the pulp forager unloads the pulp upon return and start to beg for water in the next turn. The pulp considered to build into the nest by builder wasps that are working outside the interaction platform, so that they were not modeled explicitly. This simplification is in agreement with the normal operation of wasp colonies where builders are generally very abundant compared to foragers and ready to accept the returning pulp promptly [9].

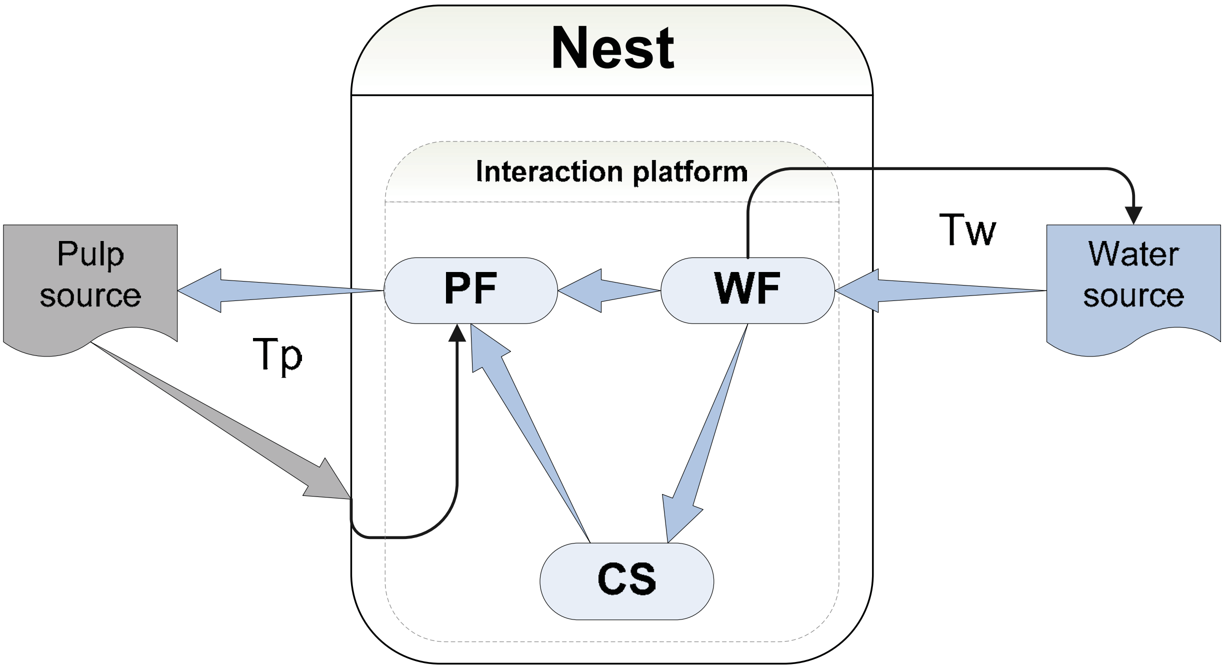

Figure 1. Schematic representation of the wasp nest. Wasp types: WF: water forager; PF: pulp forager; CS: common stomach wasp. Common stomach wasps are able to receive water when empty and able to give water when they are full. Flow of the water is shown by blue arrows. Pulp is transported from pulp source to the nest (gray arrow) and it is given to builders (not modeled explicitly). Builders build the pulp into the nest. Solid arrows show the transition of behavior of unloaded foragers for the next time step.

The simplifications above allowed us to concentrate on the water exchange among individuals that is the main focus of this study. There are 3 types of agents on the interaction platform (Figure 2):

- Water foragers who attempt to download their water load into a common stomach wasp or a pulp forager. When this succeeds they leave the nest for Tw time for collecting water again.

- Pulp foragers, who attempt to collect water from a water forager or a common stomach wasp. When this succeeds, they leave the nest for Tp time for collecting pulp again. For the pulp collection, the pulp foragers use up all their water (i.e., they leave with water and return with pulp).
- Common stomach wasps are either empty or filled with water. When they are empty they will accept water from a water forager, and when they are full they give water to a pulp forager. However, they are not exchanging water with each other.

In each time step, the agents try to land on the interaction platform randomly and interact with a single wasp in a Moore neighborhood (Figure 2). The agent in focus examines how many potential cooperative agents are in the neighbor cells and randomly choose one to interact with. There is no differentiation between the foragers and the common stomach wasps, both are considered as a potential partner in the same way. The rules of interaction are described as simple material transfer: if the states of the interaction are matching (one giver and one receiver) then material transfer happens. No interaction happens if their states are not matching (for example two foragers of the same type interact). If no interaction is possible, because there is no appropriate partner in the neighbor cells in the given time unit, then the agent retains its behavioral state and makes a random landing again on the interaction platform in the next turn. This simplified routine is close to what we can observe in real wasp colonies during a 10 seconds long time interval: the wasp either makes an interaction with a neighbor and material transfer happens or she moves around on the interaction platform [9].

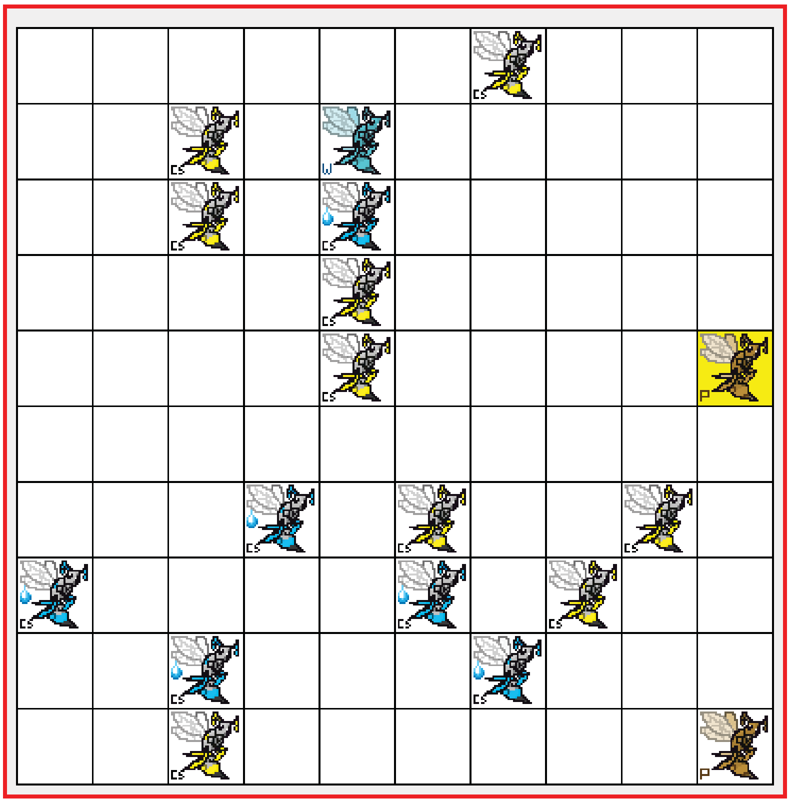

Figure 2. Interactions of workers on the interaction platform. Workers: W with blue color; water forager; P with orange color: pulp forager; CS: common stomach wasp (blue with blue dot: hold water; yellow: empty). Yellow background: currently active individual trying to interact (there is no partner for this pulp forager to interact with in this turn).

The number of delivered pulp load/pulp forager was used as a measure of efficiency in a given colony. Each simulation started with empty common stomach wasps and all forager landed on the interaction platform with full load. To avoid the effect of this colony initiation to the results, the first 100 time steps (about 20 complete foraging cycles) were discarded and only the pulp arrival of the next 100 time steps was measured. Twenty-five parallel runs were made for each colony combination and the average values are presented.

3 Results and discussion

At the first step we compared two very distinguished scenarios: colonies with only foragers (CS:WF:PF=0:1:1) vs. colonies where half of the colony members are common stomach wasps and half of the colony members are foragers (CS:WF:PF=2:1:1). With the increasing swarm size, the number of delivered pulp is increased and the colonies that had only foragers delivered approximately two times more pulp (Figure 3a). Larger colonies were more productive in per capita pulp delivery (Figure 3b), because in larger colonies the densities of the wasps were higher on the interaction platform and they could find appropriate partner in a shorter time. The number of pulps delivered by pulp foragers were higher in every swarm size when the swarm allocated half of its workforce to common stomach wasp instead of foragers with the exception of colony size four (Figure 3c). This indicates that the pulp foragers were more effective when the common stomach is available for indirect material exchange. Using the common stomach for indirect interactions and as a water buffer seems to be less efficient in case of very small colonies, because the extra interactions are involved. On the other hand, when the density is high on the interaction platform (swarm size around 60-70 or larger), the benefit of the common stomach starts to disappear, because with high probability there is at least one appropriate partner in one of the neighbor cells to interact with in each turn, therefore the material transfers are generally not delayed. Direct interactions between water and pulp collectors seem more efficient when the colony is small or when the colony is saturated. However, if collecting pulp requires more time than that of water (as it is frequent in natural colonies [9]), then even the smallest colonies will benefit from the existence of common stomach (Figure 3d). In this case most of the common stomach wasp remain filled up, given that collecting water takes shorter time than collecting pulp, therefore the pulp forager finds water giver wasps with higher probability after she returns.

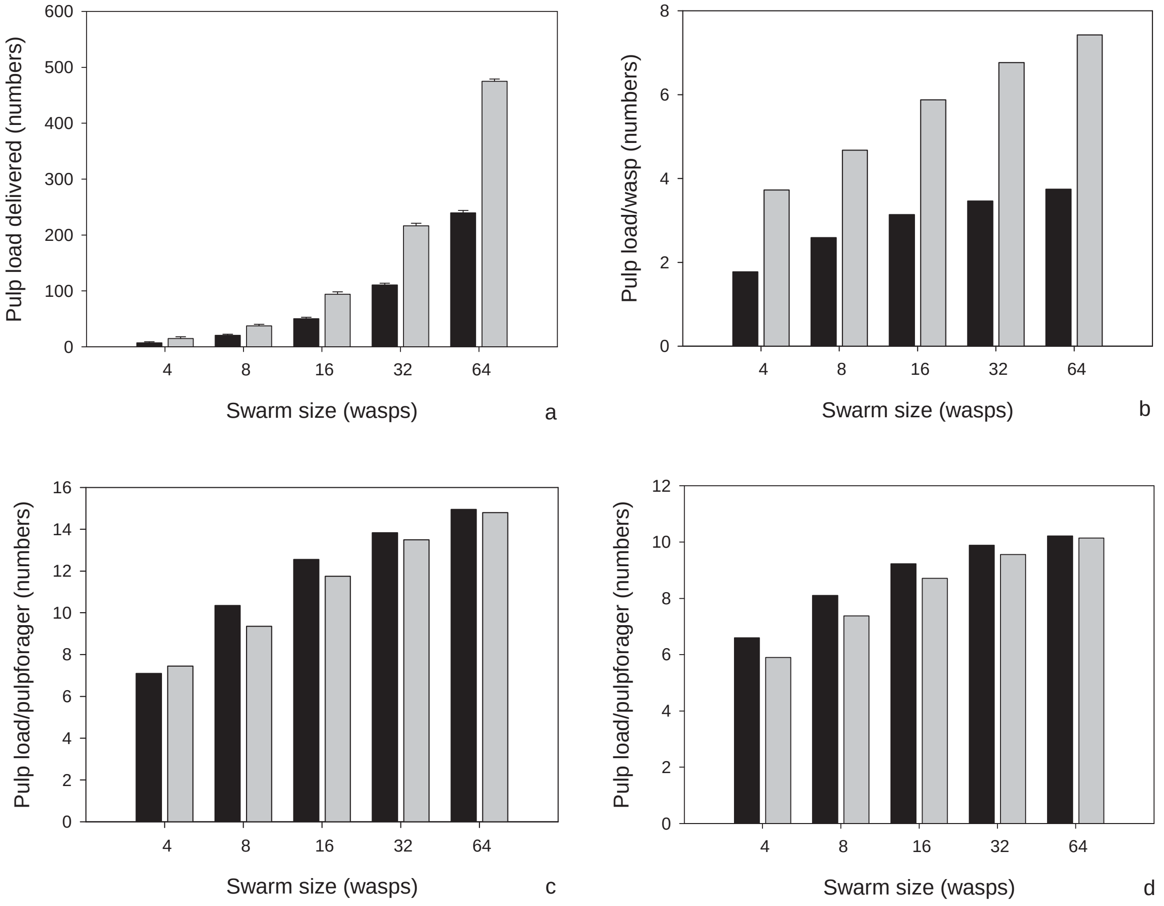

Figure 3. Function of building efficiency (pulp input) as the function of swarm size between time steps 100 and 200. Black columns: 50% of the swarm are common stomach wasp and 25- 25% are pulp and water foragers respectively; grey columns: 50-50% of the swarm are pulp and water forager, respectively. Panel a: total pulp load delivered; panel b: per capita pulp load delivered; panel c: pulp load per pulp forager (Tw=Tp=4); panel d: pulp load per pulp forager (Tw=4, Tp=8).

Examining all possible forager vs. common stomach combinations revealed that the lower boundary of the collected pulp by pulp forager is determined by the number of water foragers (Figure 4, Figure 5). The maximum pulp load per pulp forager is around 18 loads in case of a swarm size between 16 and 64, which is very close to the theoretical maximum (20) where the pulp forager has no any waiting time for finding partners for material exchange. In case of swarm size 32 (Figure 4a), the first combination that is in the range of the highest values have 3 water foragers, one pulp forager and 28 common stomach wasp (arrow). Similar high productivity can be reached via keeping the number of water foragers high or replace the part of the water foragers with common stomach wasps. The increase of the number of pulp foragers will decrease the efficiency of the pulp foragers (Figure 5), due to the competition for water on the interaction platform creating a bottleneck for pulp production. For a natural colony, keeping the number of foragers low has a considerable benefit; leaving the nest for foraging is dangerous and the mortality rate of foragers is generally high in social insects [15]. Using the minimum number of foragers with the maximum number of common stomach wasp provides maximum efficiency for the few pulp foragers with the minimum risk of losing these experienced specialists (as knowing the position of resources involves learning on the part of the forager).

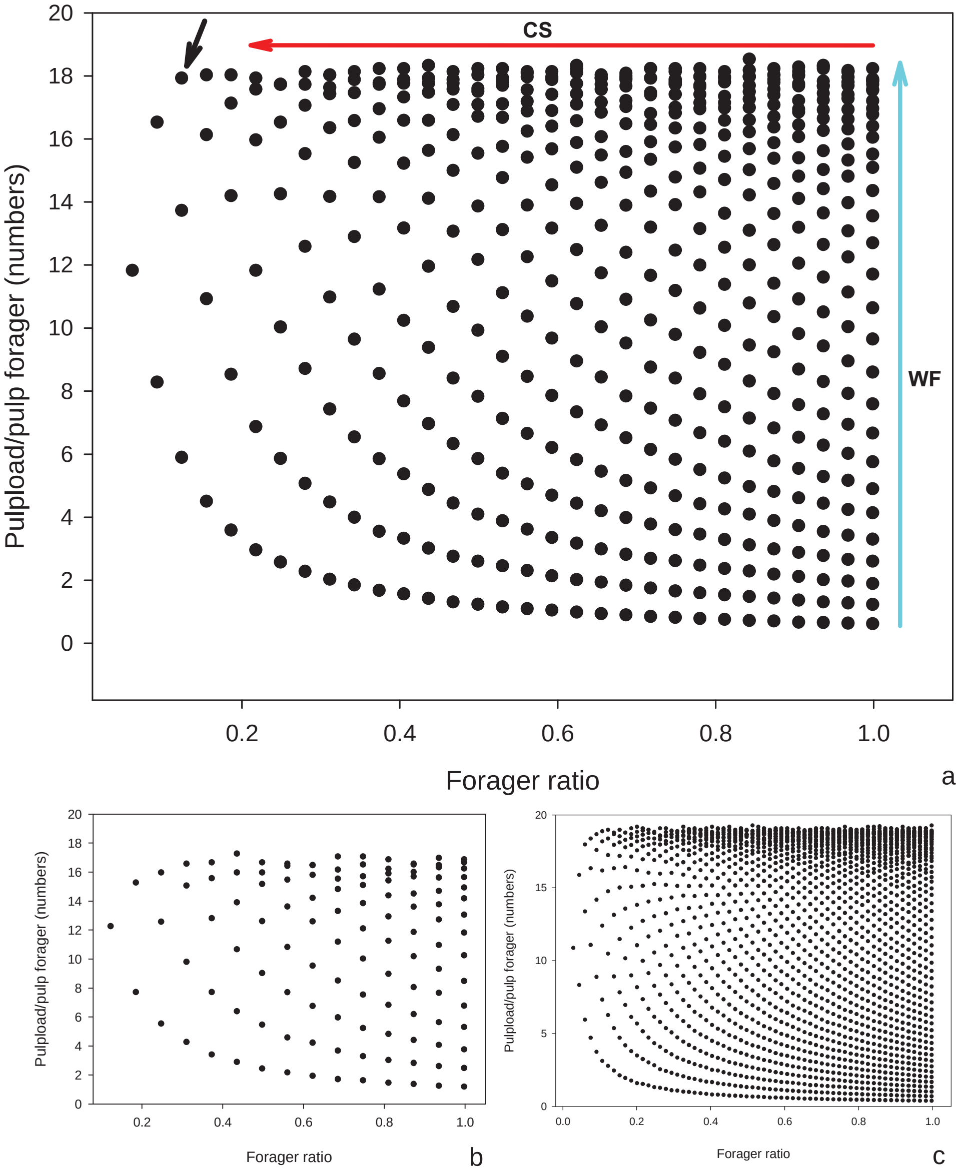

Figure 4. Effectiveness of the pulp forager (pulp load/pulp forager: pulp delivered by a single pulp forager between 100 and 200 time steps) as the function of the forager ratio ((WF+PF)/swarm size) in the swarm. Dots with the same forager ratio represents different WF and PF mix while the total number of foragers stays the same. Blue arrow shows how the number of water foragers increases in the mix. Red arrow shows how the number of common stomach wasps increases in the mix. Black arrow shows the first highly productive colony with 1 pulp forager 3 water foragers and 28 common stomach wasps. Colony size a: 32 b: 16, c: 64. Average values of 25 simulations.

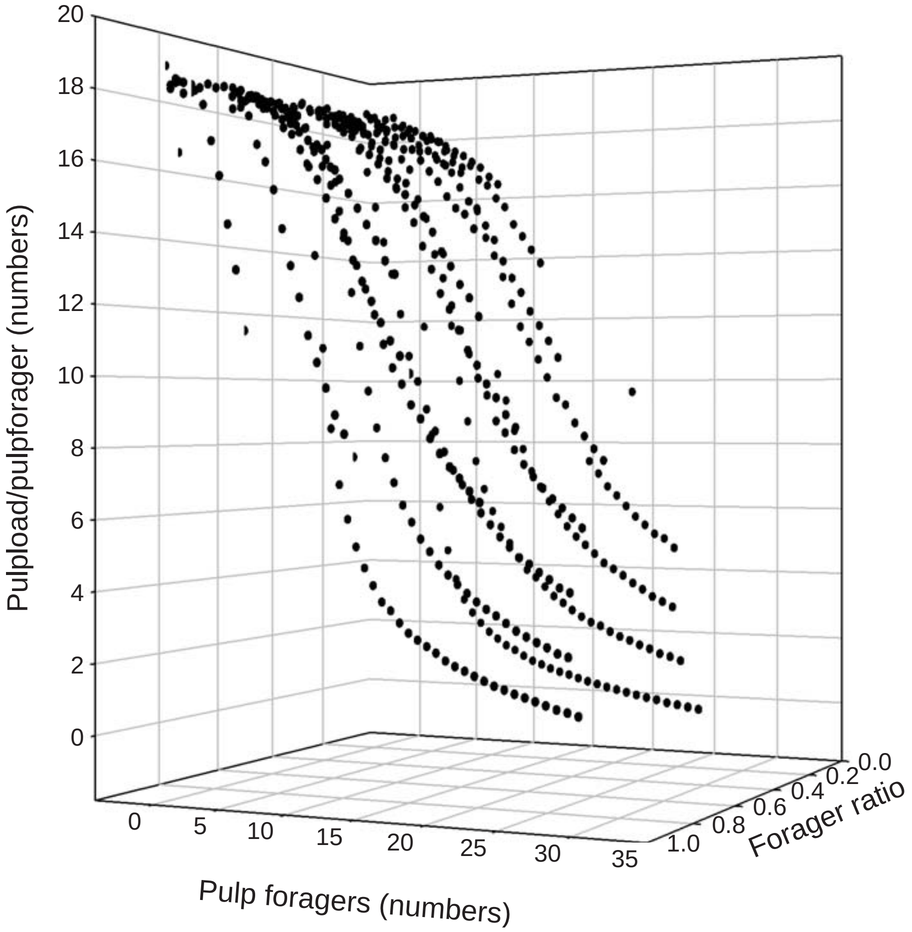

Figure 5. . Effectiveness of the pulp forager (pulp load/pulp forager: pulp delivered by a single pulp forager between 100 and 200 time steps) as the function of the forager ratio ((WF+PF)/swarm size) and the number of pulp foragers in the swarm. Dots with the same forager ratio represents different WF and PF mix while the total number of foragers stays the same (see figure 4 for more explanation). Highly effective pulp foragers exist in colonies where there is more common stomach wasps and water forager and less pulp forager. Average values of 25 simulations of swarm size 32.

Our findings imply that the effective and low risk use of worker force via worker connectivity (common stomach) is reliant upon larger colony sizes. The benefit of organizing colony level performance through worker connectivity may function as an important evolutionary pressure for increasing colony size for insect societies. Our studies showed that the usage of the common stomach wasps decreases the number of foragers and maximizes the effectiveness of the pulp forager. Using the common stomach as a regulator and buffer also keeps most wasps on the nest where they can provide additional work while they hold water, such as patrolling, defense, and cooling the nest. Only a few foragers need to take up the risky trips to the resources, and these individuals will be highly effective due to experience gained by the frequent trips [7].

Our goal with the current model was to study the effect of swarm size and division of labor on the efficiency of construction. Further studies are required to build more elaborated agent-based models for the wasp societies and in general. In our current model, the tasks of the agents did not change. While this is a realistic assumption in short term, the wasps do change behavioral profiles or adapt to the colony needs as real wasps have been shown to do [9]. Our preliminary studies show that these adjustments also depend on the state of the common stomach, [8, 9, 10] and we intend to investigate this further. Self-organization is a powerful theory to explain how minimal complexity at the individual level can generate much greater complexity at the collective level. Recently, we have more and more evidence that although genetic, physiological, and other aspects must be taken into account [6], division of labor is an emergent property of the society [1,5]. Using common stomach or social crop seem to be an efficient mechanism of self-organization in the behavior of the swarm.

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5 References

[1] Beshers, S. N. and Fewell, J. H. *Models of division of labor in social insects*. Annu. Rev. Entomol., **46,** (2001), 413-440.

[2] Calabi, P. *Behavioral flexibility in Hymenoptera: a re-examination of the concept of caste. Advances in Myrmecology*. (Ed: Trager, J. C.), Brill Press, Leiden, 1988, 237-258.

[3] Cassill, D. L. and Tschinkel W. R. *Task selection by workers of the fire ant Solenopsis invicta*. Behav. Ecol. Sociobiol. **45**, (1991), 301-310.

[4] Gordon, D. M., Paul, R. E. H. and Thorpe, K. *What is the function of encounter patterns in ant colonies?* Anim. Behav., **45**, (1993), 83-100.

[5] Gordon, D. M. *The organization of work in social insect colonies*. Complexity **8**, (2003), 43 – 46.

[6] Holldobler, B. and Wilson, E. O. *The Superorganism. The Beauty, Elegance and Strangeness of insect Societies*. W. W. Norton & Company. NY, 2008.

[7] Jeanne, R. L. *The organization of work in Polybia occidentalis: costs and benefits of specialisation in a social wasp*. Behav. Ecol. Sociobiol., **191**, (1986), 333–341.

[8] Karsai, I. and Wenzel, J. W. *Productivity, individual-level and colony-level flexibility, and organization of work as consequences of colony size.* Proceedings of the National Academy of Sciences of the United States of America, **95**, (1998), 8665-8669.

[9] Karsai, I. and Wenzel, J. W. *Organization and regulation of nest construction behavior in Metapolybia wasps*. Journal of Insect Behavior, **13**, (2000), 111-140.

[10] Karsai, I. and Balazsi, G. *Organization of work via a natural substance: regulation of nest construction in social wasps*. Journal of Theoretical Biology, **218**, (2002), 549-565.

[11] O'Donnell, S. *Polybia wasp biting interactions recruit foragers following experimental worker removals.* Anim. Behav., **71**, (2006), 709-715.

[12] O'Donnell, S. and & Bulova, S. J. *Worker connectivity: a review of the design of worker communication systems and their effects on task performance in insect societies*. Ins. Soc., **54**, (2007), 203-210.

[13] Pratt, S. C. *Quorum sensing by encounter rates in the ant Temnothorax albipennis*. Behavioral Ecology, **16**, (2005), 488-496.

[14] Robinson, G. E. *Regulation of division of labor in insect societies*. Annu. Rev. Entomol., **37**, (1992), 637-665.

[15] Sakagami, S. F. and Fukuda, H. *Life tables for worker honeybees*. Res. Popul. Ecol. **10,** (1968), 127–139.

[16] Schmickl, T. and Crailsheim, K. *Inner nest homeostasis in a changing environment with special emphasis on honey bee brood nursing and pollen supply*. Apidologie **35**, (2004), 249-263.

[17] Sherman, G. and Visscher, P. K. Honeybee colonies achieve fitness through dancing. Nature, **419**, (2002), 920-922.