

# FINDING OPTIMAL COLLECTIVE STRATEGIES USING INDIVIDUAL-BASED SIMULATIONS: COLONY ORGANIZATION IN SOCIAL INSECTS

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**Abstract.** Social insects like ants and bees live in cooperative colonies containing up to millions of individuals. These colonies are sometimes termed “superorganisms”, and have evolved tightly integrated and sophisticated collective behaviors. Different species, however, often differ in the type and mechanisms of communication and collective organization employed. I show here how individual-based models can be used to identify the non-intuitive benefits of different mechanisms of collective organization. This allows us to understand under what ecological conditions particular types of communication or division of labor may have evolved, and thus can also explain variation among species.

## 1 Introduction

Social insect colonies have to solve complex problems. For example, bee colonies collect food from flowers, whose abundance varies strongly in time and space. Finding these resources can require considerable search effort: bees will search an area of several kilometers diameter, and each forager will visit hundreds of flowers per day [1]. In addition to the search itself, effective foraging by the colony depends on an appropriate allocation of bee workers to exploration (search for new resources) and exploitation (collection of food from known resources), and an effective allocation of foragers among resource patches, which may vary in quality, distance from the nest, longevity, and reliability, leading to complex trade-offs [2-4]. The actual number of workers allocated to search and exploitation of resources is a result of the individual decisions made by these workers, which in turn are based on information available to these individuals through their own search or through communicated information from others [5]. The collective pattern is therefore self-organized, without a central leader or template directing individuals to particular resources.

The degree to which communication is used to in this process varies between species. Honey bees (genus *Apis*) can directly communicate distance and direction, and pass on information about the odor of rewarding food sources to their nestmates using the ‘waggle dance’ [6]. In addition, high availability and quality of resources causes increased frequency and duration of waggle dances, thus increases numbers of workers at those particular resources. Bumble bees on the other hand (*Bombus terrestris*) do not communicate location information. Only the presence, availability and type of rewarding resources is communicated. Recruitment to specific patches is thus not possible in bumble bees [7-10].

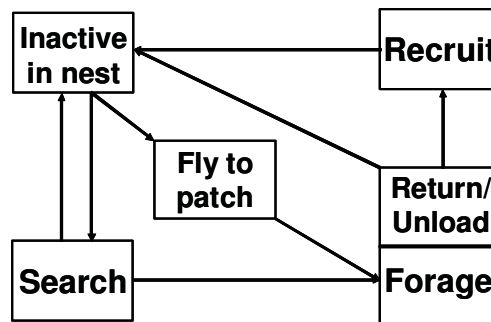
## 2 Research questions and approach

Why are there these differences? Do different communication systems work equally well, or is each system adaptive under particular ecological conditions? Previous empirical research has primarily investigated the mechanistic details of these communication systems (e.g. [11-15]), but there is little known about the benefits and costs of using one strategy over another, and how these depend on ecological conditions or internal constraints [16-18]. Here, I use an individual-based modeling approach [19-23] to investigate the benefits of particular collective strategies under different environmental and social conditions.

I will present the results of two modeling efforts, one concerned with different communication systems as described above, the second focusing on different mechanisms of task allocation within the nest. To quantify the benefits of different strategies in different environments, modeling is often necessary. In studying self-organized collective behavior, such as foraging with or without communication, individual-based models are ideal for several reasons. First, it is straightforward to implement the behaviors of and constraints on individuals as known from empirical research. Second, spatially explicit environments are used, and thus constraints on movement and spatial heterogeneity in resources and behavioral or information-heterogeneity among workers are taken into account [21-23]. However, because this usually implies that a (relatively) large number of parameters are used, whose numerical values may have an impact on the predictions produced by the model, this necessitates the use of similar techniques as empirical research, namely a strict hypothesis-testing approach and extensive sensitivity analyses [3, 24].

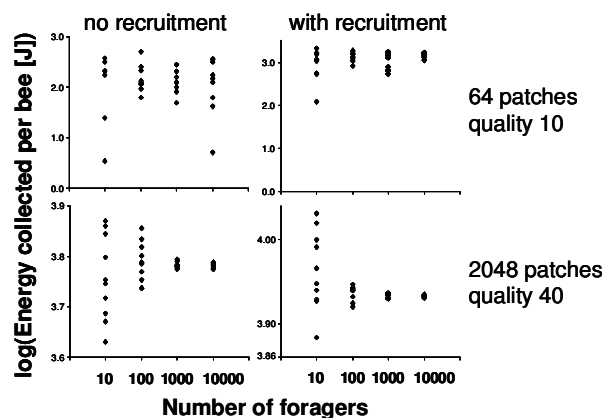
### 3 Communication in foraging: resource distribution matters!

We used a model of honey bee foraging that contained 6 behavioral states and corresponding transition rules (Fig. 1), and was parameterized using the extensive literature on bee foraging behavior [25]. In the patchiness simulations, 1000 bee foragers were simulated, foraging on between 4096 and 64 resource patches in a simulated area of 8 km x 8 km. Each bee could collect between 1.25 and 80  $\mu$ l nectar per trip ('resource quality'). Colony foraging success was measured as the net energy collected, i.e. the nectar collected by all bees in foraging trips minus the energy used by all bees over a simulated time of 50 h. Ten simulation runs were performed for every parameter combination tested. For more extensive sensitivity analysis of this model see [25]. The model was implemented using a graphical user interface in SeSam ([www.simsesam.de](http://www.simsesam.de)).

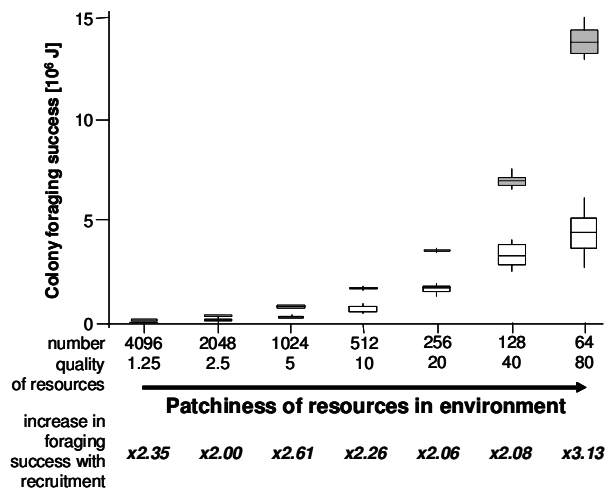


**Figure 1.** Schematic representation of the behavioural model used in the individual-based simulations. Arrows correspond to conditional/ probabilistic transitions between behavioral states. For example, 'Foraging' immediately leads to subsequent 'Returning', but to initiate 'Search', bees have a certain probability to leave the inactive state in each timestep. This leads to varying durations in each state. The transition from 'Search' to 'Foraging' depends on how quickly the bee actually finds a food source in the spatially explicit simulation.

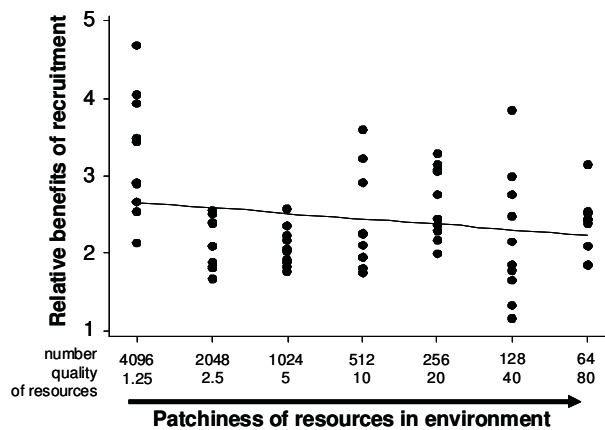
Using these methods, we quantified the benefits of a honey bee-style recruitment system in different situations. We tested for an effect of patchiness (as opposed to homogeneous distribution) of resources and effects of colony size on the benefits of communication among foragers in a group. We found that neither of these parameters had a significant effect (Fig. 2 & 3), meaning that differences in colony size or resource patchiness cannot explain why honey bees evolved a recruitment system in foraging and bumble bees did not. However, we show that communication is particularly useful in resource-poor habitats (Fig. 4, [25]). It seems that benefits of recruitment are low if resources are high quality, even if they are at low density (and thus hard to find). This is likely the case because with rich resources, the costs of search time become negligible in relation to the gain from discovering a patch, whereas with poor patches they are not (and thus search time affects overall foraging success much more strongly).



**Figure 2.** We simulated colony sizes of 10 to 10 000 forager bees. There was higher variance in foraging success (energy collected by the group) among simulation runs for smaller colonies. However, median foraging success was unaffected by colony size, and thus median benefits of recruitment (foraging success with/foraging success without communication) were also unaffected by colony size. Each data point is a simulation run. Kruskal-Wallis Test shows no significant effect of colony size for the 4 environments 64 patches, quality 10, 64/40, 2048/10, and 2048/40 (only two shown in graph) without recruitment (N=40, df=3 for each, p=0.63, 0.88, 0.10, 0.77 respectively) and with recruitment (N=40, df=3 for each, p=0.32, 0.27, 0.28, 0.12).

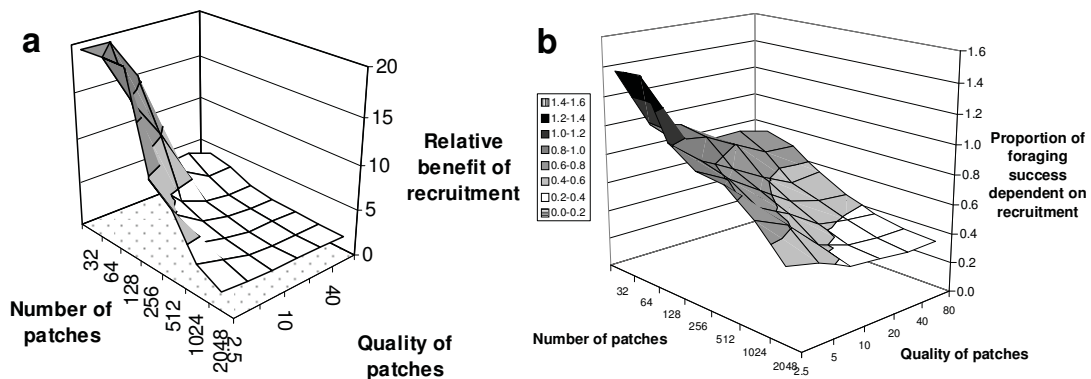


**Figure 3a:** In our model, bees had a higher net energy gain in patchy environments compared to ones with many small resources. This indicates that with our choice of parameters, searching for resource patches played a smaller role than effectively collecting nectar once patches are found (the former being harder with fewer resources, the latter when resources deliver little reward per trip). Boxes show median and interquartile interval, whiskers show range; grey: with recruitment, white: without recruitment.



**Figure 3b:** However, the benefit of recruitment (ratio of foraging success with and without recruitment) showed no increasing or decreasing trend with increasing patchiness (in simulations with recruitment, bees always collected on average about 2-3 times as much energy as without recruitment: Regression  $p=0.08$ ,  $R^2=0.03$ ).

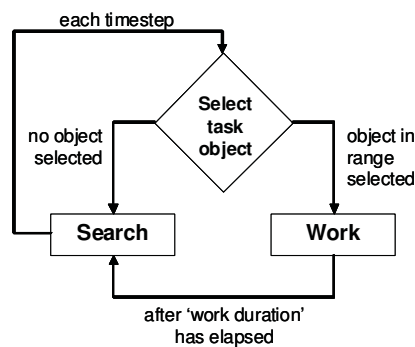
There are of course many previous modeling studies that have investigated optimal foraging strategies, and many have studied recruitment behaviors in social insects (e.g. [26-29]). However, only a few studies have looked at the benefits of differing strategies, and thus implicitly or explicitly at the evolution of such behaviors [19, 20, 30-32]. These studies have typically also investigated the role of resource characteristics and colony size for social insect recruitment. For example, one previous study found a strong role for colony size in the effectiveness of forager communication [33]. However, this study assumed that group size directly relates to the number of individuals recruited per forager who is recruiting: an entirely reasonable assumption to make in ants, where a pheromonal foraging trail may attract twice as many recruits in a colony that is twice the size, because there is essentially no limit to how many foragers can walk on one trail. However, this is not the case in the honey bee waggle dance: only about 4 bees can follow a dancer at any one time, regardless of how many bees are available to be recruited. Since a recruit has to follow on average several dances before she arrives at the indicated food source, a single forager can essentially only recruit one other individual per trip, independent of colony size [34, 35]. It is likely that this limitation, reflected in my model, is the reason that larger colonies do not show increased advantages of recruitment.



**Fig. 4a:** The previous figures (Fig. 2 & 3) showed that neither patchiness per se nor colony size affect benefits of recruitment significantly. However, other properties of the resource distribution do: here (top graph) we show relative recruitment benefits (foraging success with/foraging success without communication) with number of patches in the environment and with quality of patches (amount of nectar available per trip). Benefits of recruitment are highest with few, low quality patches (for full analysis see [25]). Both of these parameters by themselves affect benefits of recruitment, but if patchiness is increased as in Fig. 2, the effects of patch density and quality counteract each other (in this plot, patchiness increases from the bottom (front) corner to the top (back) corner of the graph). **Fig. 4b:** At low densities and low patch qualities, foraging success is sometimes negative (bees use more energy than they are able to collect); in these cases, no relative benefit was calculated (in Fig. 4a). However, we could calculate what proportion of the energy collected with recruitment was dependent on recruitment being present  $[(E_{recr} - E_{norec}) / E_{recr}]$ ; this is plotted in the lower graph (ANOVA  $df=41$ ,  $R^2=0.92$ ,  $p<0.001$  for both number and quality of resources).

#### 4 Optimal levels of variation in a group: what are the benefits of division of labor?

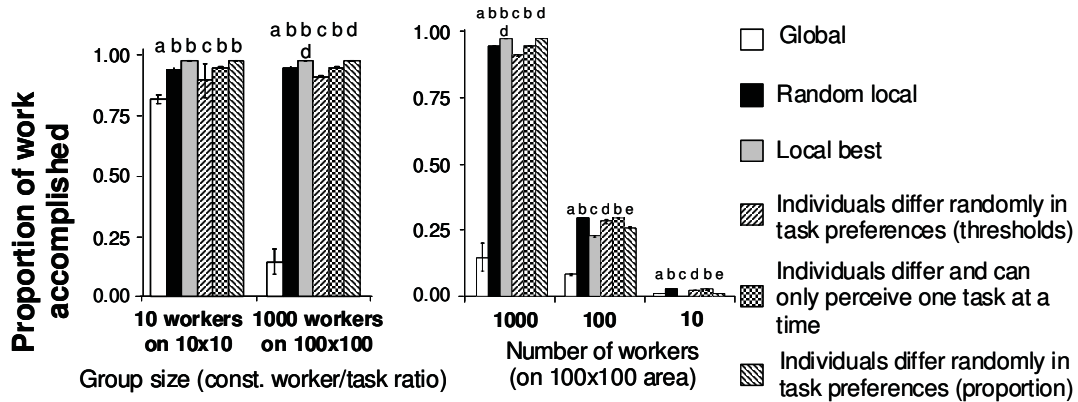
Similar to the question of optimally allocating foragers among resources, I am interested in how insect colonies allocate workers to different tasks needed in the nest, such as brood care, defense, nest repair, and cleaning. It seems that in some species this allocation of workers to tasks is determined by worker age, genetic background, or body size; in others it is the result of worker interactions or individual experience [36]. Several previous modeling studies have investigated how such mechanisms can indeed lead to individual specialization and thus division of labor [37]. However, the apparent diversity of task allocation mechanisms among social insects remains unexplained. What is the benefit of one or the other mechanism, and under what conditions is it adaptive to start with a heterogeneous group, rather than identical workers that react only to local cues? So far there is a lack of empirical studies on this [38]; here we demonstrate that individual-based models can answer some of these questions.



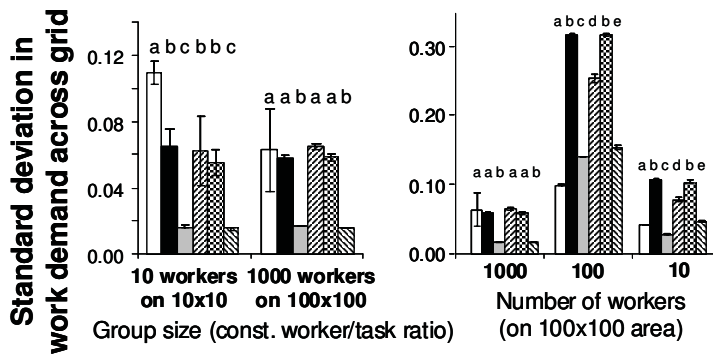
**Fig. 5:** I used a simple model of workers looking for work in a 2-dimensional nest. Each position in the nest had 2 different variables for 'work demand' associated with it, reflecting two different types of tasks. For example, one can imagine that each position in the nest needs to be regularly cleaned, repaired, the brood residing there cared for, etc. Here we only simulate two task types for simplicity. Workers in the nest move randomly while searching for work, and will check every time-step whether there is a need for work within their perception range. Depending on the task allocation mechanism used, they will then attend to this work, thus bringing local demand for work in this task down. After this, workers resume searching. The model was implemented in ObjC using the SWARM library (swarm.org).

As described in Fig. 4, I used a simplified representation of a social insect nest, containing workers and nest positions that needed work. I then compared how much of the needed work was performed depending on what behavioral rules, i.e. task allocation strategy, the workers were using. I compared global task allocation (a searching worker moves to the task that has the highest demand globally), random task choice (a worker will work at each time-step in a randomly selected local task), local task choice based on demand (a worker will work

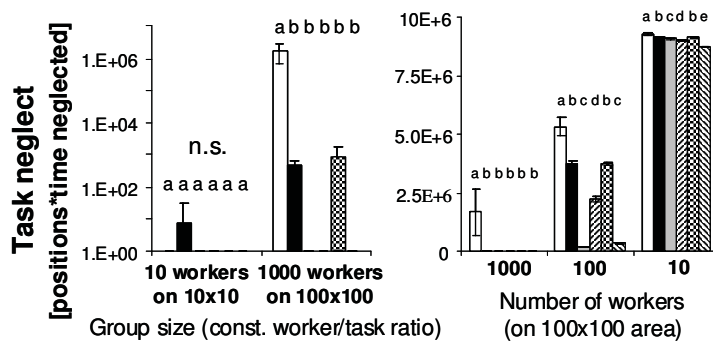
in the locally perceptible task that has the highest demand associated with it), and various threshold-based rules (each worker has a task-specific threshold, such that it only considers working in tasks whose demand exceeds this threshold). In the latter strategy, workers have inherent, fixed differences in their likelihood of working in any particular task; in the former strategies, all workers are identical. The three threshold-based strategies differ in that the first implies workers choose a task randomly as long as its demand exceeds their task-specific threshold; the second implies that workers can only test one position for its work demand at a time, and then choose to work or to continue searching; and the third implies that a worker will work on the task that has the highest demand divided by that workers task-specific threshold. Thus the last rule effectively lets workers choose the task that has the highest demand, but modulated by their task-threshold.



**Fig. 6a:** Group-level performance in the simulations was compared between different possible task allocation strategies. The intention was for workers to complete work particularly where demand was highest, and thus to keep overall demand low. In the first graph, I show proportion of work accomplished (between 0 and 1, defined as [1-average remaining demand level]) as a measure of success for the different strategies (shown are averages of 10 simulation runs with standard deviations). Details of individual behavior affect the performance of the group as a whole in all conditions (ANOVA, all  $p < 0.05$ ). It seems that a task allocation strategy in which workers are identical and select work based on highest demand ('Local best') outperforms all other strategies under many circumstances: different letters above bars indicate significant differences in Tukey's post hoc test (for each condition separately).



**Fig. 6b:** Strategies differed in the overall amount of work accomplished (see Fig. 6a), but they also differed in how accurately workers chose the tasks that were in highest demand. Here I show the amount of variation, i.e. spatial heterogeneity, produced by the different task allocation strategies.



**Fig. 6c:** This graph shows how much work was neglected under different assumptions. High values indicate bad performance (because workers fail to do the necessary work). With variation among workers in task preferences, fewer positions in the nest were neglected compared to random task choice. It is somewhat surprising that the global task allocation had so low performance; this may be caused by its tendency to send several workers to the same position, creating competition.

I was able to measure group-level task performance for the different task allocation strategies, and these strategies differed in their success (measured either as overall work accomplished, as amount of work neglected, or as amount of variation in demand across positions and task types, see Fig. 6). In particular, I also found that the worker/work ratio, i.e. whether there is always more work available than workers can complete, or whether there are more workers than needed, strongly affects which task allocation mechanism is optimal (Fig. 6). With more workers (but constant work, i.e. less work per worker), choosing based on local highest demand does best. With fewer workers (and more work per worker), completely random selection becomes better (even the best strategy). This sounds plausible, as when there is much more work than can ever be accomplished, just working anywhere randomly is as good as anything and saves travel time. However, although random selection can produce the best result in terms of work accomplished, it also causes much variation and neglect of individual positions, whereas task selection based on locally highest demand (with or without variation among workers) keep neglect to a minimum. With more work per worker, the threshold rules, i.e. those that imply variation among workers in task preferences, generally do better compared to other strategies. Thus specialization (=differences between individuals through response thresholds) may be beneficial to prevent crowding at high-demand tasks, or to spread individuals across the 2 task types. Worker crowding and worker/work ratio are factors that have not received much attention in empirical studies; it would be interesting to see what the worker/work ratio is in social insect colonies. Evolutionary considerations indicate that more work completed should always increase fitness, so in a sense one may argue that there is always more work available than workers can complete. However, it is likely that the benefits of more nest defense, more brood care, etc. level off eventually in real social insect colonies, because reproductive rates, nest size, even food collection may be constrained by other factors. Thus, whether real colonies operate near this work saturation point or not would be an interesting question, which may affect the optimal behavioral strategy in division of labor for different species.

## 5 Conclusion

In summary, individual-based models are useful for testing hypotheses about the benefits of different collective strategies under varying ecological conditions [25, 30, 32, 39-41]. Considering spatial heterogeneity and heterogeneity in individual behavior and information can be crucial to understanding how behavioral rules at the individual level can lead to complex adaptive group behavior. They can also be used to understand the evolution of particular collective strategies, if the performance of different strategies under different environmental conditions is quantified, as demonstrated here with communication and division of labor.

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