

Neural networks as mechanisms to regulate division of labor

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Abstract

In social insects, workers perform a multitude of tasks such as foraging, nest construction and brood rearing without central control of how work is allocated among individuals. It has been suggested that workers choose a task by responding to stimuli gathered from the environment. Response threshold models assume that individuals in a colony vary in the stimulus intensity (response threshold) at which they begin to perform the corresponding task. Here we highlight the limitations of these models with respect to colony performance in task allocation. First, we show with analysis and quantitative simulations that the deterministic response threshold model constrains the workers' behavioral flexibility under some stimulus conditions. Next, we show that the probabilistic response threshold model fails to explain a precise colony response to varying stimuli. Both of these limitations are detrimental to colony performance when dynamic and precise task allocation is needed. To address these problems we propose extensions of the response threshold models by adding variables that weigh stimuli. We test the extended response threshold model in a foraging scenario and show in simulations that it results in an efficient task allocation. Finally, we show that response threshold models can be formulated as artificial neural networks, which consequently provide a comprehensive framework for modeling task allocation in social insects.

Keywords task allocation, social insects, division of labor, response thresholds, neural networks.

Introduction

High levels of cooperation are often cited as the primary reasons for the ecological success of social insects (Oster and Wilson 1978; Hölldobler and Wilson 1990; Robinson 1992). In social insects, workers perform a multitude of tasks such as foraging, nest construction and brood rearing without central control of how work is allocated among individuals (Wilson and Hölldobler 1988; Seeley 1989; Gordon 1996; Pratt 2005). Experimental evidence indicates that individuals in a colony vary in their propensity to perform different tasks (Oldroyd et al 1993; Julian and Cahan 1999; Kryger et al 2000; Jones et al 2004; Robinson et al 2009). It has been suggested that workers choose a task by responding to stimuli gathered from the environment (e.g., presence or absence of food) or from interactions with other workers (Bonabeau et al 1996).

Empirical studies have identified a variety of factors affecting the stimulus intensity (response threshold) at which workers initiate to perform a given task (Duarte et al in press). First, in many species there is a strong division of labor based on the age of workers, a phenomenon designated age polythe-

ism (Oster and Wilson 1978; Wilson 1971). Second, size and morphology is also strongly correlated with the likelihood of workers to undertake the various tasks in species with distinct morphological castes (Wilson 1980). Third, in species with multiply-mated queens or multiple queens per colony, different patriline and matriline tend to differ in their tendencies to perform certain tasks demonstrating a genetic component in response threshold (e.g., Robinson and Page (1988)). Finally, individual experience has been shown to influence task preference in the ant *Cerapachys biroi* (Ravary et al 2007).

The combined effects of age, size, genetic background and individual experience should lead to substantial intra-colony variation in response thresholds. The resulting individual difference in the response of workers to a given stimulus intensity leads to individuals with a lower threshold for a given task being more likely to perform that task than individuals with a higher threshold. A variety of models have been proposed to account for the emergence of intra-colony division of labor on the basis of variation in response thresholds (Robinson 1987, 1992; Bonabeau et al 1996; Page Jr and Mitchell

1998; Theraulaz et al 1998; Graham et al 2006; Jeanson et al 2007) (see Beshers and Fewell (2001) and Smith et al (2008)).

The two most often used models are the deterministic response threshold model (DTM) (Page Jr and Mitchell 1998), and the probabilistic response threshold model (PTM) (Bonabeau et al 1996). Both models assume that all workers receive information of the colony needs via commonly perceived stimuli. With the DTM each worker performs the task with the highest positive difference between the stimulus and its own corresponding response threshold. If all the stimuli are lower than the corresponding thresholds the worker remains idle. With the PTM the relation between stimulus and threshold is interpreted as a probability to perform the task. While these response threshold models are frequently used to explain division of labor in colonies of social insects (Bertram et al 2003; Graham et al 2006; Jeanson et al 2007), no attempts have been made to quantify their efficiency in task allocation. Here we show with analysis and quantitative simulations that DTM (Page Jr and Mitchell 1998) and PTM (Bonabeau et al 1996) lead to sub-optimal colony performance under some stimulus conditions. To overcome these problems we propose an extended response threshold model (ETM) that can result in an efficient task allocation for any stimulus conditions. We experimentally compare all models by means of directed evolution (Nolfi and Floreano 2000; Floreano and Keller 2010) in a foraging scenario that requires a dynamic re-allocation of workers to different tasks according to colony needs (Tarapore et al 2010). Finally, we show that the response threshold models can be formulated as artificial neural networks (McClelland et al 1986; Haykin 1998), which consequently constitute a comprehensive framework for modeling task allocation in social insects.

Materials and Methods

Task allocation mechanism

We assumed that workers receive information of the colony needs via commonly perceived stimuli and that workers' thresholds do not vary during their lifetime. We considered a colony composed of 1000 workers facing two distinct tasks. In DTM every worker has two thresholds corresponding to each of the two tasks. A worker performs the task with the highest positive difference between the stimulus and its own corresponding response threshold, or remains idle if both of its thresholds are higher than the stimuli (Page Jr and Mitchell 1998; Jeanson et al 2007). If the difference between the stimulus and the worker's corresponding response thresholds is the same for all tasks, one of them is randomly chosen and performed by the worker. In PTM, every worker has two thresholds corresponding to each of the two tasks and the difference between stimulus and corresponding response threshold constitutes the probability of being engaged in the corresponding task. In *Electronic Supplementary Material (ESM) Appendix* we show that our probabilistic model is very similar to the original probabilistic response threshold model (Bonabeau et al 1996), as both models lead to similar colony performance and patterns of division of labor [*ESM Appendix D*]. In ETM, every worker has two thresholds corresponding to each of the two tasks and two weights corresponding to each of the two stimuli. A worker performs the task with

the highest positive difference between the weighted stimulus and its own corresponding response threshold, or remains idle if both of its thresholds are higher than the weighted stimuli. If the difference between the weighted stimulus and the worker's corresponding response threshold is the same for all tasks, one of them is randomly chosen and performed by the worker. For formal definitions of all models see [*ESM Appendix A*].

The response threshold models (DTM and PTM) and the extended response threshold model (ETM) can all be formulated as a more general class of parallel distributed processing models, known as artificial neural networks (McClelland et al 1986; Haykin 1998; Lek and Guégan 1999). Artificial neural networks have been successfully used to control the behaviour of individuals in a colony (see e.g. Floreano et al (2007); Waibel et al (2009)) making it a useful approach to consider in modeling task allocation in social insects. An artificial neural network is a computational model that consists of a set of units (neurons) connected by weighted links, where the response of the output units is the sum of weighted inputs (McClelland et al 1986). In DTM and PTM, each stimulus constitutes an input, the thresholds are the weights of the additional input constantly set to -1 and the allocated task for the worker is derived from the output neurons (Fig. 1A and 1B). While in DTM and PTM the weights for task stimuli are set to $+1$, in ETM they can vary between workers (Fig. 1C). In DTM and ETM a worker performs the task corresponding to the output unit with highest positive value, or remains idle if both outputs are lower or equal to 0. In PTM the values of the output units are interpreted as probabilities of performing the corresponding tasks.

In artificial neural networks with so-called hidden neurons, a non-linear activation function that transforms the output of the neuron is often used. Because the artificial neural networks used here do not need non-linear activation functions and do not have hidden units, we do not mention such a function explicitly. Mathematically speaking, we consider the activation function to be the identity function. If the neuronal formalism gets extended, one may use the activation function, depending on the needs of the architecture.

Colony tasks

To quantify the workers' efficiency in task allocation we used a stochastic agent-based simulation to model a situation in which workers had to perform two distinct tasks (Tarapore et al 2010). Our aim was to mimic situations with two vital tasks such as foraging and regulation of nest temperature. If the colony is efficient in foraging but does not regulate nest temperature well, the brood may die. Conversely, if nest temperature is well regulated, but little food is collected, only few offspring can be reared. A colony consisted of 1000 workers placed in an environment with an infinite number of two types of items, foraging and regulatory. The colony lifespan was divided into 100 time-steps. At the beginning of each time-step, a worker was presented with two task stimuli, one for the foraging items and the other for the regulatory items. If there were no items in the nest, the corresponding stimulus was set to its maximal intensity, which was 1. Otherwise, the intensity of the stimulus for each task was inversely proportional to the number of corresponding items in the nest. At each time step, every worker performed the chosen task

(or stayed idle) according to the task allocation mechanism (DTM, PTM, ETM) considered in the experiment. At each time step, a worker had a probability of 0.1 to successfully collect one item corresponding to the task performed and, at each time-step, the number of foraged and regulated items in the nest were depleted by ten items with an expected probability of 0.4. For formal definitions of the stimulus dynamics and the foraging scenario see [ESM Appendix C].

The colony performance directly depended on the number of collected foraging items, but these were counted only when the number of regulatory items in the nest was within predefined bounds (140 – 160 items). At the first time-step of a simulation, there were no items of the foraging and regulatory tasks in the nest. The colony performance (fitness) f was calculated by adding the partial performance obtained at each time-step, with $f = \sum_{t=1}^{100} f(t)$ where the colony performance at each time-step ($f(t)$) was quantified as the number of items of the foraging task collected when the number of items of the regulatory task present in the nest was between 140 and 160: $f(t) = b(t) \cdot g^F(t)$ where $b(t) = 1$ if $140 \leq g^R(i) \leq 160$ and $b(t) = 0$ otherwise, $g^F(t)$ represents the number of items foraged at time-step t and $g^R(t)$ the number of items being regulated within the nest at time-step t . Thus, if colonies performed well in only one of the two tasks, their fitness was low. We normalized the resulting fitness values by 10000, which is the expected amount of foraging items collected if all 1000 workers were foraging for all 100 time-steps with the probability of success equal to 0.1.

In all simulations the regulatory bounds were constantly fixed to the same values (140 – 160 items) (Tarapore et al 2010). Changing the regulatory bounds would not qualitatively affect our results. First, the regulatory bounds have to be narrow for the regulatory task to require a dynamic reallocation of workers. Thus, the difference between the regulatory upper bound and the regulatory lower bound should not be varied. Second, placing the regulatory bounds on a different level (e.g., 100 – 120 or 200 – 220 items) would change only the relative length of the “initialization” phase (i.e., when the regulatory items are accumulated to reach the lower bound for the first time) and the “control” phase (i.e., when the regulatory items are maintained within the regulatory bounds). Such a change does not qualitatively affect any of the models’ properties that we investigated.

The fitness function used here lead to a strong influence of the efficient performance of the regulatory task on the benefits of foraging. It is likely that the efficient performance of two tasks frequently does not interact so strongly under natural conditions. However, we used such a strong on-off transition to get clearer results on the processes regulating the efficient performance of two complementary tasks. In some cases such a strong on-off transition may also occur in natural situations, for example as a result of dramatic variation in temperature affecting brood survival or colony response to flooding (which requires rapid movement of all individuals to avoid colony extinction). Note also that, for simplicity we assume no conflict of interest among colony members about task allocation (i.e., the fitness of all colony members is proportional to overall colony performance). This would, for example, be the case of a species where workers are completely sterile or when task performance does not affect the likelihood of an individual to reproduce in the future.

Genetic architecture

In experiments with DTM each worker had a genome consisting of two thresholds, both ranging from -1 to $+1$ (8-bit encoding, 256 possible real values with a resolution of $\frac{1}{128}$). In experiments with PTM each worker had a genome consisting of two thresholds, both ranging from -1 to $+1$ (8-bit encoding, 256 possible real values with a resolution of $\frac{1}{128}$). In experiments with ETM each worker had a genome consisting of two thresholds and two weights, all ranging from -1 to $+1$ (8-bit encoding, 256 possible real values with a resolution of $\frac{1}{128}$).

Although threshold values are typically expected to be non-negative (Bonabeau et al 1996; Page Jr and Mitchell 1998; Graham et al 2006; Jeanson et al 2007) we allowed values between -1 to $+1$ in order to be consistent with the formalism of neural networks weights. We conducted a control experiment for DTM with thresholds in the range from 0 to $+1$ (8-bit encoding, 256 possible values with a resolution of $\frac{1}{256}$) to make sure that our choice did not significantly affect the result of the experiments. We support this claim in [ESM Appendix D], showing that the different range of threshold values does not importantly alter the division of labor patterns and colony behavior in the treatments with DTM.

Reproduction and selection

Artificial selection was conducted in thirty independent replicates for each of the three treatments. We used populations of 1000 colonies, each consisting of 1000 workers. At the first generation of each replicate, the alleles of all 1 000 000 workers were set randomly to one of the 256 values between -1 and $+1$ with a resolution of $\frac{1}{128}$. To construct the 1000 colonies of the following generation we selected the 300 colonies with the highest fitness (performance). This selected pool of 300×1000 workers was used to create the next generation of workers by using fitness proportional selection (i.e., the probability of a worker to contribute to the next generation was proportional to its colony fitness). The newly created 1 000 000 workers were then randomly distributed among the new 1000 colonies of the following generation. Finally, the alleles of the workers were mutated, i.e., with a probability of 0.001 each allele was set randomly to one of the 256 values between -1 and $+1$ with a resolution of $\frac{1}{128}$.

Worker behaviour and statistical analysis

To compare the task allocation efficiency for DTM, PTM and ETM we averaged, for each treatment and replicate, the performance of the 1000 colonies (30 replicates per treatment) at generation 1000. The same procedure was applied to compare other characteristics of the models. In order to understand the difference in performance between the models, we compared the proportion of workers in each of the three states (foraging, regulating, idle) averaged over all 100 time-steps (Fig. 3). We also compared the proportion of workers in each of the three states as a function of the time-step (Fig. 4). Next, we compared the number of workers’ transitions between states summed over all 1000 workers and all 100 time-steps, normalized by the number of all state transitions (separately for each model). Next, we compared the time that the regulatory items were out of the predefined bounds dur-

ing the entire colony lifespan (Fig. 6A). We also compared the time until the regulatory items were within the predefined bounds (140-160) for the first time (Fig. 6B). Finally, we compared the proportion of colonies that kept the regulatory items within the predefined bounds as a function of the time-step (Fig. 7). In a statistical test we compared the proportion of colonies that kept the regulatory items within the predefined bounds after they were within the predefined bounds for the first time (in order to provide a fair comparison it was performed at the 50th time-step for all treatments). Statistical significance within all treatments was determined with the Kruskal-Wallis test (nonparametric one-way analysis of variance) and between a pair of treatments with the Wilcoxon test (rank sum test for equal medians). The statistical tests were performed after the 1000th generation.

Results

Theory

The common understanding of the response threshold models is that the workers' tendency to perform various tasks depends on its thresholds and that, by changing the threshold values, the worker can express any behavior, from generalist (switching between tasks) to specialist (dedicated to a specific task) (Robinson 1992; Bonabeau et al 1996; Beshers and Fewell 2001). However, a mathematical analysis of the DTM reveals that the worker's behavioral flexibility depends not only on the worker's thresholds, but also on the difference between stimulus intensities. In particular, a worker can switch from task A to task B, only if there is a decrease in the difference between stimulus intensities of task A and task B. A worker can switch back from task B to task A, only if there is an increase of the aforementioned difference. [see *ESM Appendix B* for more details]. Thus, contrary to the intuition standing behind the response threshold models (Robinson 1992), the workers' behaviors were influenced not only by the absolute intensities of the stimuli, but also by their relative intensities. Consequently, the values of the stimuli constrain the worker's ability to switch tasks regardless of the values of the individual thresholds. In the PTM this constraint is less marked, because the workers' responses are stochastic, thus allowing them to switch tasks more easily. However, stochastic individual responses make the response at the colony level more unreliable, even under fixed stimuli conditions (i.e., for the same stimuli intensities the response of a worker may be different, due to its random component). Thus, both the DTM and the PTM have limitations, which could be detrimental to colony performance. These problems can be overcome by extending the DTM with additional variables that weigh stimuli (ETM, Fig. 1). The weights relax the constraints on the flexibility of task allocation by allowing the workers to scale the stimuli if needed [see *ESM Appendix B* for more details]. At the same time, the deterministic decision rules employed in the ETM allow the workers to precisely respond to changing colony needs.

Simulations

To test whether the ETM allows a higher behavioral flexibility of workers and/or more precise responses at the colony

level to varying stimuli, hence translating in a higher colony performance, we conducted experimental evolution with a stochastic agent-based simulation to model a situation in which workers had to perform two distinct tasks. The first was a regulatory task where workers had to maintain the amount of a given food item in their colony within predefined bounds. This would, for example, be the case of a honeybee colony maintaining about one kilogram of pollen in the hive or workers regulating within-hive temperature (Seeley 1995). The other was a foraging task where workers had to collect the highest possible amount of a second type of food item. Consequently, at a given point in time a worker could be engaged in the regulatory task, could be engaged in the foraging task (foraging worker) or could be inactive (idle worker). The fitness of colonies was a function of workers being able to perform both tasks efficiently (Tarapore et al 2010, see *Methods*).

For each of the three models, the performance of the colonies rapidly increased within the first 200 generations of selection, and converged within 1000 generations (Fig. 2). However, there were important efficiency differences between the models (Kruskal-Wallis test, $df = 2$, $p < 0.001$). The highest performance was achieved for the ETM (PTM: -10.3% ; DTM: -20.4% ; all pairwise Wilcoxon tests $df = 29$, $p < 0.001$).

The difference in performance between threshold models was associated with differences in the proportion of workers engaged in the foraging task (Kruskal-Wallis test, $df = 2$, $p < 0.001$). The proportion of foraging workers was the highest for the ETM (PTM: -1.1% ; DTM: -10.5% ; all pairwise Wilcoxon tests $df = 29$, $p < 0.001$; Fig. 3). The proportion of workers staying idle also differed (Kruskal-Wallis test, $df = 2$, $p < 0.001$) and was the lowest for the ETM (PTM: $+2293.2\%$; DTM: $+21907.5\%$; all pairwise Wilcoxon tests $df = 29$, $p < 0.001$; Fig. 3). By contrast, there was only little variation in the proportion of workers engaged in the regulatory task (Fig. 3), although the differences among models were significant (Kruskal-Wallis test: $df = 2$, $p < 0.001$). Furthermore, with the PTM the proportion of foraging workers was not constant during the entire colony lifespan and decreased in time, which was not observed for other models (Fig. 4).

The differences in workers' distribution among the three threshold models was associated with the differences in the frequency of worker transitions between being engaged in the foraging and regulatory tasks and staying idle (six Kruskal-Wallis tests, one for each type of transition: all $df = 2$, all $p < 0.001$; Fig. 5). In line with theoretical predictions the behavioral flexibility between the foraging and regulatory tasks was constrained with the DTM, with the effect that the workers switched much more often between the regulatory task and staying idle, than with other models (all pairwise Wilcoxon tests: $df = 29$, $p < 0.001$; Fig. 5). This lack of flexibility in switching tasks resulted in a high proportion of idle workers with DTM so as to respond efficiently to changes in colony needs (Fig. 3). By contrast, with the PTM and ETM the workers readily switched between the regulatory and foraging tasks (all pairwise Wilcoxon tests: $df = 29$, $p < 0.001$; Fig. 5), thus not requiring the colonies to maintain a high proportion of idle workers (Fig. 3).

The difference in foraging strategies induced by the three

threshold models translated in variation in the proportion of time during which the regulatory items were out of the predefined bounds during colony lifespan (Kruskal-Wallis test: $df = 3$, $p < 0.001$). The most efficient regulation was with the ETM (all pairwise Wilcoxon tests: $df = 29$, $p < 0.001$; Fig. 6A). The difference between models in the efficiency of regulation was primarily due to two factors. First, there were differences in the time until the regulatory items were within the predefined bounds for the first time (Kruskal-Wallis test: $df = 3$, $p < 0.001$), the most efficient model being the ETM (PTM: +267.5%, DTM: +384.2%; all pairwise Wilcoxon tests: $df = 29$, $p < 0.001$; Fig. 6B). Second, there were differences in the proportion of colonies that successfully kept the regulatory items within the predefined bounds, after they first were within predefined bounds (Kruskal-Wallis test: $df = 3$, $p < 0.001$), the most efficient models being both the DTM and ETM (PTM: -2.1%; Wilcoxon test between DTM and ETM: $df = 29$, $p = 0.11$; all other pairwise Wilcoxon tests: $df = 29$, $p < 0.001$; Fig. 7).

We investigated the sensitivity of our findings to changes in the implementation of mutations and in the population's size. We conducted additional experiments with two alternate mutation's implementations (Gaussian mutations and mutations switched off instead of uniform mutations) and two smaller population's sizes (100 and 500 colonies instead of 1000). These experiments showed that the results were robust to changes in both cases [see *ESM Appendix E* for more details].

Discussion

A comparison of the deterministic (Page Jr and Mitchell 1998), probabilistic (Bonabeau et al 1996) and our new extended response threshold models showed that they affect the workers' responses to varying stimuli and colony performance. As predicted by our formal analysis, the deterministic response threshold model was found to constrain the workers' ability to switch tasks because workers with a high foraging threshold and a low regulatory threshold became idle when the regulatory items were within bounds and the foraging stimulus was lower than the workers' thresholds. Consequently, the colony performance was low with the deterministic response threshold model when a dynamic task allocation was required. In the case of the probabilistic response threshold model, the workers' behavioral flexibility was less limited, but the colony was unable to precisely respond to changes in the stimuli values as a response of the stochastic switching between tasks. This led to a relatively low colony performance. Additionally, when the stimuli decreased, the probability that a worker performed a corresponding task decreased too (even if the stimulus was above the threshold). Thus, when the foraging stimulus was low, workers more often switched between being engaged in the foraging task and staying idle, which also had a detrimental effect on colony performance. The extended model did not suffer from these limitations because the weights of the stimuli allowed the workers to switch tasks, while keeping their response deterministic.

We showed that the response threshold models (Bonabeau et al 1996; Page Jr and Mitchell 1998) and the extended models proposed in this paper could be formulated as artificial

neural networks. The neuronal formalism introduced here will be useful for further extension of models, such as for example changing the threshold values with age or the integration of adaptive learning, where the connection weights of the neural network are updated using experience-based learnings rules (Floreano and Urzelai 2001; Floreano et al 2008). Furthermore, one could use neural networks with recurrent connections (Mandic and Chambers 2001), to equip the workers with a memory. These, and other, extensions would facilitate addressing increasingly complex and biologically relevant questions on division of labor in social insects. Of note, although we considered a situation with only two tasks, the neuronal formalism can be easily scaled for a higher number of tasks.

We focused on a situation with two tasks, one of which is regulatory (the number of items in the nest ought to be kept within boundaries) and the other that is maximizing (the number of foraged items ought to be maximized). The results allow us to speculate how the models compare in three other situations: 1) with both foraging tasks, 2) with both regulatory tasks and 3) with more than two tasks. First, with two foraging tasks the simulation is strongly simplified, and of little interest, because there is no need to dynamically reallocate the workers between the tasks. Thus, all models should lead to high colony performance. Second, with two regulatory tasks, there could be two outcomes, depending on whether or not a dynamic reallocation of the workers is required. If not, the workers could split into two distinct subsets and handle the tasks independently. The workers from the first subset would perform the first task, or be idle, and the workers from the second subset would perform the second task, or be idle. In such a case, high performance should be obtained under both the deterministic and extended response thresholds models. While the probabilistic response threshold model, which is unable to provide a precise colony response to a stimulus change, should lead to a lower performance. On the contrary, if the dynamic reallocation of workers is required, the tasks cannot be handled independently by distinct subsets of workers. Consequently, this constitutes similar conditions to those of one regulatory task and one foraging task, and thus the colony performance and behavior should not differ from the ones observed in this study. Finally, if there are more than two tasks, all the limitations of the considered models still hold, and this should not qualitatively affect the results.

Our foraging system implicitly assumed that it was beneficial to minimize the number of idle workers. This might not always be the case in nature, as some idle workers may be beneficial for the colony, for example because of energy constraints (Gordon 1989; Robinson 1992; Krieger et al 2000) or to serve as reserve force that can be mobilized when needed (Wilson 1983; Gordon 1989; Robinson 1992). It would be possible to include such effects in more complex foraging scenario and study for example the expected relationship between the proportion of idle workers and colony size (Jeanson et al 2007; Dornhaus et al 2009). Finally, we assumed that the task stimuli are available to all workers in the colony. What happens to the workers' behavioral flexibility and task allocation efficiency in cases when stimuli are available to only a subset of workers, or depend on spatial configurations, is a question that remains to be investigated.

To further investigate the possible consequences of partial information, we performed a simulation with the version of the deterministic response threshold model proposed by Jeanson et al (2007). The stimuli are presented to each worker sequentially in a random order, and not all at once, as is assumed by Page Jr and Mitchell (1998). In particular, the workers always perform the first encountered task for which their threshold is lower than the corresponding stimulus. Thus, although the decisions made by the workers are deterministic, the model does not limit the workers' ability to switch tasks, because of the random order of task encounters. The performance and the behavior of the colonies evolved with the deterministic response threshold model with random task encounters are similar to the ones obtained for treatments with the extended response threshold model [*ESM Appendix D*]. This similarity of the phenotypic traits evolved using very different mechanisms of task allocation is interesting and might be a promising direction for further studies.

The main focus of the paper was to compare several commonly used models of task-allocation. We showed that by allowing for variation not only in stimulus response thresholds, but also by adding the weights to these perceived stimuli, one obtains a much more flexible task allocation system. In contrast to the original response thresholds models, the extended response thresholds model performs well under a wide range of environmental stimuli. However, it remains to be investigated what rule ants and other social insects use. In particular it would be interesting to study whether social insects employ more sophisticated rules than fixed threshold. While evolution is often considered to be an effective optimization process (Parker and Smith 1990) there are many factors such as stochasticity, genetic drift, insufficient time to reach the optimum or the existence of local maxima and other developmental and physiological constraints that may lead to non-optimal behavior (Pérez-Escudero et al 2009). With social insects the question of evolutionary optimality is especially difficult to address, because colonies are complex, multi-component systems. There are multiple functions on which persistence of the colony depends (e.g., foraging, colony maintenance, defense) and many constraints that the colony must respect (e.g., spatial, energy). Consequently, one cannot rule out the possibility that if a foraging strategy is sub-optimal, this might be due to increase performance of some other tasks that are also important.

It has recently been suggested that in systems of many components, the largest deviations from optimality are expected in those components with less impact on the indirect measure of fitness (Pérez-Escudero et al 2009). Applying this idea to social groups leads to some predictions associated with colony size differences. For example, an efficient and flexible task allocation is expected to be particularly important in small colonies which typically contain only few idle workers. By contrast, deviations from optimality in task switching might have a lower impact in large colonies which usually contain a substantial reserve force that can be mobilized when needed (Wilson 1983; Gordon 1989; Robinson 1992). Of interest would thus be to compare the mechanisms of task allocation among species varying in colony size and also investigate whether there are differences within species during the ontogeny of the colony.

Overall, our analyses highlight the limitations of the re-

sponse threshold models that are currently used in the literature (Robinson 1987, 1992; Bonabeau et al 1996; Page Jr and Mitchell 1998; Theraulaz et al 1998; Beshers and Fewell 2001; Bertram et al 2003; Graham et al 2006; Jeanson et al 2007; Smith et al 2008). We extended these models by weighting the stimuli. We also showed that the response thresholds model could be formulated as artificial neural networks thus providing a solid theoretical framework for further studies. Finally, it is worth mentioning that although threshold models have been developed to explain division of labor in social insect, they may also be used to devise efficient systems of task allocation and dynamic scheduling in engineering (Bonabeau et al 2000; Campos et al 2000; Matarić et al 2003; Berman et al 2009).

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A Online Appendix. Task allocation models

We assume that workers receive information of the colony needs via commonly perceived stimuli (Bonabeau et al 1996; Page Jr and Mitchell 1998) and that the workers' thresholds, and weights, do not vary during their lifetime (Bonabeau et al 1996; Page Jr and Mitchell 1998; Jeanson et al 2007). Following are the formal definitions of the deterministic response threshold model (DTM, Page Jr and Mitchell (1998)), the probabilistic response threshold model (PTM), the extended response threshold model (ETM) and the original probabilistic response thresholds model (oPTM) adopted from (Bonabeau et al 1996).

Let $T = \{1, 2, 3, \dots, n\}$ be the set of all time-steps indices. Let $M = \{1, 2, 3, \dots, m\}$ be the set of all workers indices. Let $s^A(t)$ be the stimulus of task A at the time-step t . Let $s^B(t)$ be the stimulus of task B at the time-step t . For every worker j there are two decision variables $o_j^A(t)$ and $o_j^B(t)$ that translate into being engaged in task A or B , or staying idle.

DTM and PTM: $o_j^A(t) = 1 \cdot s^A(t) - \theta_j^A$ and $o_j^B(t) = 1 \cdot s^B(t) - \theta_j^B$ where θ_j^A and θ_j^B are the thresholds of the worker j for tasks A and B , respectively.

ETM: $o_j^A(t) = w_j^A \cdot s^A(t) - \theta_j^A$ and $o_j^B(t) = w_j^B \cdot s^B(t) - \theta_j^B$ where w_j^A and w_j^B are the weights of the worker j for stimuli A and B , respectively.

oPTM: $o_j^A(t) = \frac{(s^A)^2}{(s^A)^2 + (\theta_j^A)^2}$ and $o_j^B(t) = \frac{(s^B)^2}{(s^B)^2 + (\theta_j^B)^2}$.

Let $W_j(t) \in \{A, B, I\}$ be the state of the worker j at the time-step t , where A and B stand for being engaged in task A and B , respectively, and I stands for staying idle.

DTM, ETM

$$W_j(t) = \begin{cases} A & \text{if } o_j^A(t) > 0 \text{ and } o_j^A(t) > o_j^B(t) \\ B & \text{if } o_j^B(t) > 0 \text{ and } o_j^B(t) > o_j^A(t) \\ Z & \text{if } o_j^A(t) = o_j^B(t) > 0 \\ I & \text{otherwise} \end{cases} \quad (1)$$

PTM, oPTM

$$W_j(t) = \begin{cases} A & \text{if } P_j^A(t) = 1 \text{ and } P_j^B(t) = 0 \\ B & \text{if } P_j^A(t) = 0 \text{ and } P_j^B(t) = 1 \\ Z & \text{if } P_j^A(t) = 1 \text{ and } P_j^B(t) = 1 \\ I & \text{otherwise} \end{cases} \quad (2)$$

Z is a random variable, which takes value A with probability $\frac{1}{2}$ (otherwise B). $P_j^A(t)$ and $P_j^B(t)$ are random variables, which take value 1 with probability $o_j^A(t)$ and $o_j^B(t)$, respectively (otherwise 0).

B Online Appendix. Formal analysis of DTM and ETM

Let us consider the DTM (see *ESM Appendix A*). In practice, the third condition from Equation 1 is rarely met, therefore

for further analysis the model can be simplified:

$$W_j(t) = \begin{cases} A & \text{if } s^A(t) - \theta_j^A > 0 \text{ and } s^A(t) - \theta_j^A > s^B(t) - \theta_j^B \\ B & \text{if } s^B(t) - \theta_j^B > 0 \text{ and } s^B(t) - \theta_j^B > s^A(t) - \theta_j^A \\ I & \text{otherwise} \end{cases} \quad (3)$$

Let us denote by $T_j^A = \{t \in T \mid W_j(t) = A\}$ the set of time-steps in which worker j is engaged in task A and let us denote by $T_j^B = \{t \in T \mid W_j(t) = B\}$ the set of time-steps in which worker j is engaged in task B . From Equation 3 it follows:

$$\begin{aligned} \forall j \in M \forall t_j^A \in T_j^A \forall t_j^B \in T_j^B : \\ s^A(t_j^A) - s^B(t_j^A) > \theta_j^A - \theta_j^B \text{ and} \\ s^A(t_j^B) - s^B(t_j^B) < \theta_j^A - \theta_j^B \end{aligned} \quad (4)$$

From Equations 4 it follows:

$$\begin{aligned} \forall j \in M \forall t_j^A \in T_j^A \forall t_j^B \in T_j^B : \\ s^A(t_j^B) - s^B(t_j^B) < s^A(t_j^A) - s^B(t_j^A) \end{aligned} \quad (5)$$

Equation 5 holds true if and only if

$$\begin{aligned} \forall j \in M | T_j^B \neq \emptyset \wedge T_j^A \neq \emptyset : \\ \max_{t \in T_j^B} (s^A(t) - s^B(t)) < \min_{t \in T_j^A} (s^A(t) - s^B(t)) \end{aligned} \quad (6)$$

Equation 6 means that the difference between stimulus for task B and task A ($s^B(t) - s^A(t)$) in moments when a worker is performing task A ($t \in T_j^A$), is always smaller than the analogous difference ($s^B(t) - s^A(t)$) in moments when a worker is performing task B ($t \in T_j^B$). Note that Equation 6 holds true 1) for every worker, 2) regardless of the values of the thresholds and 3) regardless of the type of the two tasks (i.e., the tasks do not need to be foraging and regulation). Equation 6 limits the task allocation flexibility, because the sets T_j^A and T_j^B must be such that the Equation 6 is met. In other words, regardless of the individual thresholds, the values of stimuli may by definition constrain the workers' ability to switch tasks by restraining the T_j^A set and/or the T_j^B set (and thus restraining the time when the worker j can perform tasks A and B). In the extreme case, if one of the sets T_j^B and T_j^A is empty, then Equation 6 is always met, regardless of the other set. Note that if T_j^B or T_j^A is empty, it means a worker j is a specialist (performs only one task or is idle). This explains the experimental results where the number of transitions between performing a regulatory task and staying idle (which corresponds to the number of specialists) was higher while evolving the colonies for treatments with the DTM, than with other treatments [see *Results* in the *Main article*].

We obtained an analogous constraint (compare Equations 6 and 7) for the ETM by applying the same reasoning as for the DTM:

$$\begin{aligned} \forall j \in M | T_j^B \neq \emptyset \wedge T_j^A \neq \emptyset : \\ \max_{t \in T_j^B} (w_j^A \cdot s^A(t) - w_j^B \cdot s^B(t)) < \min_{t \in T_j^A} (w_j^A \cdot s^A(t) - w_j^B \cdot s^B(t)) \end{aligned} \quad (7)$$

The additional parameters in Equation 7 (the weights w_j^B and w_j^A) lift the constraints on the flexibility of task allocation.

Every worker has its own set of weights, which can evolve as such, that Equation 7 is met even if both T_j^B and T_j^A are not empty. Note that if both sets T_j^B and T_j^A are not empty, a worker j is a generalist (switches tasks). This explains the experimental results where the number of transitions between performing distinct tasks (which corresponds to the number of generalists) is higher while evolving the colonies for treatments with the ETM, compared to the DTM [see *Results* in the *Main article*].

The PTM escapes this analysis, because the model is not deterministic and basis on probabilities.

C Online Appendix. Simulation definition

Let $T = \{1, 2, 3, \dots, n\}$ be the set of all time-steps indices ($n = 100$). Let $M = \{1, 2, 3, \dots, m\}$ be the set of all workers indices ($m = 1000$). The state of each worker j in every time-step t ($W_j(t)$) is decided according to one of the models presented in *ESM Appendix A*, where task A is foraging task F and task B is regulatory task R . The foraging stimulus $s^F(t)$ and the regulatory stimulus $s^R(t)$ are defined as

$$\begin{aligned} s^F(t) &= 1 - 0.0001 \cdot a^F(t-1) \\ s^R(t) &= 1 - 0.005 \cdot a^R(t-1) \end{aligned}$$

$a^F(t)$ and $a^R(t)$ are the number of items accumulated in the nest at the time-step t , and are defined as

$$\begin{aligned} a^F(0) &= 0 \\ a^R(0) &= 0 \\ a^F(t) &= \sum_{i=1}^t (g^F(i) - d^F(i)) \\ a^R(t) &= \sum_{i=1}^t (g^R(i) - d^R(i)) \end{aligned}$$

$g^F(t)$ and $g^R(t)$ are the number of items gathered at the time-step t , and are defined as

$$\begin{aligned} g^F(t) &= \sum_{j=1}^m X_j^F(t) \\ g^R(t) &= \sum_{j=1}^m X_j^R(t) \end{aligned}$$

$X_j^F(t)$ and $X_j^R(t)$ are random variables such that

$$X_j^F(t) = \begin{cases} 1 & \text{with probability } p^F \text{ if } W_j(t) = F \\ 0 & \text{otherwise} \end{cases}$$

and

$$X_j^R(t) = \begin{cases} 1 & \text{with probability } p^R \text{ if } W_j(t) = R \\ 0 & \text{otherwise} \end{cases}$$

The probability of successful foraging p^F is set to value 0.1. The probability of successful regulation p^R is set to value 0.1. Values $d^F(t)$ and $d^R(t)$ are the number of items depleted from the nest at the time-step t , and are defined as

$$d^F(t) = \begin{cases} 0 & \text{if } d^F(t-1) = 10 \\ D & \text{if } d^F(t-1) = 0 \text{ and } d^F(t-2) = 10 \\ 10 & \text{if } d^F(t-1) = 0 \text{ and } d^F(t-2) = 0 \end{cases}$$

and

$$d^R(t) = \begin{cases} 0 & \text{if } d^R(t-1) = 10 \\ D & \text{if } d^R(t-1) = 0 \text{ and } d^R(t-2) = 10 \\ 10 & \text{if } d^R(t-1) = 0 \text{ and } d^R(t-2) = 0 \end{cases}$$

where D is a random variable, which takes value 10 with probability $\frac{1}{2}$ (otherwise 0).

D Online Appendix. Other response thresholds models

Deterministic response threshold model with non-negative values of thresholds. Although threshold values are typically expected to be non-negative (Bonabeau et al 1996; Page Jr and Mitchell 1998; Graham et al 2006; Jeanson et al 2007), in our experiments we allowed values between -1 to $+1$ in order to be consistent with the formalism of neural networks weights. We conducted a control experiment to confirm that our choice did not affect the results of the experiments. We found support for this claim, showing that there is a reasonable good agreement between the DTMs with different range of threshold values with respect to colony performance (Fig. D1, left) and colony dynamics (Fig. D2, top).

Original probabilistic response threshold model. We conducted a control experiment to test whether the PTM (which is in fact a probabilistic interpretation of the deterministic response threshold model proposed by Page Jr and Mitchell (1998)) produces a similar colony performance and workers' behavior, as the original probabilistic response threshold model proposed by Bonabeau et al (Bonabeau et al 1996) (oPTM). We found support for this claim, showing that there is a reasonable good agreement between different probabilistic response thresholds models with respect to the colony performance (Fig. D1, right) and colony dynamics (Fig. D2, bottom).

Deterministic response threshold model with random order of task encounters. We conducted a control experiment to test the effects of using the DTM as formulated by Jeanson et al (2007) (DTMR). The stimuli are presented to each workers sequentially in a random order, and not all at once, as in the DTM. In particular, the workers always perform the first encountered task for which their threshold is lower than the corresponding stimulus. Thus, although the decisions made by the workers are deterministic, the model does not limit the workers' ability to switch tasks, because of the stochastic order of task encounters. Interestingly, there is a very good agreement between the DTMR and ETM with respect to the colony performance (compare Fig. 2 and D1, right) and dynamics of the system (compare Fig. 4 and D2, top). It seems that the DTMR and ETM, which are different with respect to the mechanisms of task allocation, lead to the evolution of similar phenotypic traits. The possible implications of this finding still require to be solidly investigated.

Methods. In treatments with the DTM $[-1,1]$, PTM $[-1,1]$, oPTM $[-1,1]$ and DTMR $[-1,1]$ each worker had a genome consisting of two thresholds, both ranging from -1 to $+1$ (8-bit encoding, 256 possible values with a resolution of $\frac{1}{128}$). In treatments with the DTM $[0,1]$, oPTM $[0,1]$ each worker had a genome consisting of two thresholds, both ranging from 0

to +1 (8-bit encoding, 256 possible values with a resolution of $\frac{1}{256}$). We tested the oPTM with non-negative values of the thresholds, because in this way the model was defined originally Bonabeau et al (1996). Of note, on contrary to the models based on artificial neural networks proposed in the *Main article*, using negative thresholds with the oPTM does not increase the explanatory power of the model. This is because in the oPTM the thresholds are risen to the second power and thus information about the sign of the thresholds is disregarded. We used the same experimental methods and settings as in the *Main article* [see *Methods*].

E Online Appendix. Sensitivity analysis.

Using different population sizes. To test the sensitivity of the results to different population size we performed two control experiments, with populations consisting of 100 colonies and with populations consisting of 500 colonies. Other simulation settings were the same as in the *Main article* [see *Methods*]. In particular, we used the same mutation (i.e., with a probability of 0.001 each allele was set randomly to one of the 256 values between -1 and $+1$ with a resolution of $\frac{1}{128}$), to which we refer as uniform mutation. We found that both control experiments are in agreement with the results reported in the main text, with respect to the colony performance (Fig. E1.A,B) and colony dynamics (Fig. E2.A,B).

Using different mutation. To test the sensitivity of the results to different mutations we performed two control experiments. In the first one, the mutation was switched off. In the second one, all alleles of the workers were mutated by adding a random value with a resolution of $\frac{1}{128}$. The values of mutations were generated using a Gaussian distribution (mean \pm s.d.: 0 ± 0.0075), so that the magnitude of the value was inversely proportional to its probability of occurrence. We refer to this mutation as frequent Gaussian mutation. All alleles that by mutation became lower than -1 or greater than $+1$ were reflected back above -1 or below $+1$ accordingly (i.e., if the value after mutation was $v > +1$ we used $2 - v$ instead, and if the value after mutation was $v < -1$ we used $-2 - v$ instead). Other simulation settings were the same as in the *Main article* [see *Methods*]. We found that both control experiments are in agreement with the results reported in the main text, with respect to the colony performance (Fig. E1.C,D) and colony dynamics (Fig. E2.C,D)

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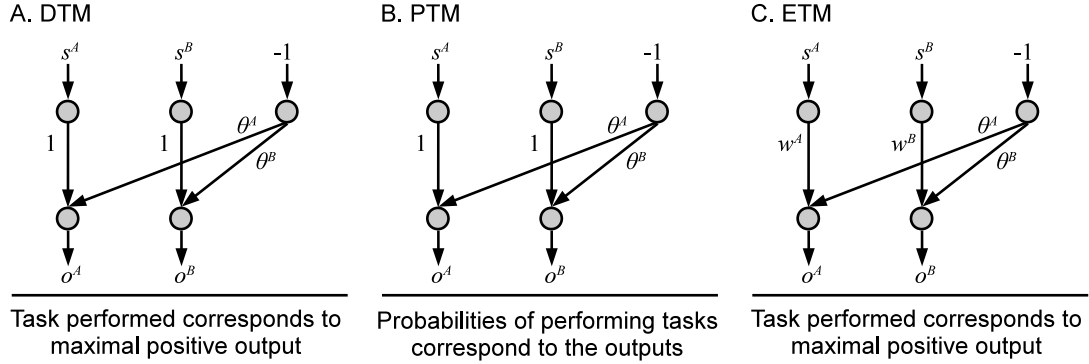


Figure 1: Task allocation mechanisms: A) deterministic response threshold model (DTM), B) probabilistic response threshold model (PTM), C) extended response threshold model (ETM). Consider a colony composed of multiple workers facing two tasks: A and B . s^A stands for the task A stimulus, s^B for the task B stimulus, θ^A and θ^B are the corresponding thresholds. Outputs are the sum of the weighted inputs and are calculated as $o^A = 1 \cdot s^A - \theta^A$ and $o^B = 1 \cdot s^B - \theta^B$ (for DTM and PTM), and as $o^A = w^A \cdot s^A - \theta^A$ and $o^B = w^B \cdot s^B - \theta^B$ (for ETM). Note that ETM uses two additional variables, namely w^A and w^B which are the weights for the connections between corresponding input and output neurons. In the case of the DTM and PTM these weights are constant and set to $+1$. In A and C each worker collects items of the type corresponding to the output unit with highest positive value, or remains idle if both outputs are lower or equal to 0. In B the values of the output units are interpreted as probabilities for the worker to choose the corresponding task. For the sake of simplicity we considered a situation with only two tasks, but the presented formalism scales to any number of tasks.

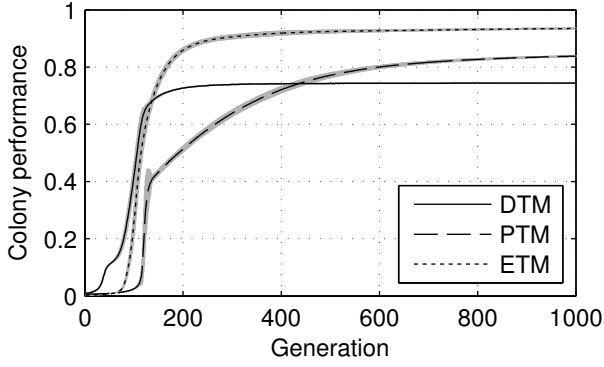


Figure 2: Mean \pm s.d. (in grey) performance of each of the three response threshold models over 1000 colonies (30 replicates). The performance directly depended on the number of the collected items of the foraging task, but these were counted only when the number of items of the regulatory task was within predefined bounds. Thus, the performance was high only if the workers efficiently performed both the regulatory and foraging tasks.

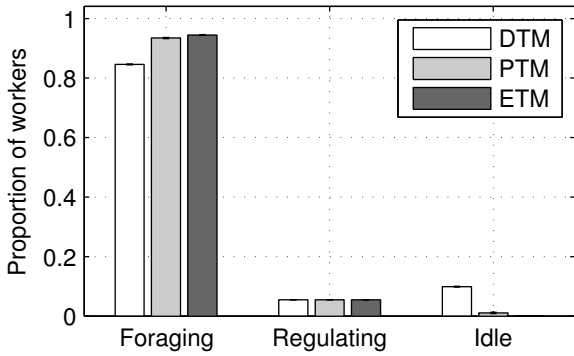


Figure 3: Mean \pm s.d. proportion of workers engaged in foraging, regulating or staying idle. Results are given for each of the three models, over 100 time-steps and 1000 colonies of the 1000th generation (30 replicates).

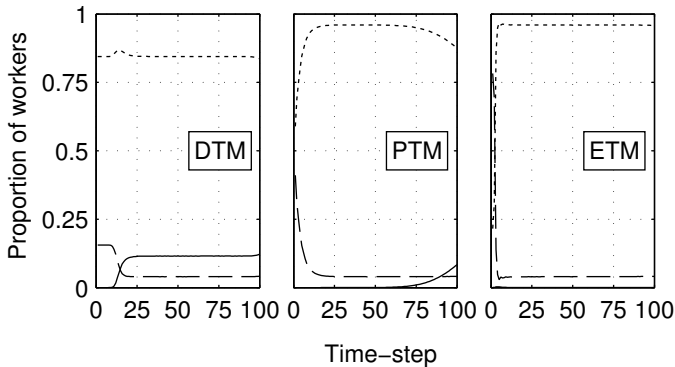


Figure 4: Mean proportion of workers engaged in the foraging task (short-dashed line), in the regulating task (long-dashed line) or staying idle (solid line) as a function of time-steps. Results are given for each of the three models, over 1000 colonies of the 1000th generation (30 replicates).

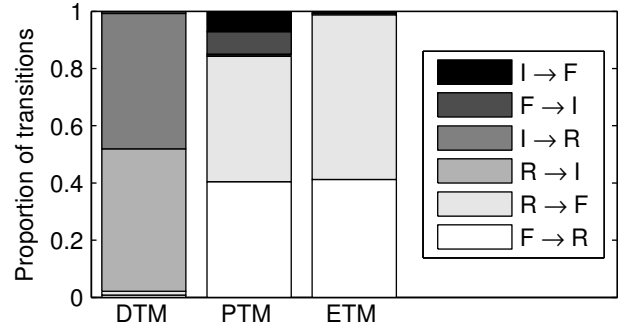


Figure 5: Mean proportion of transitions between being engaged in foraging and regulatory tasks and staying idle, summed over 1000 workers. R stands for the regulatory task, F stands for the foraging task, I stands for idle and \rightarrow stands for the direction of the transition. Results are given for each of the three models, over 100 time-steps and 1000 colonies of the 1000th generation (30 replicates). Normalized separately for each model, by the number of all state transitions (number of all state transitions DTM: 3829 ± 147 , PTM: 10926 ± 296 , ETM: 4543 ± 327).

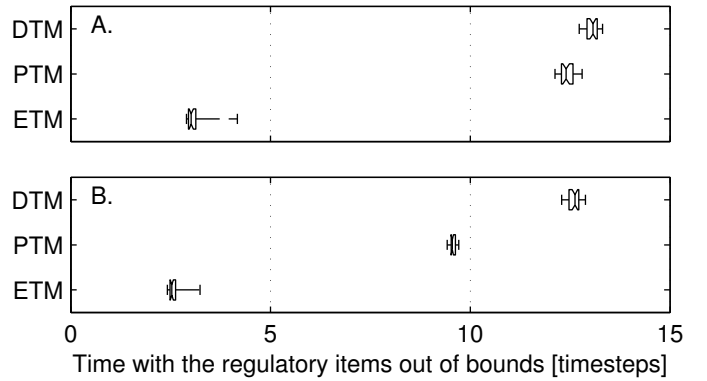


Figure 6: Box and Whisker plots showing the number of time-steps: A) that the regulatory items were out of the predefined bounds during entire colony lifespan, B) until the regulatory items were within the predefined bounds for the first time. Results are given for each of the three models, over 1000 colonies of the 1000th generation (30 replicates).

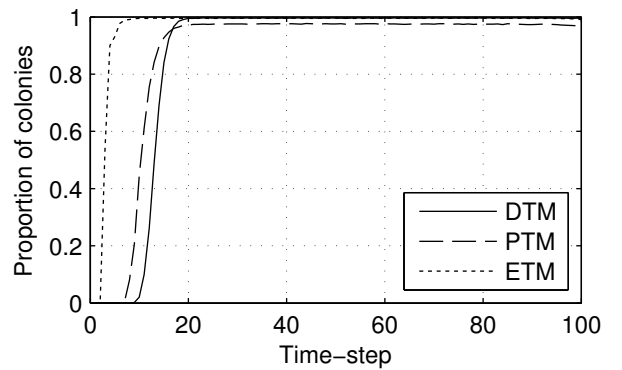


Figure 7: Mean proportion of colonies, with regulatory items within the desired bounds as a function of time-step. Results are given for each of the three models, over 1000 colonies of the 1000th generation (30 replicates).

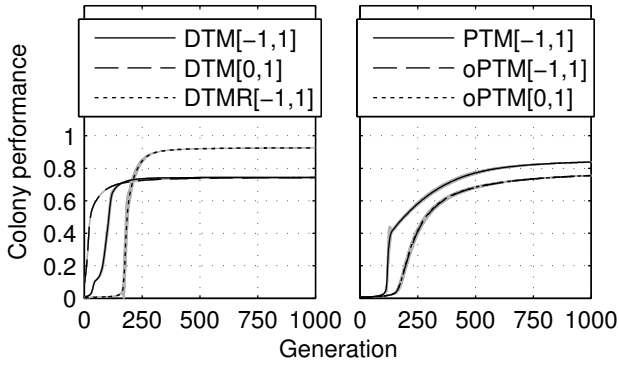


Figure D1: Mean \pm s.d. (in grey) performance for three deterministic (left) and three probabilistic (right) response threshold models over 1000 colonies (30 replicates). Note that values of oPTM[-1,1] and oPTM[0,1] match, making the corresponding plots indistinguishable.

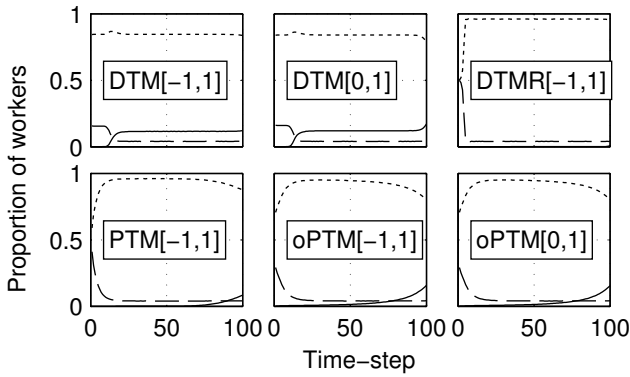


Figure D2: Mean proportion of workers engaged in the foraging task (short-dashed line), in the regulating task (long-dashed line) or staying idle (solid line) as a function of time-steps. Results for three deterministic (top) and three probabilistic (bottom) response threshold models, over 1000 colonies of the 1000th generation (30 replicates).

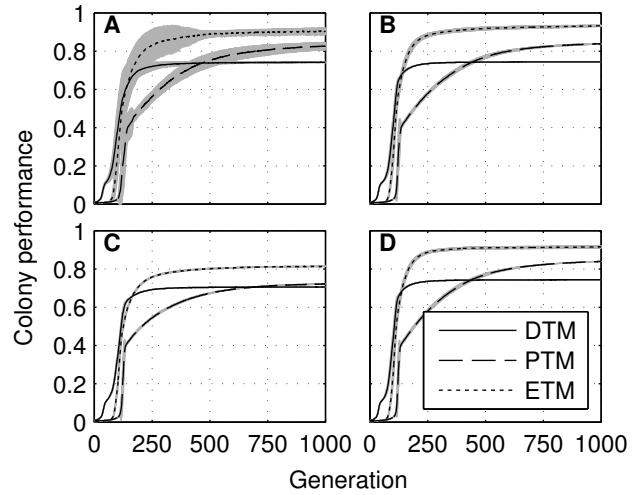


Figure E1: Mean \pm s.d. (in grey) performance of each of the three response threshold models (30 replicates). A) 100 colonies were evolved with uniform mutations. B) 500 colonies were evolved with uniform mutations. C) 1000 colonies were evolved with frequent Gaussian mutations. D) 1000 colonies were evolved with mutations switched off.

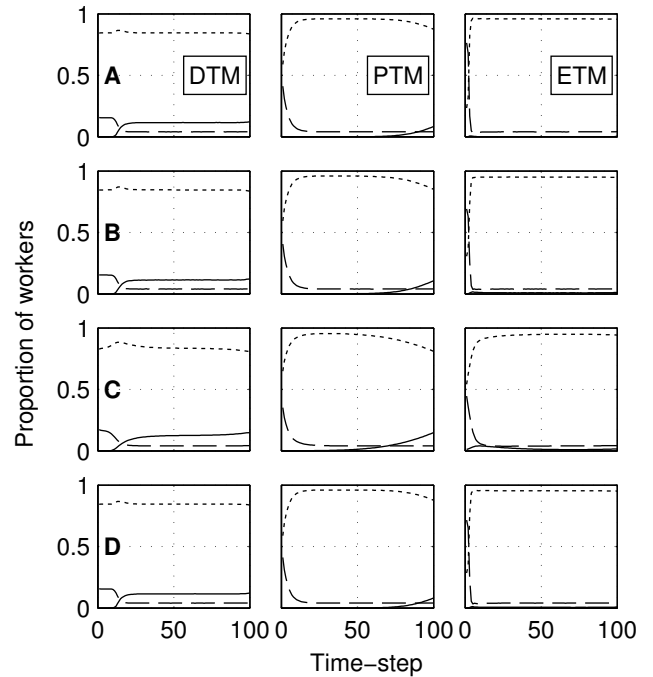


Figure E2: Mean proportion of workers engaged in the foraging task (short-dashed line), in the regulating task (long-dashed line) or staying idle (solid line) as a function of time-steps. Results for three response threshold models, over all colonies of the 1000th generation (30 replicates). A) 100 colonies were evolved with uniform mutations. B) 500 colonies were evolved with uniform mutations. C) 1000 colonies were evolved with frequent Gaussian mutations. D) 1000 colonies were evolved with mutations switched off.