The Common Stomach as a Center of Information Sharing for Nest Construction

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Abstract. Construction of wasp nests is a self organized process that requires building materials, pulp and water foragers, and builders to cooperate. In this paper we study how the society of agents use a social crop, or common stomach, to store water that also provides a mechanism for worker connectivity, which in turn regulates building. Our model predicts that via the common stomach usage, medium sized colonies enjoy the benefit of having highly effective foragers and this in turn means that the colonies need only endanger a few foragers to ensure steady construction. When pulp foraging becomes more costly than water foraging, the colonies adjust via recruiting more pulp foragers and less water foragers, but keep high numbers of common stomach wasps on the nest. The common stomach provides an adaptable platform for indirect worker connectivity and a buffer for water storage.

Keywords: communication, swarm, social insect, superorganism, agent.

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 [1]. The ability of social insects to divide the colony's work via specialization, polyethism, and task partitioning has fascinated scientists for centuries. Many of these studies are commonly concerned with the integration of the individual worker behavior into colony-level task organization and with the question of how regulation of division of labor may contribute to colony efficiency. For example, bee colonies collect food from flowers, whose abundance varies strongly in space and time. Finding these resources requires considerable search effort [2] and effective foraging by the colony depends on an appropriate allocation of bee workers to exploration versus exploitation (collection of food from known resources) [3].

Colony-level flexibility in response to environmental changes and internal perturbations is an essential feature of division of labor [4, 5]. The actual number of workers allocated to different tasks is a result of the individual decisions made by these workers, which in turn are based on information available to these individuals through direct and indirect communication with their nest-mates and the environment. The collective colony-level pattern is therefore self-organized, without a central leader or

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template directing individuals to particular resources. Colony size correlates with productivity, body size, behavioral flexibility and colony organization [6].

Studies 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 [7]. O'Donnell and Bulova [8] propose that relying on shared and connected information can be beneficial: 1. Connectivity permits sharing of information among more workers and across greater distances than direct perception of stimuli. 2. Connectivity can foster task switching or can overcome task inertia. 3. "Catalytic individuals" with better or more information can propagate the information through the connected colony faster. The possible mechanisms of worker connectivity range from simple pair-wise encounters [9, 10] to specialized communicative displays [11].

While pheromones and dances are well-developed communication systems, even bees and ants use a wide variety of other types of communication to regulate or fine tune their division of labor [12]. For example, Cassill and Tschinkel [13] found that the division of labor in *S. invicta* ants depends on worker size and age and is fine tuned by the states of their crop volume and content. In honeybees, food reserves not only ensure homeostasis, but also regulate division of labor [14]. In social wasps, construction behavior is regulated indirectly by the temporally stored water in the crop of the insects [15, 16].

In this paper our goal is not to construct a detailed model the behavior of wasp societies, but rather to investigate in a more abstract way some important features of the common stomach. While our model is inspired by the colony regulation of wasps, the presented model is minimalistic; our agents are much simpler than the wasps, and we focus on the function of the common stomach rather than on the dynamically evolving agents. Specifically, we investigate how colony efficiency changes as a function of colony size and the constitution of task force. We also demonstrate how colony efficiency changes with the increase of the time cost of pulp foraging.

2 The Model

We constructed a multi-agent model (implemented in Java) inspired by the nest construction of Metapolybia wasps [15]. Nests are built by builder wasps using wooden pulp. For collecting pulp, 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 predetermined task group and her job does not change. Our goal was to focus on short term efficiency and to study the efficiency of different workforce combinations. For a more complex approach of the same phenomena see [16].

Collection of water and pulp take place outside the nest at the water and pulp source respectively (Fig. 1). The time required for collecting these materials is parameterized with Tw (water) and Tp (pulp) which represent the time in which the forager wasp is outside the nest collecting materials. We assumed that there is no variation in collection times or the amount of water and pulp collected. Collection of pulp generally takes longer [15] and we explicitly studied the effect of collecting time and the effectiveness of different colony compositions. Construction of the nest is simplified into a sink and the shape and the size of the nest do not change or play any role in this model. The pulp is considered to build into the nest by builder wasps that are working outside the interaction platform (therefore they were not modeled explicitly). Upon arrival the pulp forager unloads the pulp (into a sink that represents nest building) and starts to collect water on the interaction platform in the next turn. This simplification is in agreement with the usual operation of wasp colonies where individuals that are willing to build are generally abundant and they ready to accept the pulp promptly from the pulp forager [15].

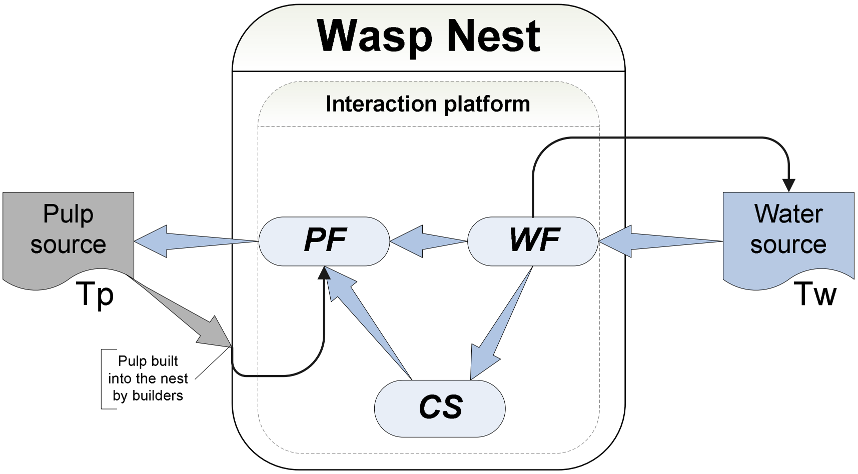

Fig. 1. Schematic representation of the wasp nest. Wasp types: water forager (*WF*); pulp forager (*PF*); common stomach wasp (*CS*). Common stomach wasps are able to receive water when empty and able to give water when they are full. Flow of the water (*blue arrows*), pulp transported from pulp source to the nest (*gray arrow*). Pulp is given to builders (not modeled explicitly). Transition of behavior of unloaded foragers for the next time step (*solid arrows*).

The simplifications above permitted us to focus on the water exchange among individuals as the main focus of this study. There are three types of agents on the interaction platform (Fig. 2):

- Common stomach wasps are either empty or filled with water. When they are empty they accept water from a water forager, and when they are full they give water to a pulp forager. However, they do not exchange water with each other.
- Pulp foragers attempt to collect water from a common stomach wasp or from a water forager. After this happens, they leave the nest for Tp time for collecting pulp. The pulp foragers use up all their water for the pulp collection (i.e., they leave with water and return only with pulp).
- Water foragers attempt to download their water load into a pulp forager or a common stomach wasp. After this happens, they leave the nest for Tw time for collecting water.

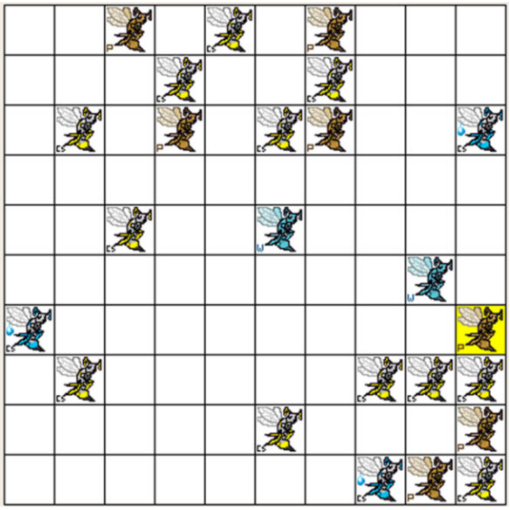

Fig. 2. Interactions of agents on the interaction platform. Wasps: water forager (*W: blue color*); pulp forager (*P: orange color*); common stomach wasp (*CS: blue with blue dot: holding water; yellow: empty*). Currently active pulp forager (*yellow background*) are able to receive water from a W agent in its Moore neighborhood. The two CS agent in its neighborhood are empty and cannot interact with this pulp forager in this turn.

In each time step, the agents attempt to land on the interaction platform randomly and interact with a single wasp in a Moore neighborhood (Fig. 2). The agent in focus examines how many potential cooperative agents are in the neighbor cells and randomly chooses one to interact with. Both foragers and common stomach wasps are considered a potential partner in the same way. For example, both a water forager and a common stomach wasp that hold water can give water to the pulp forager wasp. 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. If no interaction is possible, 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 second long time interval: the wasp either makes an interaction with a neighbor and material transfer happens or she moves around on the interaction platform [15]. The small size of the interaction platform and the speed the wasps travel between material exchanges allowed us to simplify the movement patterns to a series of random landings.

The number of delivered pulp load divided by the number of foragers (PF+WF) was used as a measure of efficiency in a given colony. We assumed that colonies which operate with fewer foragers and provide high pulp input are more effective, because it results in a high construction rate with a minimized risk of losing foragers to predation. Each simulation started with empty common stomach wasps and all foragers landed on the interaction platform with full load. To avoid the effect of this colony initiation, 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. The average of twenty parallel runs for each colony combination was calculated and used.

3 Results

First, we compared two very distinct scenarios: colonies which only operate with foragers (CS:WF:PF=0:1:1) versus 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 increasing colony size, the amount of pulp delivered to the nest is larger [17] because of the increasing number of pulp foragers. Colony efficiency (pulp delivered/number of foragers) is significantly higher (MW U test $p<0.05$, $N=40$) in case of a larger colony size in both scenarios (Fig. 3).

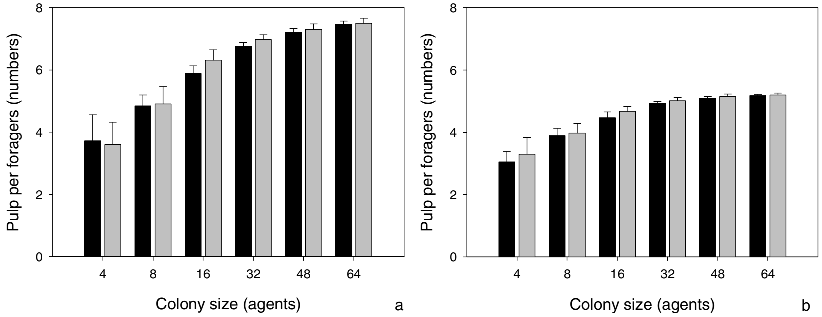

Fig. 3. Construction efficiency (total pulp returned/(WF+PF)) (*average and std.dev*) as a function of colony size. Workforce: 50% of the colony is common stomach wasp and 25- 25% are pulp and water foragers, respectively (*grey*); 50-50% of the colony are pulp and water foragers, respectively (*black*). Panel a: Tw=Tp=4; panel b: Tw=2, Tp=8.

When pulp foraging was 4 times more time consuming than water foraging (Fig 3, a vs.b), the efficiency of the colonies was significantly smaller (MW U test $p<0.05$, $N=40$) except in the smallest colony size where common stomach wasps were also present (MW U test $p>0.1$ (two tailed), $N=40$). Comparing the effectiveness of the 2 scenarios at each colony size showed significant differences (MW U test $p<0.05$, $N=40$) at colony sizes 16, 32 and 48, and the same pattern also emerged when pulp foraging was more time consuming. These indicated that using non-forager common stomach wasps can result in a more efficient solution for middle-sized colonies in these special mixes of workforces (Fig 3).

After studying two specific combinations of workforce along the wide range of population size above, we focused on two colony sizes (8 and 48), but generated all possible workforce combinations. In cases of small colonies when collection of pulp and water took the same time (TP=TW=4) the most effective workforce combination consists of 6 common stomach wasps, and 1 pulp and water forager, respectively.

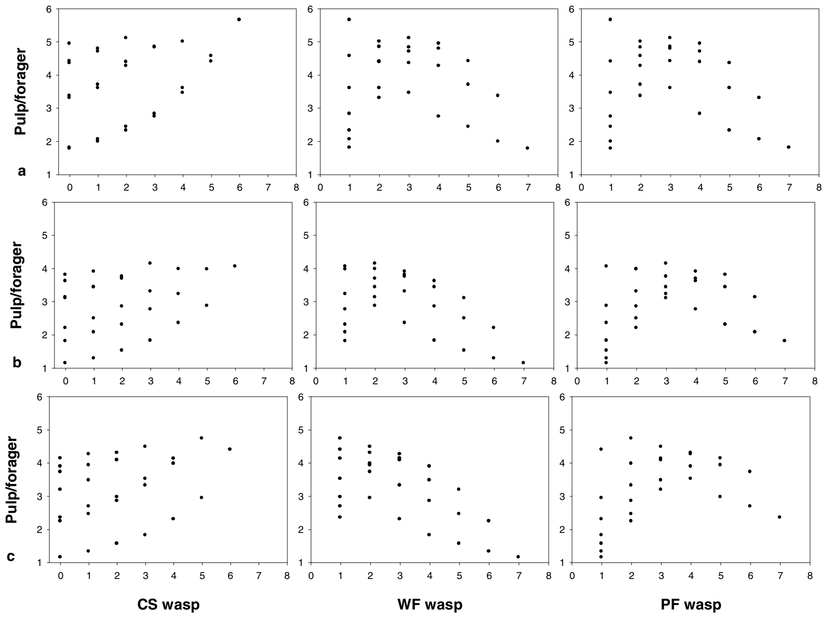

Fig. 4. Average efficiency (*dots*) of every possible workforce combination in small (8 individuals) colonies. Efficiency (pulp delivered/(WF+PF)) are calculated from 20 parallel runs of the same type of colony mix; a: TP=TW=4; b: TW=4, TP=8, c: TW=2, TP=8.

The increase of the number of foragers beyond 2-3 foragers clearly decreased the efficiency. On the other hand, as the number of common stomach wasps increased the efficiency (especially its lower bound) increased. Making pulp foraging more costly than water foraging (Fig. 4. b, c) resulted in a similar picture with a slight preference for more foragers. When pulp foraging was very costly, the most effective mix consisted of 5 common stomach wasps, 2 pulp foragers and 1 water forager (Fig 4 c).

In the larger colonies (colony size 48), the main trends were similar to the observed patterns of small colonies, but due to the larger workforce, there were a larger number of highly effective combinations (Fig. 5). The most effective colonies consist of a few foragers of both types and many common stomach wasps, but there were other combinations with less common stomach wasps and more foragers that provided only slightly less efficiency. When foraging for the two resources required the same time (Tw=Tp=4), then if either forager types dominated in numbers (more than half of the colony belonged to that forager types), the effectiveness of the colony is dropped sharply. As the time cost of pulp foraging increased compared to water foraging, the effective colonies had fewer water foragers, but they operated with high range (5-35) of pulp foragers (Fig 5. c). However, even in this case the most effective colonies are operated by small number of foragers and large number of common stomach wasps.

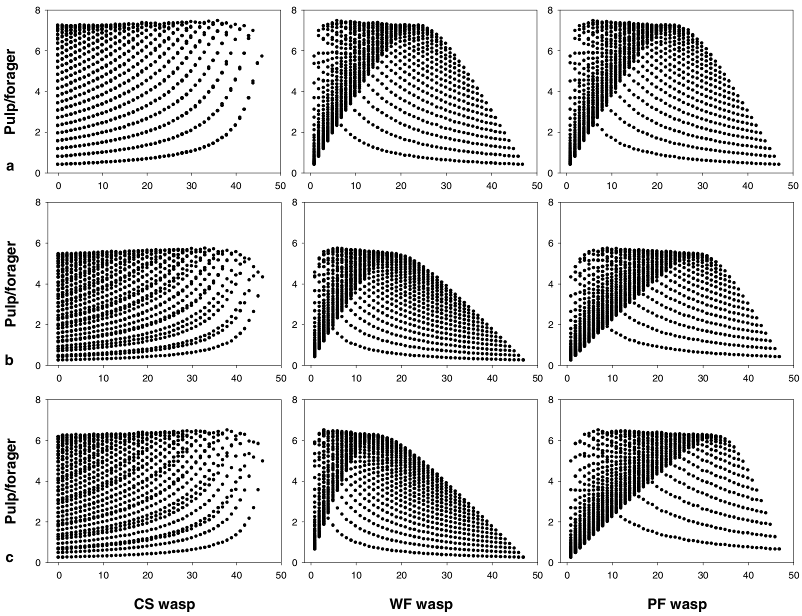

Fig. 5. Average efficiency (*dots*) of every possible workforce combination in large (48 individuals) colonies. Efficiency (pulp delivered/(WF+PF)) are calculated from 20 parallel runs of the same type of colony mix; a: TP=TW=4; b: TW=4, TP=8, c: TW=2, TP=8.

4 Conclusions

Our model predicted that the effective and low risk use of worker force via worker connectivity (common stomach) is affected by both colony size and the time required for retrieving the resources. We showed that the usage of the common stomach was beneficial in most cases, except if the density of the wasps is very low (hard to find partners) or very high (easy to find a partner for direct transmission). The size of the interaction platform could be a consequence of evolutionary pressures that prefer to keep most wasps on the nest. The regulation mechanism we presented is also able to adapt to the changing cost of resource collection via adjusting the number of foragers, but still retaining high number of common stomach wasp to ensure highly effective low-risk foraging. Using the common stomach as a regulator and buffer also provides secondary advantages in the form of additional work that these common stomach wasps can provide while they hold water, such as patrolling, defense and so on. Keeping the number of foragers low is beneficial, because foraging is dangerous [18]. By using the common stomach, 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 [19]. Using the common stomach or social crop seems to be an efficient self-organizing mechanism for regulation of work of agents.

Acknowledgments

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References

1. Holldobler, B., Wilson, E.O.: The Superorganism. The Beauty, Elegance and Strangeness of insect Societies. W. W. Norton & Company, New York (2008)
2. Seeley, T.D.: Honeybee ecology. A study of adaptation in social life. Princeton University Press, Princeton (1985)
3. Bartholdi, J.J., Seeley, T.D., Tovey, C.A., Vande Vate, J.H.: The Pattern and Effectiveness of Forager Allocation Among Flower Patches by Honey Bee Colonies. J. Theor. Biol. 160, 23–40 (1993)
4. Calabi, P.: Behavioral flexibility in Hymenoptera: a re-examination of the concept of caste. In: Trager, J.C. (ed.) Advances in Myrmecology, pp. 237–258. Brill Press, Leiden (1988)
5. Robinson, G.E.: Regulation of division of labor in insect societies. Annu. Rev. Entomol. 37, 637–665 (1992)
6. Karsai, I., Wenzel, J.W.: Productivity, individual-level and colony-level flexibility, and organization of work as consequences of colony size. PNAS USA 95, 8665–8669 (1998)
7. O'Donnell, S.: Polybia wasp biting interactions recruit foragers following experimental worker removals. Anim. Behav. 71, 709–715 (2006)
8. O'Donnell, S., 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, 203–210 (2007)
9. Gordon, D.M., Paul, R.E.H., Thorpe, K.: What is the function of encounter patterns in ant colonies? Anim. Behav. 45, 83–100 (1993)
10. Pratt, S.C.: Quorum sensing by encounter rates in the ant Temnothorax albipennis. Behav. Ecol. 16, 488–496 (2005)
11. Sherman, G., Visscher, P.K.: Honeybee colonies achieve fitness through dancing. Nature 419, 920–922 (2002)
12. Dornhaus, A.: Finding optimal collective strategies using individual-bases simulations: colony organization in social insects. In: Troch, I., Breitenecker, F. (eds.) Proceedings MATHMOD 2009, Vienna, pp. 888–894 (2009)
13. Cassill, D.L., Tschinkel, W.R.: Task selection by workers of the fire ant Solenopsis invicta. Behav. Ecol. Sociobiol. 45, 301–310 (1991)
14. Schmickl, T., Crailsheim, K.: Inner nest homeostasis in a changing environment with special emphasis on honey bee brood nursing and pollen supply. Apidologie 35, 249–263 (2004)
15. Karsai, I., Wenzel, J.W.: Organization and regulation of nest construction behavior in Metapolybia wasps. Journal of Insect Behavior 13, 111–140 (2000)
16. Karsai, I., Balazsi, G.: Organization of work via a natural substance: regulation of nest construction in social wasps. J. Theor. Biol. 218, 549–565 (2002)
17. Karsai, I., Runciman, A.: The effectiveness of the "common stomach" in the regulation of behavior of the swarm. In: Troch, I., Breitenecker, F. (eds.) Proceedings MATHMOD 2009, Vienna, pp. 851–857 (2009)
18. Sakagami, S.F., Fukuda, H.: Life tables for worker honeybees. Res. Popul. Ecol. 10, 127–139 (1968)
19. Jeanne, R.L.: The organization of work in Polybia occidentalis: costs and benefits of specialization in a social wasp. Behav. Ecol. Sociobiol. 191, 333–341 (1986)