Journal of Theoretical Biology 294 (2012) 98–113

Contents lists available at SciVerse ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

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

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ARTICLE INFO

Article history:
Received 10 June 2011
Received in revised form
27 October 2011
Accepted 31 October 2011
Available online 7 November 2011

Keywords:
Common stomach
Regulation of behavior
Social wasp
Agent based model
Social crop

ABSTRACT

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.

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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doi:10.1016/j.jtbi.2011.10.037

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