



Self-complexification through integral feedback in eusocial paper wasps of various levels of sociality

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ABSTRACT

We investigate how simple physical interactions can generate remarkable diversity in the life history of social agents using data of social wasps, yielding complex scalable task partitioning. We built and analyzed a computational model to investigate how diverse task allocation patterns found in nature can emerge from the same behavioral blueprint. Self-organizing mechanisms of interwoven behavioral feedback loops, task-dependent time delays and simple material flows between interacting individuals yield an emergent homeostatic self-regulation while keeping the global colony performance scalable. Task allocation mechanisms based on implicitly honest signaling via material flows are not only very robust but are also highly evolvable due to their simplicity and reliability. We find that task partitioning has evolved to be scalable and adaptable to life history traits, such as expected colony size or temporal bottlenecks in the available workforce or materials. By tuning solely the total number of agents and a social connectivity-related parameter in the model, our simulations yield the whole range of emergent patterns in task allocation and task fidelity akin to observed field data. Our model suggests that the material exchange (“common stomach mechanism”) found in many paper wasps provides a common functional “core” across these genera, which not only provides self-regulation of the colony, but also provides a scalable mechanism allowing natural selection to yield complex social integration in larger colonies over the course of their evolutionary trajectory.

1. Introduction

Complex adaptive systems are characterized as such when patterns emerge on upper system levels due to both localized interactions and selection processes acting at lower system levels [1]. Such systems are characterized by nested hierarchical networks of components which are organized as interconnected modules [2,3] and exhibit nonlinear dynamics with multiple possible outcomes [4].

Complex adaptive systems are composed of multiple components and can exhibit an increase in global performance with increasing system size [5,6]. However, instead of observing an unbounded performance increase (Gustafson’s law), it is more common to observe diminishing returns in performance (Amdahl’s law and Gunther’s universal scalability law) with increasing system size [7]. In technical systems, parallelizing the execution of tasks is constrained by limitations and bottlenecks. These limitations can be structural, for example if serial operations are required to perform well. Limitations can also be logistical, for example, when parallel processing is

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limited by the costs of coordination [8,9]. In biological systems, a similar phenomenon is known as ‘Michener’s paradox’ or as the ‘Per Capita Paradox’ [10], where the per-capita productivity in social insect colonies does not increase with colony size. Rationalizations for Michener’s paradox include biological (kin selection, phylogeny) and statistical (sampling error, central limit theorem) explanations [10–12]. We hypothesize here that both physical constraints and fundamental interaction mechanisms can explain the ‘Per Capita Paradox’ as well as the observed emergence of task fidelity (individual agents repeat a given task instead of switching between tasks frequently) in insect societies.

The evolution of emergent biological complexity requires the development of information-processing systems at multiple scales [13]. This information processing fosters the evolution of short-term response mechanisms, enabling better adaptations in dynamic environments. In turn, the structure and the constraints of the surrounding environment mutually link to the evolving biological system, allowing for co-evolution. Both biological and cultural evolution operate under many constraints of different magnitude [14]. Some of these constraints stem from the fundamental rules of network size, which in turn strongly limit the repertoire of potential designs [15]. We adopt the view that the fundamental principles of a system are shaped by natural selection as a result of the interference between the constraints of the system and the demands of the tasks that are required to survive and to reproduce [16]. We use insect societies to demonstrate how complexification can emerge as a function of constraints and how this process can be beneficial for the evolution of the complex adaptive system as a whole.

Insect societies can be described as analogues to ‘liquid brains’, ‘active matter’, or swarms of interactive agents [17,18]. We emphasize two important characteristics of cognitive living networks: first, their agents move in space and thus their interactions are local and dynamic, constraining the system in a non-trivial way; second, the attractors of these systems are not always based on the strength of interactions (connection weights) but are also dependent on population abundances [17]. The fundamental mechanisms of colony functioning must work over a large scale of population sizes, given that many colonies start with one or few individual(s) and can reach a size of thousands or millions of animals within a few years [19]. The evolution and function of such simple robust mechanisms have been one of the central questions in understanding complex societies [12,20].

Division of labor is one of the most important and common phenomena in social animal groups [21–23]. Insect colonies need to perform a set of tasks, such as constructing nests or gathering food and materials, under changing environmental conditions. Thus, each colony must be capable of sensing the internal state of the colony utilizing distributed information processing. Ants, for example, use pheromones to mark trails that lead to food sources. This pheromone network influences the behavior of the individuals, which in turn can reinforce or adapt the network. This broadcast-type signaling amongst individuals via pheromones allows the whole colony to access global system states, ultimately yielding a plethora of emerging collective behaviors [17,24].

In a previous study [20], we analyzed the task allocation mechanisms of honeybees [25,26], ants [27], and wasps [12,28–34]. We discovered a common core mechanism akin to an integral control regulation, which had previously only been identified in biological systems at the physical and cellular-molecular levels [35–37], but not above the individual organization level [20]. The common core element of this closed loop regulation, which we call the “common stomach”, ensures that foraging for a crucial substance and the consequent use of it in a colony is regulated by the very substance itself. This is achieved via a network of behavioral feedback loops, which are facilitated by local physical worker-to-worker interactions. This regulatory core exhibits a high level of redundancy, ensuring resilience, reliability, and robustness within the self-regulation. Besides its role as an information center, the common stomach also provides a material buffer against fluctuations in substance flows and also acts as a natural integrator, reducing the impact of system noise [37].

Our study demonstrates the spontaneous emergence of parallel processing and an increase of task fidelity on the macroscopic system level as a function of increasing colony size. This phenomenon arises exclusively from the microscopic mechanics of self-regulation via the common stomach. An increasing level of task fidelity will increase the degree of system redundancy at the sub-unit level (parallel processing), which according to the reliability theory, is more efficient than redundancy at the system level [38]. We propose that a scalable integral control mechanism has evolved for ensuring the operability of the system across different environmental and colony size fluctuations. In addition, we show that although task fidelity increases with colony size, the average per-capita efficiency stays similar across all tested colony sizes, which agrees with Michener’s Paradox [10]. This suggests that several important biological traits may have the same mechanistic explanation at their core, which is captured by our model.

2. Methods

Our model of a wasp colony is implemented as an individual-based spatially resolved multi-agent model in which one agent represents one wasp that is active in the nest construction. The model allows to vary the size of the modeled colony’s population, as well as to set specific genera-specific behavioral patterns of interaction, such as parameters that govern the transfer of substances (pulp and water) concerning their general occurrence, their duration, and their frequencies of occurrence (SI file: [Movie S1](#)). This way the model can be parametrized to the typically observed behaviors of several wasp genera, which exhibit significant differences in these behavioral aspects. It is not our goal to model specific wasp species in detail. Instead, we chose four distinct wasp genera which exhibit distinct life histories and in our model building process we only focused on relevant mechanisms concerning the wasps’ construction behavior. These four strategies are defined in the result section and labeled to the corresponding name of a wasp genera. The derivation of our model parameters is detailed in the Appendix (SI file).

Supplementary video related to this article can be found at <https://doi.org/10.1016/j.heliyon.2023.e20064>

Modeling different wasp genera: The four different wasps societies are selected to serve as model systems to demonstrate how higher levels patterns (task partitioning and task fidelity), can emerge from localized interactions and simple physical processes acting at lower levels. In order to be able to model the macroscopic emergent results of the interplay of microscopic mechanisms between

multiple actors, we implemented an individual-based model of the system (Fig. 1(a)) in the Netlogo v6.2 programming environment [39] (SI file). A finite state automaton models the agents' behavioral transitions purely based on its loading-status-dependent task transition probabilities and time periods (see Fig. 1(b)).

Modeling space and initial conditions of agents: In our model space is modeled explicitly by ensuring that each agent always occupies exclusively one cell in a discrete lattice environment. The environment is structured into four specific locations important for the nest construction and for the associated foraging behaviors (Fig. 1). These working sites are modeled as three rectangular areas which correspond to specific locations: a water foraging site (Fig. 1(a): blue area), a pulp foraging site (Fig. 1(a): brown area), a nest building site (Fig. 1(a): red area), and a social interaction platform (Fig. 1(a): grey area). The interaction platform is defined as the part of the nest and its surroundings where the insects commonly interact. These high traffic areas are commonly located near the nest entrance or landing site in each of the modeled species. This area is where water and pulp transfers (if any) happen. Such transfers usually do not occur in the construction sites, which may be located deeper in the nest, The material foragers in wasps, like the nectar foragers in honeybees, rarely visit the sites when the collected material is used. The area of this interaction platform location scales linearly with the workforce size in our model, so that the density of agents, that move around there, is kept constant. In contrast to that, the foraging and nest building sites always have the same size as agents do not interact there and thus density differences cannot show an effect. Their sizes are chosen to be large enough that access to these resources and building sites are not spatially constrained, thus the availability of material resources is modeled ad-libitum. All agents start in the interaction platform area. They are initialized with uniformly randomized water loads and pulp loads in the “unemployed wasp” behavioral state.

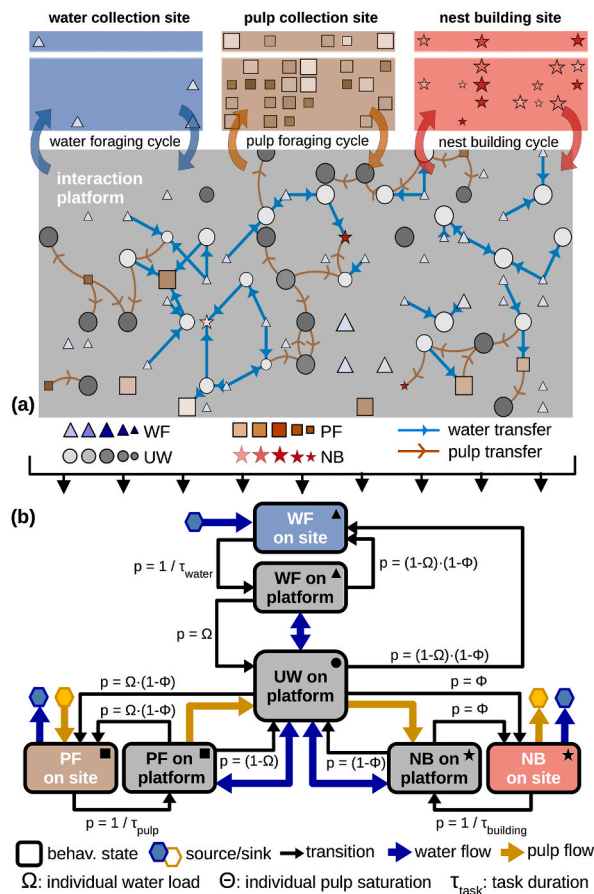


Fig. 1. Model of construction behaviors in wasp societies. (a): Snapshot of spatial organization and interaction of wasps and material flows. Size and color of symbols corresponds to the relative quantity of material the individual carries. The symbols (circles, triangles, squares, and stars) indicate agents in specific behavioral states, their size indicates their individual water loads ($\Omega(i, t)$), their darkness indicate their individual pulp load saturation ($\Phi(i, t)$). Blue arrows between agents indicate water transfers, brown arrows indicate pulp transfers. (b): Finite state automaton representation of the model. Boxes represent behavioral states, thin arrows indicate possible state changes, also indicating their probabilities (p-functions). Agents' behavioral transitions are purely dependent on their loading-status, on probabilities (p) or on time periods (τ). WF: water foragers, PF: pulp foragers, UW: unemployed wasps, NB: nest builders. For details on these probabilities and task-associated time periods, see SI, section “Behavioral state transitions” and the following sections on the specific task modeling. The thick yellow arrows indicate pulp flows within the system, while the thick blue arrows indicate water flows. The dimensions of the collection sites and of the building site are larger (higher) than depicted in this picture, as is indicated by the slim white separator of these sites at the top of the picture. The full extent of these sites can be seen in the SI video from minute 4:50 onwards.

Modeling the task selection by wasps: In each simulation run all wasps are modeled to have the same physical properties and start in a random location of the nest's interaction platform. Each wasp has an individual loading status that describes how much and what kind of building material (water and pulp) they hold as a result of previous interactions with the environment and other wasps. In every time step, each unemployed worker (UW, Fig. 1(a): circles) agent decides, purely on its own individual loading status, whether it will engage in one of the three working tasks of water foraging (WF, Fig. 1(a): triangles), pulp foraging (PF, Fig. 1(a): squares) or nest building (NB, Fig. 1(a): stars). In a similar way, each already employed agent decides, based on its own loading status only, whether it will stay in its task or abandon it to become unemployed. The time durations for water foraging, pulp foraging and nest building are constant (τ_{water} , τ_{pulp} , $\tau_{building}$) in our model. All agents that have assigned a job and that are located at the interaction platform can – again based purely on their own loading status – choose whether they stay at the platform or leave it for foraging or for nest building. All these behavioral decisions are made in a stochastic way based on transition probabilities that scale linearly with the agents' water loads and/or pulp loads.

Modeling task performance and the resulting material flows: When a wasp leaves the interaction platform, it is placed on an empty spot at the corresponding working area for a specific amount of time steps. During this task-dependent handling time, the wasp will collect material or add building material to the nest. Afterwards it will return to the nest's social interaction platform. At the social interaction platform, the wasp will perform material-transfer interactions with (maximally) a maximum number of c_{max} other wasps for a period of $\tau_{contact}$ (SI file). This transferred water can then be utilized by pulp foragers to collect a maximum amount of Ψ_{max} of pulp at the pulp foraging site, where this water is used up during pulp maceration. After returning to the interaction platform, this collected pulp can be transferred to building wasps which construct on the building site (for details see SI file). A steady small proportional loss of pulp and water in the nest reflects to the fact that other tasks, which have not been explicitly modeled here, also use materials or materials can be lost by evaporation over time or be dropped by wasps occasionally. The spatial model, the finite state automaton with its transitional properties between the behavioral states as well as the material flows within the system is shown in Fig. 1 (See also Fig. S4 in the SI file for the emerging water and pulp flows in different social systems).

Model parametrization, initialization and evaluation metrics: All model parameters are based on field studies [28] and were also used in our previous models [29–34] or logical derivations (see S1 table in the Supplementary Information file). In simulation experiments, the model ran with a time step size of $\Delta t = 20 \text{ sec}$ with a minimum of 10 repetitions per parameter set, but with randomized random seeds and starting conditions. The length of simulation runs corresponds to a time span of several days. Neither colony ontogeny nor any long terms changes or reinforcements were thus considered. Due to the focus of the model on construction behavior, other processes such as reproduction, food gathering were not modeled explicitly and only the workforce that play a role in the construction ($N_{construction}$) is considered, not the total colony size. The wasps which participate in the construction behaviors ($C_{construction}$, a set of agents of size $N_{construction}$) are considered to be a subset of the total colony population (C_{colony} of size N_{colony} , see Fig. S1 and subsection "Model framework implementation" in the Supplementary Information document). We chose the predicted emergent dynamics of the constructed nest building as a measure of efficiency of the emergent task allocation. We used three metrics to characterize the per capita efficiency of the given experiment (see subsection "Parameters of the model and efficiency calculations" in the SI file for more information). The building efficiency metric takes into account the amount of building material that has been accumulated in the nest ($\Xi(t)$) during the simulation run until time step t : $E_{building}(t) = \Xi(t)/N_{construction}/t$. This metric normalizes the total building against worker numbers (per-capita) and per time step to support comparisons between differently sized colonies and different length of simulation runs. Higher per-capita efficiency is expressed with higher values in this metric. The foraging activity metric accounts for the time spent with foraging ($\Gamma(t)$) that was necessary to collect the building material used for construction: $A_{foraging}(t) = \Gamma(t)/N_{construction}/t$. This metric is also normalized per capita and per time step to accommodate different runtimes of experiments. As foraging is a risky task, this is a metric that should be minimized for increasing colony efficiency. Finally, a colony-level efficiency metric expresses a combination of the 2 previous efficiency metrics by describing the total amount of material built into the nest in proportion to the required foraging activity: $E_{colony}(t) = \Xi(t)/\Gamma(t)$. This metric shows high similarity with the assessment principles that honeybee foragers perform concerning their quality assessment of nectar sources, where they also maximize the energetic gain per invested costs [40]. In our model, highly efficient colonies will maximize pulp gained for building by minimizing the risk (cost) for collecting it. These efficiency measurements are focusing only the construction activities and do not relate to reproductive output or other efficiencies that was not modeled in this study.

3. Results

3.1. Scalable regulation of task partition and task fidelity

Social wasps are a diverse group with a variety of life histories [28], but they all construct their nests via a self-organized close-loop mechanism [20]. We distinguish here four life history strategies which correspond to four phylogenetically different genera:

Polistes wasps have small colonies, and one or very few individuals construct the nest by performing three tasks in a sequential order: 1, water foraging; 2, pulp foraging; 3, building. No water transfer between individuals and no pulp sharing can be observed. These wasps show no task fidelity, as all individuals perform all their tasks in a sequence.

Vespula wasps have medium sized colonies. Few individuals participate in the nest construction, pulp sharing is not observed, but occasional water transfer between individuals can occur. This results in a weak specialization of water forager wasps (partial task partitioning). Pulp forager wasps will construct the nest with the pulp they collected themselves. Wasps show low task fidelity.

Metapolybia wasps have medium sized colonies. Several dozens of individuals participate in the nest construction. Both pulp

sharing, in which the pulp loads collected by pulp foragers are processed by several builders, and water transfers between individuals are common. Their construction behavior shows full task partitioning between water foraging, pulp foraging, and nest building. However, wasps still switch between tasks occasionally (medium task fidelity).

Polybia wasps exhibit a life history similar to *Metapolybia* wasps, except that the colonies and their nest constructing workforce groups are larger. Both pulp sharing and water transfers occur extensively. Full task partitioning with rare task switching is observed (high task fidelity).

To study the general principles of the core mechanism of such complex adaptive system, we developed a multi-agent computer model based on the mechanistic interactions between wasps and their construction materials (Fig. 1, SI file). The aim is to investigate whether these biologically distinct life histories, which we can observe in insect societies, could be derived from a unified mechanism (the common stomach task partitioning). We argue that a single scalable mechanism on the microscopic system layer, could result in both different observed macroscopic patterns of task fidelity and diminishing returns as the colony size increases. We compare data on the construction behavior of these four genera [28] to the predictions yielded by our model. These specific simulations are parameterized to represent the interaction mechanisms and the size of the task cohorts of these four genera in construction behavior. Due to the simplicity of our model and the generality of the modeled mechanisms, we consider strong qualitative agreements with empirical data as conclusive results and thus, important for model validation. In order to investigate whether or not our model yields nature-like emergent regimes of task allocation among the wasps, we compare the predicted frequencies of task changes after completion of one bout of task performance to the observed frequencies from natural wasp colonies (Fig. 2). We found that only minor quantitative differences between modeled and field data and these differences can be attributed to factors that were not included into our model (see discussion section).

In the case of a singular constructor (*Polistes*), the model predicted a sequential construction strategy like it was also observed in real *Polistes* wasps (Fig. 2): The simulated *Polistes* wasps rarely repeated or switched back to the previous task, but more frequently carried out the next task in the sequence WF → PF → NB → (WF) and so on. This happened as an emergent property of the system, the algorithm did not force the wasp to carry out any sequential order in a pre-programmed way. In contrast, this task cycling emerged frequently due to the wasp-material interactions and material processing. In real colonies other variables (not included in the model) can canalize the sequence further such as the pulp will dry out if it is not built into the nest soon after it is processed. As the colony size

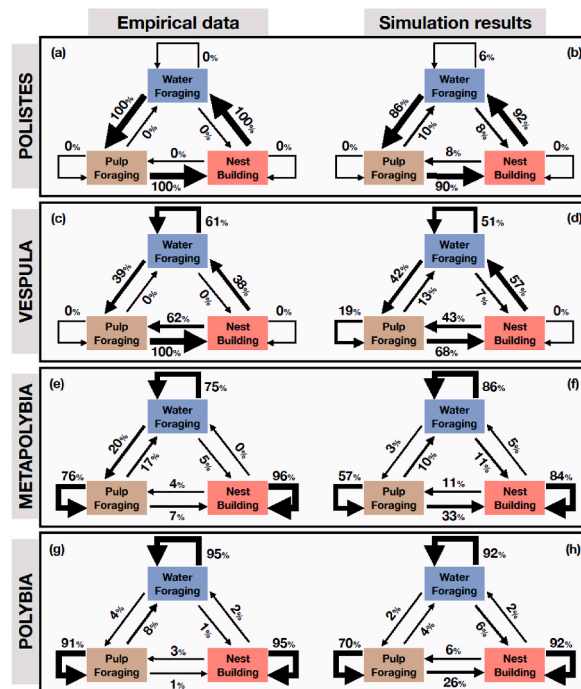


Fig. 2. Emergent task fidelity and task switching probabilities in natural and simulated wasp colonies. The number of wasps participating in construction behaviors increases from the top to bottom: *Polistes* (a,b): 1; *Vespula* (c, d): 7; *Metapolybia*; (e,f): 30; *Polybia* (g,h): 125 active wasps. These numbers are based on observations and estimations of corresponding natural colonies [28]. Empirical data from natural colonies (a,c,e,g) are compared to simulation results (b,d,f,h). In these simulations, the first 2000 of 3800 timesteps were discarded since colony initiation with all wasps starting in the ‘idle’ state. This generates an initially strongly fluctuating transient. With each colony parameter setting we recorded all task switches and all task repetitions of each simulated wasp. From the resulting a 3 × 3 task transition matrix we derived the percentages (indicated numerically at the arrows and also by the arrow thickness) of task switching happened during the final 1800 time steps across all simulations. Each setting was repeated for 100 trials. This approach gave an analogous method to long term observations of individual wasp behavior for task switching we calculated for real colonies.

and hence the number of wasps participating in construction behavior increases, the system complexifies in response to it: the construction behavior becomes more and more partitioned into several subtasks as the workers' task fidelity increases, which corresponds to observed natural patterns (Fig. 2). In simulated *Vespula* colonies a rather specialized group of water foragers emerged. These wasps rather repeated the water foraging throughout consecutive work cycles rather than switching to another tasks. In simulated *Metapolybia* and *Polybia* colonies the construction behavior automatically becomes strongly partitioned into 3 distinct worker groups and each task (especially in larger colonies) gets performed by wasps that rarely change their jobs (high task fidelity). The rise of high task fidelity of larger colonies emerged from the same mechanism which resulted the sequential behavior in *Polistes* wasps. This specialization to tasks emerges without any reinforcement mechanism being implemented into our multi-agent model, such as learning, threshold-reinforcement mechanisms. There is also no a-priori predisposition of wasps to specific jobs, as they are all modeled with identical properties. The only variables that can change in a wasp agent is its location and its current loadings, but they do not differ in loading capacity or speed (flight cycle times) and do not have any initial preference for a task. Thus, the observed emergent symmetry breaking arises purely from the social interaction and the material handling.

3.2. Performance depends on life history and workforce size

In general, the per capita performance of the colonies does not improve in our simulation runs, and in some cases even shows diminishing returns with increasing workforce (Fig. 3(a-c)). The average foraging activity is very high in *Polistes*, and *Vespula* performs only slightly more efficiently in foraging than *Polistes* (Fig. 3(a)). The emergent strategy of the *Polybia* group (*Metapolybia* and *Polybia* species) shows a decrease of 50% in the total time spent at foraging sites. However, none of the emerging strategies show a notable change in per capita foraging activity with respect to workforce size. The *Polybia* group has the lowest foraging activity but the highest average per capita building efficiency in most cases (Fig. 3(b)). This high building efficiency is paired with an economical low foraging activity, and thus provides the highest per capita colony efficiency for the *Polybia* group (Fig. 3(c)). The *Polistes* and *Vespula* strategies have lower building and colony efficiencies than the *Polybia* group, except in very small colonies. The simple sequential *Polistes* building behavior and the very rudimentary task partitioning of the *Vespula* wasps is more efficient in very small colonies than in the *Polybia* group. While the building efficiency of *Polistes* and *Vespula* does not change with workforce size, the efficiency improves in the *Polybia* group steeply for small workforce sizes but shows diminishing returns after the workforce exceeds 50 or more workers (Fig. 3

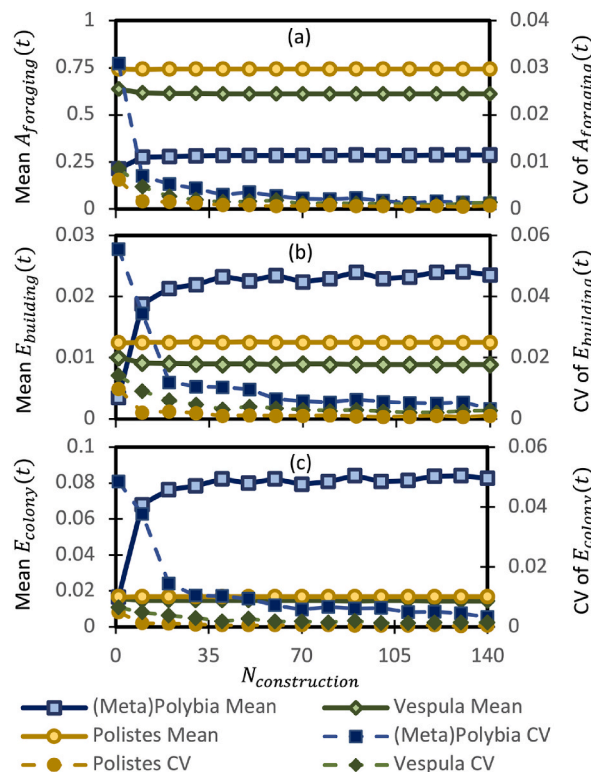


Fig. 3. Averages (large symbols) and coefficients of variation (small symbols) of the final per capita efficiencies as functions of the workforces participating in the construction behaviors for the four life history strategies. Labels: (a): foraging activity: $A_{foraging}(t)$; (b): building efficiency $E_{building}(t)$; (c): colony efficiency $E_{colony}(t)$. *Metapolybia* and *Polybia* strategies are pooled here as colonies of these genera differ only in workforce size in our model. All data were calculated as per capita per timestep from the total work that had been done until $t = 10,000$ timesteps. The average and coefficient of variation (CV) of 20 parallel runs were plotted as a function of workforce size.

(b)). The coefficient of variation (CV) shows a significant decrease from a small to a medium sized workforce. This indicates that a workforce that is medium size or larger provides a more reliable performance than a small one (Fig. 3(c)).

A simulated perturbation of the wasp construction behavior, by inducing a water leakage out of the system, also supports the stabilizing role of larger colony sizes and the buffering effect of the common stomach in the genera that exchange water (Fig. 4(a–d)). Most water is used for construction behavior, but water is occasionally also used for other functions such as cooling and drinking. Such a water loss decreases the efficiencies of construction behavior but rearranging the workforce can be an emergent contingency for this problem. In consequence, with intensive losses, such compensation mechanisms counterbalance the efficiency declines. *Polybia* and *Metapolybia* colonies perform considerably better when water exchanges are allowed. Larger *Polybia* colonies perform better than smaller *Metapolybia* colonies, although they use the same water exchange mechanisms. Water losses will be compensated for in the *Polybia* group by increasing water foraging activity if the water exchange is suppressed externally. *Polistes* building efficiency is surpassed only by the *Polybia*, because *Polistes* do not spend extra time on social interactions (Fig. 4(a,c)). However, *Polistes*’ colony efficiency is the lowest due to their very inefficient foraging (Fig. 4(b–d)). When water exchange is fully suppressed, *Polybia* and *Metapolybia* react by increasing their foraging activity with increasing water loss rate, up to a point above which the foraging activity level stays constant. All other groups’ foraging activities show slight linear decreases with increasing water losses, as losses of water decrease their pulp foraging and their building activities (Fig. 4(a d)).

3.3. Sensitivity analysis

Sensitivity analysis is crucial for ascertaining that the results of the simulations are not dependent on a set of specific values of the parameters and that the overall stability of this system is emerging from the proposed control mechanism. We performed a sensitivity analysis of our multi-agent model by conducting 1000 repetitive runs with different random seeds for 40,500 time steps. All core parameters of the model (τ_{water} , τ_{pulp} , $\tau_{building}$, $\tau_{contact}$, c_{max} , Ψ_{max}) were varied $\pm 50\%$ of their standard values, for details see Table S2 in the supplementary materials (SI) file. In case of integer-type parameters rounded afterwards, kept constant within each model run. All other parameters were set to the standard settings for the genus *Metapolybia* with a population size of $N_{construction} = 125$ wasps. Every 100 time steps the most important system variables (wasps at the foraging/working sites and at the interaction platform) (Fig. 5(a–c)) and efficiency metrics ($E_{colony}(t)$, $E_{building}(t)$, $A_{foraging}(t)$, $\Xi(t)$) were saved and the data are plotted to indicate the spread of the results (Fig. 5(d–h)). In order to investigate the stability of our model we conducted four consecutive perturbation experiments over the course of each simulation run. We randomly selected 10 wasps that were on the interaction platform in each time step and performed one of the following procedures, depending on the current period:

- between $t = 4500$ and $t = 9000$ timesteps we removed all water from these selected wasps,
- between $t = 13,500$ and $t = 18,000$ we filled the crops of these wasps with additional water,
- between $t = 22,500$ and $t = 27,000$ we removed all pulp loads from these wasps,

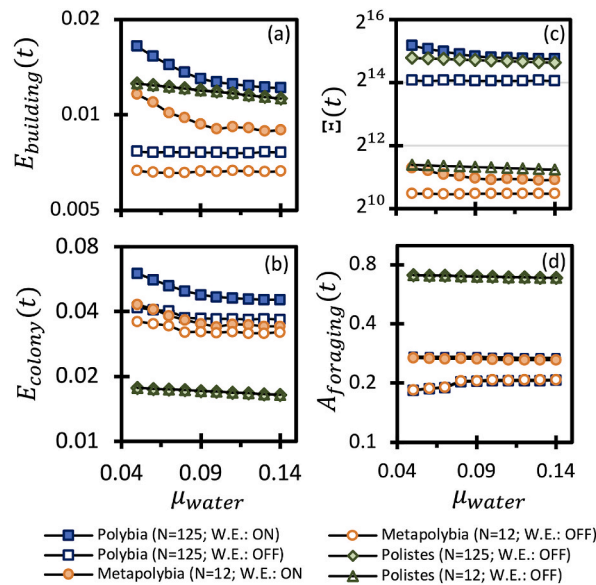
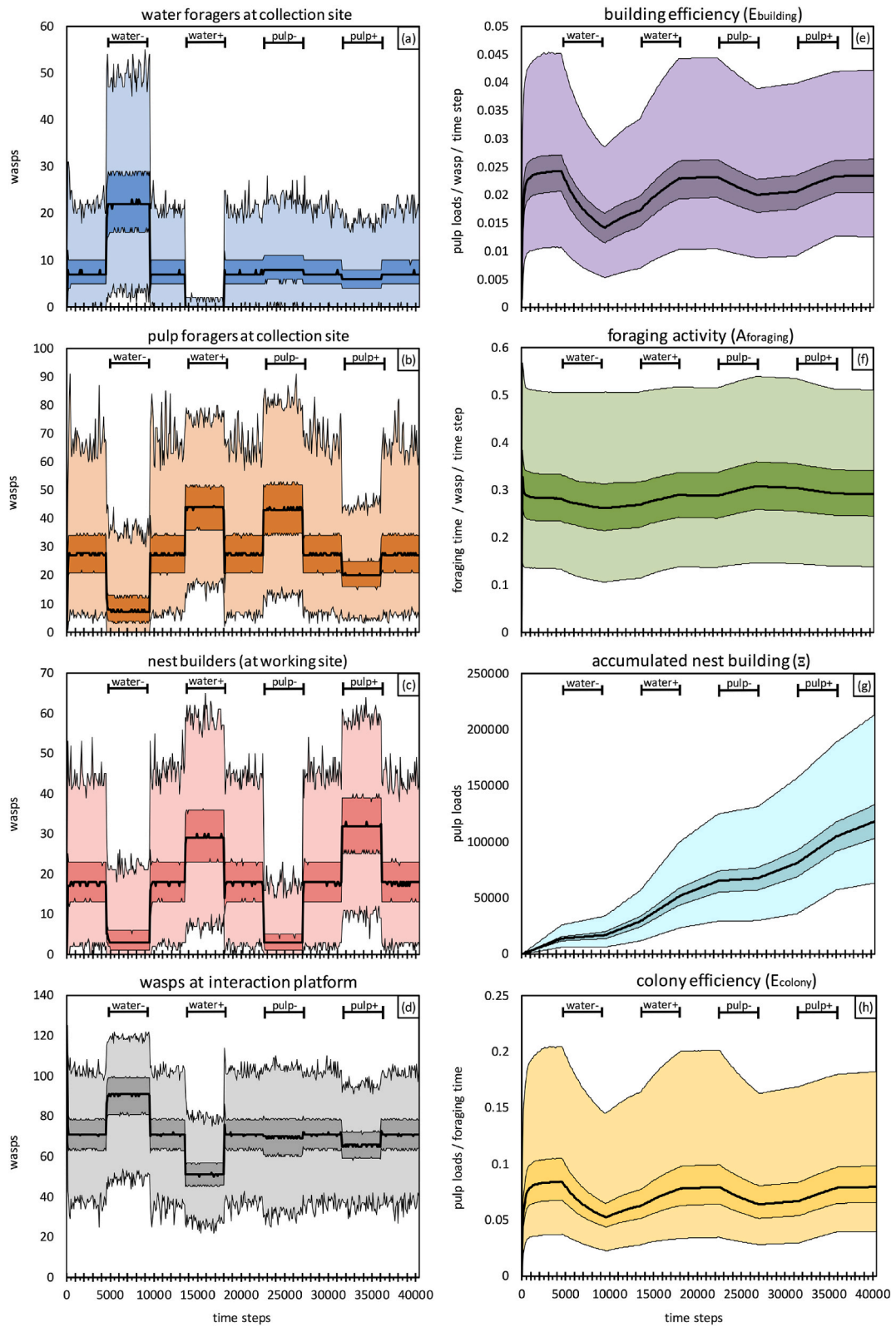


Fig. 4. The efficiency responses of different strategies to varying degrees of water loss. Water loss is implemented as constant water leakage from all wasps located on the interaction platform. Labels: (a): building efficiency $E_{building}(t)$; (b): colony efficiency $E_{colony}(t)$; (c): per capita accumulated building material $\Xi(t)$; (d): foraging activity: $A_{foraging}(t)$. The medians of the final metric values of 10 runs of small ($N_{construction} = 12$ wasps) and large colonies ($N_{construction} = 125$ wasps) of *Polistes*, *Metapolybia* and *Polybia* with and without water exchange are plotted from the total efficiency data at $t = 18,000$ timesteps.



(caption on next page)

Fig. 5. Sensitivity analyses of the *Metapolybia* model ($N_{\text{construction}} = 125$ wasps). Labels: (a): number of water foragers at collection site; (b): number of pulp foragers at collection site; (c): number of builders at working sites; (d): number of wasps at interaction platform; (e): building efficiency; (f): foraging activity; (g): accumulated building material; (h): colony efficiency. The strong middle line represents the median across all 1000 runs, the darker colored inner ribbons indicate the range of results into which 50% of these runs fall, the lighter colored outer ribbons show the whole range of results of these runs in the course of our simulations. The span-indicators on top of each figure indicate the specific perturbation periods' timings.

- between $t = 31,500$ and $t = 36,000$ we gave each of those wasps a full pulp load.

Combining these perturbation experiments with an extensive parameter sweep shows that the system is very robust and generally compensates for strong perturbations by keeping the foraging activity stable, while counteracting the perturbations by rearranging the workforce (Fig. 5). This sensitivity analysis is also crucial for understanding the general core model we present here. It allows to ascertain that the observed stability of this system is emerging from the proposed control mechanism and that this effect does not have a strong dependency on the initial values of the variables we used. The model did never predict infeasible results, such as a negative number of wasps or a negative quantity of materials or any runaway explosions in the efficiency measurements. In general, the system shows a quick convergence towards an equilibrium, followed then by a robust counterbalancing against external perturbations, and a fast return to the original equilibrium after each perturbation was switched off. The model system reacted similarly to these perturbations compared to the observed reactions in natural colonies [28]. For example, adding water to the system resulted a drop in the number of water forages, while the number of pulp foragers and builders increased. Due to the plentiful availability of water, less water-exchange interaction was needed among the wasps to accomplish their jobs and this in turn increased the building efficiency and colony efficiency and the foraging activity. Removing water resulted in a similar cascade of colony responses in an opposite direction. Adding pulp decreased the number of pulp foragers and the builders, but it caused less dramatic change in the number of water foragers. The building and colony efficiency increased, but the foraging activity did not change in a significant way. Removing pulp from the system resulted in a similar degree of colony level reaction, but in an opposite direction. In summary, our agent-based model reacted similarly to the perturbations carried out as experimental treatments on natural colonies [28] or simulated experiments in our previous ODE model [29].

4. Discussion

Previous work [20] showed that the core of task regulation in wasp, bee, and ant societies can be considered akin to a form of integral control regulation, which has previously been described for cellular and subcellular levels in biology. Here we present an explanation on how such a mechanism can explain both the commonality in the construction behavior of social wasps and the differences in life history aspects of different wasp genera. Mechanisms of interaction and material exchange among workers are shaped by natural selection into emergent complex pulp and water sharing systems that are scalable and robust. We stress that scalability is one of the most important properties of/in a complex adaptive system, especially in a “swarm system” or a “hive mind” as social insect colonies are often called. Our simulation experiments showed not only interesting scalability properties of the system, which are often the effect of emergent strategy changes in the modeled social interaction systems, but we observed also remarkable emergent counterstrategies in our perturbation experiments. The specifically modeled mechanisms of water and pulp sharing showed to be crucial elements that allow the wasps to switch to alternative behaviors in response to alterations of work force sizes or environmental conditions.

The model we present here strictly follows the parsimony principle: the explanation should be as simple as possible and as complex as necessary. In this model the mechanisms we modeled are material transfers and linear modulations of work engagement or abandonment. No other mechanism were assumed and implemented into our model, such as learning processes, genetic dispositions, physiological or morphological agent heterogeneity, individual preferences or other specific neuroethological predispositions, as they are often expressed by heterogenous sigmoid stimulus-response curves in agent-based models. One of our key findings here is, that we do not require to hypothesize about colony-size-dependent adaptations of proximate mechanisms, as our model can predict the observed ultimate effects without such a layer of additional complexity. In this paper we emphasize that the common stomach mechanism, due to its scalable nature, will result in different colony level outcomes with differing workforce sizes. Ultimately, a complex task partitioning process is the emergent consequence of more interactions, as the workforce size increases, using the same basic construction mechanism. Thus, our findings show that complexity can arise from simplicity in wasp societies.

Our agent-based common-stomach model differs significantly from ODE models on the common stomach found in literature. We avoid here the implicit assumptions of mean-field ODE modeling, such as assuming an optimal mixture of agents or allowing infinite interaction distances. Such assumptions are implicitly made in previous common stomach models on where the task allocation of several species (ants, honeybees, wasps) was described [25–27,29,30], or when crosscutting comparisons between these insect societies have been made [20]. In contrast to these studies, we focus here on investigating task allocation of paper wasps at different levels of eusocial complexity concerning their colony integration mechanisms. Our bottom-up model presented here implements only a small set of basic proximate mechanisms and physical interaction principles, which then yield ultimate colony-level effects as emergent property in simulation runs. Such emergent properties were found to be flexible task division and allocation (Fig. 2) and colony-level resilience against environmental perturbations (Fig. 5). Ultimately, our model allows investigating how simple physical interactions, that are modeled purely locally, can yield different performance metrics of the overall colony, allowing to scale the colony

concerning the number or modulating specific aspects of interaction.

Our model keeps the modeled workplaces (water collection sites, pulp collection sites, construction site) very abstract and ad libitum concerning the ability of the wasps to perform their work there. In their natural habitat, there will always be water and wood to be found for the wasps. However, there are intrinsic limitations of work: Water foraging requires empty crop space, pulp foraging requires a full water load and nest building requires pulp loads. These limitations are modeled explicitly, but the resources for construction are assumed to be available ad libitum. In addition, environmental fluctuations in the resource accessibility can be modeled via modulating the corresponding length of a given collection duration. For example, in the dry season the water collectors may need to travel farther for water. To account for sudden changes of resource availability we implemented additional influx of water or pulp, to analyze the sensitivity of these systems (Fig. 5). Jensen et al. [41] concluded that the optimization of material flows appears to be a universal feature of biological transport systems. They emphasized that most transport systems are also subject to a set of limiting constraints. In insect societies *Michener's (Per-Capita) Paradox* [10] describes a diminishing return of per capita productivity with increasing colony size. The reason for the emergence of this paradox in these societies remains elusive, even though it also seems to emerge from other facets of social life [42]. This paradox is similar to *Amdahl's Law* [43] found in technical computation systems, which shows that technical bottlenecks impede unbounded increases of computation rate with increasing system size. Our study demonstrates how local and simple physical interactions (material exchanges) can give rise to such emerging patterns with similar key properties. Although *Michener's Paradox* was neglected at first and criticized thereafter [44], it is a significant biological observation of biological scalability that is highly relevant beyond biology today. Michener discovered, years ahead of Amdahl, a general law of scalability that became crucial in understanding complex systems such as economy and complex computational systems. Michener's views were crucial to recognize that insect societies are complex adaptive systems and they operate under the same physical rules as other similar systems.

Our simple agent-based model shows that strategies with no or little interaction between wasps will not scale up well with increasing work force size. *Polistes* wasps do not share materials and work as jack-of-all-trades individuals in a sequential manner. Task partitioning will consequently not emerge in their colonies. These wasps do not spend much time in social interactions and are working as independent individuals on nest construction even if the colony size increases. Our model shows that this strategy is efficient for construction, but it is costly when foraging. In nature, the cost of this strategy is mostly incurred by the potential loss of the foragers, which is largely due to predation. *Polistes* colonies evolved to remain small and to grow slowly. This ensures small nests and moderates total foraging traffic, which makes them less detectable by predators.

Vespula wasps have a life history very similar to *Polistes* wasps. For example, their nest is initially built by a single queen in a sequential manner. However, *Vespula* colonies will develop a rudimentary form of task partitioning (emergence of water foragers) when their colony's size increases. These wasps spend more time with social interaction while transferring water, so their building efficiency is a bit smaller than of the *Polistes*, but their foraging is more economical. In natural colonies, the smaller number of specialized foragers will find the resources faster and will thus be exposed for less time to predation risks. Characteristically, *Vespula* colonies grow larger than *Polistes* colonies, even if their per-capita efficiency, similar to *Polistes*, does not change with colony size.

Metapolybia and *Polybia* wasps have similar life histories, but *Polybia* wasps generally build larger colonies. These wasps share pulp and water via worker-to-worker interactions, and they thus spend considerable time at the interaction platform region of the nest. Our model predicts that this strategy would be very detrimental to their efficiency in small colony sizes. In nature, these colonies never reside in small colonies, as they reproduce by swarming rather than via a single queen like *Polistes* and *Vespula*. Our model shows that the construction strategy using pulp and water sharing is clearly superior for the building and the colony efficiency except at very small colony sizes. This high efficiency of large colonies is achieved by a greatly reduced foraging activity than is observed in other wasp genera. Task partitioning is well defined in these genera and the workers' task fidelity is high. These colonies operate with small numbers of specialist foragers that can carry out foraging quickly, therefore decreasing predation risk. This emergent phenomenon of task fidelity does not cause rigidity of the colony-level behavior. Our perturbation analyses show that in fact these societies are very resilient against environmental changes, and that this resilience property is essentially achieved via dynamic rearrangements of the workforce governed by common stomach regulation [20].

Our model focuses only on the construction behavior of some important wasp genera, this way it emphasizes some key elements and neglects less important factors from their complex behavior. Our model is based on previous empirical and modeling work that we did on these wasp societies [12,28, 29, 30–34], thus this model cannot be directly generalized to other groups of organisms. However, the core mechanism of this model stems from our previous studies [25–27] where we showed that the task regulation of bees, ants and wasps relies on an integral control mechanism that we named “common stomach”. The common stomach is a functioning colony-level regulatory system, based on explicitly defined local worker-to-worker interactions. This is a significant finding, as our previous ODE models have demonstrated that the common stomach's key principles are generalizable also to other organism groups [20].

Diverse biological complexity can emerge from simple physical laws and from mechanisms such as transport processes and material flows, paired with physical constraints and restrictions to local interactions [45]. Natural selection acts upon the involved proximate mechanisms and a rich diversity of ultimately colony-level regulation systems can emerge. For example, task fidelity has been presented in previous literature to be a consequence of a lack of learning abilities, or that it requires specific genetic makeup, and such specialists are able to be “activated” or “deactivated” while staying in their task's role [46]. In contrast to these hypotheses, we here show that task fidelity can be an emergent property purely resulting from the simple construction behavior of wasp societies, and that it can be explained via physical material-exchange interactions without any specific worker precondition or specific properties required [20,28,32,47,48]. Task fidelity and task partitioning will automatically emerge in larger colonies, a testimony to the power of scalable general mechanisms in explaining the diversity of life histories.

Data availability

The authors declare that the empirical data used for Fig. 2 were published in Karsai, I. & Wenzel, J. W. Productivity, individual-level and colony-level flexibility, and organization of work as consequences of colony size. *Proc. Natl. Acad. Sci. USA* **95**, 8665–8669 (1998). All other data supporting the findings of this study are available within the paper and its supplementary information files.

Code availability

The code of the multi-agent simulation will be made available on request by the authors.

Author contribution statement

Thomas Schmickl: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper. Istvan Karsai: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary Information

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.heliyon.2023.e20064>.

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