

Dynamic Polyethism and Competition for Tasks in Threshold Reinforcement Models of Social Insects

Daniel Merkle, Martin Middendorf

Parallel Computing and Complex Systems Group, Department of Computer Science, University of Leipzig

In this paper we study the dynamics of task division in threshold reinforcement models of social insect societies. Our work extends other models in order to include several factors that influence the behavior of real insect colonies. Main extensions of our model are variable demands for work, age-dependent thresholds and finite life span of the individuals. It is shown how these factors influence the degree of task specialization of the individuals in a colony. Moreover, we show that the introduction of a threshold-dependent competition process between the individuals during task selection leads to the occurrence of specialists and differentiation between individuals as an emergent phenomenon that depends on the colony size. This result can help to explain the proximate mechanisms that lead to specialization in large insect colonies. Our results have implications for the fields of multi-agent systems, robotics, and nature inspired scheduling where threshold response models are used for control and regulation tasks.

Keywords task division · threshold models · polyethism · simulation

1 Introduction

Division of labor and specialization of individuals to different tasks are complex phenomena that occur in many social insect societies. Possible benefits of task division and specialization for insect colonies and the ultimate reason why specialization occurs predominantly in larger colonies have been studied extensively by biologists (e.g., Jeanne & Nordheim 1996; Karsai & Wenzel, 1998; Seely, 1982). However, not so well understood are the proximate mechanisms that lead to colony size-dependent specialization.

Threshold models have been used successfully to explain and study different phenomena of social behav-

ior (e.g., Bonabeau, Théraulaz, Schatz, & Deneubourg, 1998b; Robinson, 1992). Division of labor can be explained with stimulus–response threshold models where each individual has an internal threshold for every task (e.g., see Bonabeau, Théraulaz, & Deneubourg, 1996, 1998a). If an individual encounters a task with a stimulus that is higher than the threshold of the individual it starts working on the task with high probability. Recently, threshold reinforcement models have been proposed which allow to model learning and forgetting effects (see the interesting paper of Gautrais, Théraulaz, Deneubourg, & Anderson, 2002) for an overview). Learning/forgetting is modeled by decreasing/increasing threshold values.

Correspondence to: Daniel Merkle, Parallel Computing and Complex Systems Group, Department of Computer Science, University of Leipzig, Augustusplatz 10-11, D-04109 Leipzig, Germany.
E-mail: merkle@informatik.uni-leipzig.de
Tel.: +49(0)341-9732279, *Fax:* +49(0)341-9732329.

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In this paper we use threshold reinforcement models of social insect societies to study the dynamics of labor division. We first re-examine the model that was introduced in Gautrais et al. (2002) and give a different explanation why specialization occurs in this model. Then we extend the model to include some aspects that are important for the behavior of real insect colonies. In particular, we study the effects of differing demands for work, the introduction of a finite life span for the individuals, and the influence of age-dependent maximal threshold values. Finally, we introduce competition for work between the individuals. This is done through a threshold-dependent selection process between the individuals during task selection. It is shown that this can lead to the occurrence of specialists as an emergent phenomenon that depends on the colony size. For finite time or finite age models this leads also to colony size-dependent differentiation between the individuals with respect to their degree of specialization.

Since the emergence of colony size specialization in insect colonies is not well understood it is an interesting research problem to find out where in social insect societies a competition for work mechanism occurs in connection with a learning/forgetting behavior and whether this leads as predicted by the model to the emergence of colony size-dependent specialization and differentiation. Other interesting applications of our results are expected in the areas of multi-agent systems, robotics, and nature-inspired scheduling. In these areas threshold models are used to implement cooperation and tasks specialization between agents or robots. For instance, Agassounon and Martinoli (2002) use fixed and variable response threshold models for the worker allocation of robots to work for a puck clustering problem. Krieger and Billeter (2000) use a response threshold model for a group of robots where the task of the robots is to search and collect food items in a foraging area and bring them back to their nest. The robots have different personal activation thresholds for different subtasks. An example for the use of threshold models for scheduling is the work of Cicirello and Smith (2004). Each machine has a wasp-like agent that is in charge of choosing which jobs to bid for possible assignment to the associated queue of waiting tasks for that machine. A threshold model for real wasps behavior by Théraulaz, Goss, Gervet, & Deneubourg (1991) is the foundation for the distributed task allocation scheme that is used by the agents.

In the next section we describe the threshold reinforcement model. The re-examination of colony size-dependent specialization is presented in Section 3. Section 4 discusses the influence of finite life span and maximal thresholds. Age-dependent thresholds are introduced in Section 5. In Section 6 we discuss the influence of competition to colony size-dependent specialization and differentiation. Conclusions are given in Section 7.

2 The Threshold Reinforcement Model

In this section we describe the threshold reinforcement model that has been introduced in Gautrais et al. (2002). It is assumed that there are N individuals and m tasks T_1, \dots, T_m . Each task T_j has an associated stimulus value $S_j \geq 0$. Each individual i has an associated threshold value $\Theta_{i,j}$ for each task T_j such that $0 \leq \Theta_{i,j} \leq \Theta_j^{\max}$ for a given maximal value $\Theta_j^{\max} \geq 0$.

In each time step an individual is idle or actively engaged in exactly one task for which it will do α units of work during the time step for a given $\alpha > 0$. An active individual becomes idle with given probability $p \geq 0$. When it becomes idle it is idle for at least one time step. An individual i that was idle starts to work on task T_j with probability $(1/m)(S_j^2/(S_j^2 + \Theta_{i,j}^2))$. Observe that the maximal amount of work that the colony can perform in one time step on average per task is $W_{\max} = (N/m) \cdot (\alpha/(1+p))$.

In each time step the threshold values are changed for each task T_j and each individual i according to the following rules: (i) if i is engaged in T_j then $\Theta_{i,j} = \max\{\Theta_{i,j} - \xi, 0\}$, (ii) otherwise, $\Theta_{i,j} = \min\{\Theta_{i,j} + \phi, \Theta_j^{\max}\}$. ξ is called learning parameter and ϕ is the forgetting parameter.

In each time step the stimulus values are changed for each task T_j according to $S_j = S_j + \sigma_j - E_j \cdot \alpha$ where $\sigma_j = D \cdot W_{\max}$, $0 < D \leq 1$ is the demand parameter, and E_j denotes the number of individuals that are currently engaged in task T_j . Note that parameter D allows to model situations with different demands for work: e.g., for $D = 1$ the colony must work at full capacity in order to hold the stimulus values at the same level.

In order to study the specialization of an individual the following measure was introduced by Gautrais et al. (2002) for a system with 2 tasks. A period of work of an individual is defined as the time from the start of working at some task until the next idle time. If

the task an individual has worked on during a period of work differs from the task of the next period of work this is called a transition. For some time period let C_i be the number of transitions divided by the total number of periods of work minus 1 for individual i . The degree of specialization F_i of individual i is measured by $F_i = 1 - 2C_i$. Then $-1 \leq F_i \leq 1$ holds. Observe that $F_i = 1$ when an individual has not switched between tasks (high specialization), $F_i = 0$ when an individual has switched randomly between two tasks (no specialization), and $F_i = -1$ when an individual has switched alternately between the tasks. The activity of an individual over a time period is measured as the proportion of time steps it was working at a task.

3 Re-examination of Colony Size Dependent Specialization

Gautrais et al. (2002) have investigated the degree of specialization (measured over all simulation steps) of the individuals for a 2-task model for different colony sizes and different demands. It was shown that for medium ($D = 0.5$) or high ($D = 0.8$) demands specialists occur but only for colonies that are not too small ($N \geq 20$). It was argued that the magnitude and time scale of fluctuations of the difference between the stimulus values ($S_1 - S_2$) is the crucial factor because in small colonies large absolute differences are sustained for longer periods than in large colonies. The interpretation was that a high stimulus difference $S_1 - S_2$ will break down any specialization that individuals may have for task 2 because they are more likely to tackle task 1 (and so learn) while forgetting task 2 (and vice versa for high $S_2 - S_1$). In large colonies where the fluctuations were less longer sustained the individuals have sufficient time working on the same task for the positive feedback of learning to take effect. The conclusion was that differentiation in activity levels and specialization only occurs when colony size exceeds some critical value.

In our simulation we obtained the same results but cannot agree with the given interpretation of the results. In the following we give a different explanation and show that the reason why there are no specialists in the small colonies has only to do with the specific colony size-dependent situation during the first steps after the chosen initialization of the simula-

tion model. Recall that for initialization the thresholds and the stimuli are set to zero (or nearly zero) and the maximal threshold values are presumably equal ($\Theta_{\max} := \Theta_1^{\max} = \Theta_2^{\max}$).

Given this initialization during the first time steps in small colonies the stimuli will grow much more slowly than in large colonies because the value of σ_j , $j \in [1 : 2]$ is proportional to colony size. The threshold values grow independently of the colony size. Hence, the chance for an individual to start working and therefore the activity level are much smaller when colony size is small. The effect is that for each individual in a small colony both threshold values will grow until they reach the maximum values Θ_j^{\max} . But such individuals are not specialists and all have a similar activity. The stimuli will continue to grow until the chances to start working become so high for an idle individual (even with threshold values that are maximal) that the demand for work can be satisfied by the colony. In later phases of the simulation an individual with threshold values that nearly equal are the maximum threshold values has nearly no chance to become a specialist (especially when the maximal thresholds values are high).

In contrast, in a large colony the stimulus values grow fast during the first steps after initialization. The effect is that the activity of the individuals strongly increases during the first time steps. But when an individual has started to work early at say task T_1 then the chances are high that it will work again at task T_1 in the following period because its threshold values for task T_1 and T_2 are quite different. The reason is that the threshold for the task the individual is working on remains to be nearly zero and the other threshold increases each time step by ϕ .

See Figure 1 for an illustration of the evolution of threshold and stimulus values in small and large colonies. The figure shows the stimulus values and threshold values for a typical individual of a small ($N = 10$) and a large ($N = 1000$) colony. The individual in the small colony starts to work randomly for 6 steps on task T_1 . But then it never works again during the first 30 steps because the stimulus values for both tasks grow slowly whereas the threshold values for both tasks grow much faster. The individual in the large colony starts to work randomly for task T_2 . But the stimulus values grow relative to the threshold values much faster compared to the small colony. Since the

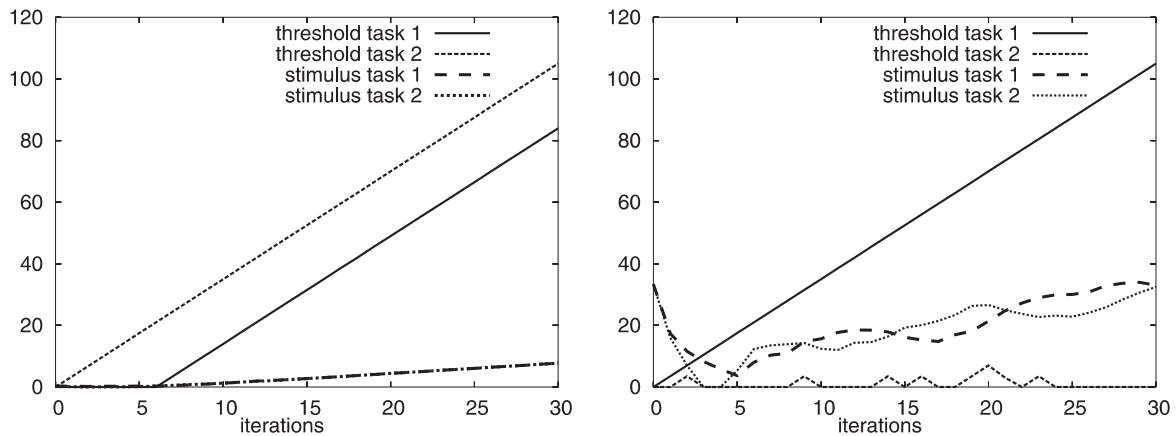


Figure 1 Stimulus values and threshold values of typical individual for a small colony with $N = 10$ (left) and a large colony with $N = 1000$ (right) over the first 30 iterations: $D = 0.8$, $\Theta_{\max} = 1000$.

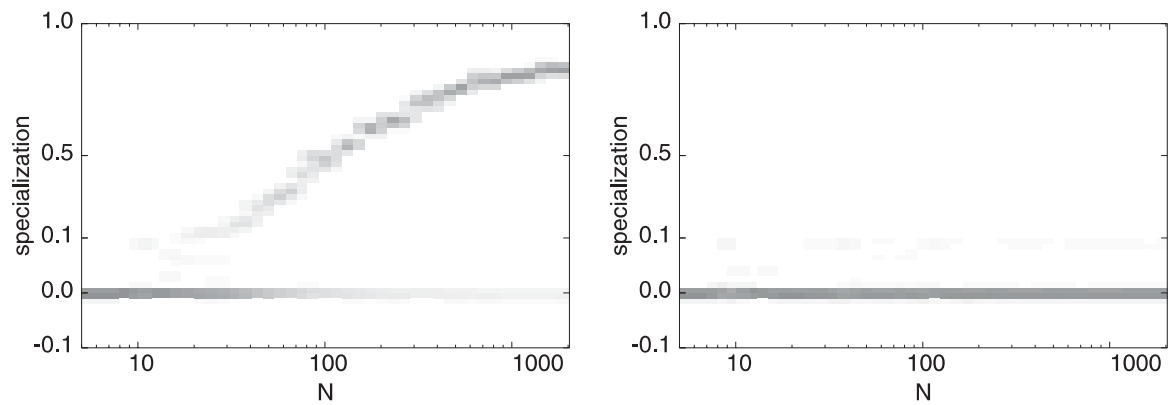


Figure 2 Specialization for different colony sizes $N \in [5 : 2000]$ for $D = 0.8$, $\Theta_{\max} = 2000$, with (right) and without (left) demand variation phase; the darker the color the larger is the fraction of individuals that have the corresponding specialization level.

threshold for task T_2 remains at a low level for some iterations the individual starts again several times to work for task T_2 during the first 30 iterations. Therefore, it keeps its threshold for task T_2 low (while the threshold for task T_1 has become high) and thus specializes in task T_2 .

Hence, we conclude that the observed difference in specialization between small and large colonies is not an emergent phenomenon because it is the consequence of the colony size-dependent growth of stimulus values during the initial phase of the simulation model (for the chosen initial parameter values). We made several experiments in order to back our explanation. One experiment was to reset explicitly the threshold values of some individuals in the small colony when it has reached a stable state to $\Theta_1 = \Theta_{\max}$ and $\Theta_2 = 0$. The result was that these individuals become

specialists (with respect to the F_i measure) and remained to be specialists (over the observed simulation steps). Thus, specialization does not break down over the simulation time in the small colony.

In order to remove the effect of the initialization phase to some extent we studied a system where after initialization the demand for work was changed between longer periods of very high demand and longer periods of very small demand. After this demand variation phase the system is no longer dependent on the initial conditions (more exactly, the values of the initial stimulus and threshold values). No significant differences between small and large colonies occur in such systems with respect to activity levels or specialization. This is illustrated in Figure 2 which shows the different behaviors of the system with and without demand variation phase for a (constant) demand $D = 0.8$ (after

the demand variation phase). When thresholds and stimuli are initialized (close) to zero specialization occurs only for larger colony sizes. But after a demand variation phase nearly all individuals have a specialization very close to 0.0 no matter what the colony size is. If not stated otherwise, we apply a demand variation phase to every test run and the standard colony size that is used is $N = 100$.

Another aspect of the threshold reinforcement model of Gautrais et al. (2002) that we should point out is that differentiation between individuals with respect to activity level or specialization is a phenomenon that can exist only when measured over finite time periods. Recall that individuals differ in the model only by their actual threshold values and whether they are engaged in some task or not. Since each individual has a nonzero probability to change from its current state to every other possible state (this might take several iterations) there is no difference in the behavior of individuals over infinite time. Thus, all observed differentiation between individuals depends fundamentally on the simulation time because in the limit over infinite time all individuals in a colony have exactly the same degree of specialization and activity. This is different for the variant of the model that is introduced in the next section where individuals have a finite time life span and where differentiation can occur independently from simulation time (see also Section 6).

4 Finite Life Span and Maximal Thresholds

In this section we introduce individuals with a finite life span to the threshold reinforcement model. One reason is that individuals in natural systems have a finite life span. Since new individuals might be different from older individuals it can be expected that the introduction of finite life span can possibly change the behavior of the model significantly. The other reason is to avoid the fundamental problem of the infinite lifetime model that specialization and differentiation can only be a phenomenon over a finite time as explained in Section 3. For simplicity we assume here that each individual has the same maximal age a_{\max} . In order to make the interpretation of our results easily comparable with the infinite life time model it is assumed that the colony size remains always fixed.

This implies that there is a constant inflow of new individuals, that is when an individual has left the system because its lifetime ended it is replaced by a new individual. The initialization is done with individuals that have a random age which is uniformly chosen from $[0, a_{\max}]$. In the following we study a system that is in a stable state after a demand variation phase. The specialization for a system with individuals of finite life span is measured as the average specialization over all individuals that left the system.

In this section we study also the influence of the size of the maximal threshold value Θ_{\max} . As has been argued in Section 3 large maximal threshold values make it unlikely that an individual with threshold values that are nearly maximal will ever become a specialist. This might be different in a system with small maximal threshold values. In Gautrais et al. (2002) maximal threshold values of 1000 have been used for the simulations. Here we consider also systems with much smaller such maximal threshold values. This is important because for some natural systems small values are more realistic. A large threshold of size 1000 in combination with learning parameter $\xi = 4$ (forgetting parameter $\phi = 3.5$) implies that an individual has to improve its skills by 250 learning steps (respectively ≈ 285 forgetting steps) until threshold 0 is reached when starting with threshold 1000 (respectively vice versa). Hence large maximal threshold values are realistic in situations where learning/forgetting is a slow process that leads over many different levels of skills. But for insects many learning processes are fast and improve only over a few steps until the individual reaches its final level of skill (analogously for forgetting processes). As an example consider experiments that have been done by Scheiner, Erber, and Page (1999) with honey bees to study the learning of tactile patterns. Another example is odor learning of honey bees that was investigated by Ben-Shahar, Thompson, Hartz, Smith, and Robinson (2000). In these works it was shown that the maximal response of a bee to a learned pattern or odor (measured by the proboscis extension response, PER) was reached after only about 5–6 learning steps. A pattern or odor has been forgotten after about 5 contacts with a different pattern or odor. For this example of bee learning it means that for $\xi = 4$ and $\phi = 3.5$ the maximal threshold value in the model should be set to about $\Theta_{\max} = 20$.

We compared the threshold response model with infinite life span to the model with individuals of finite

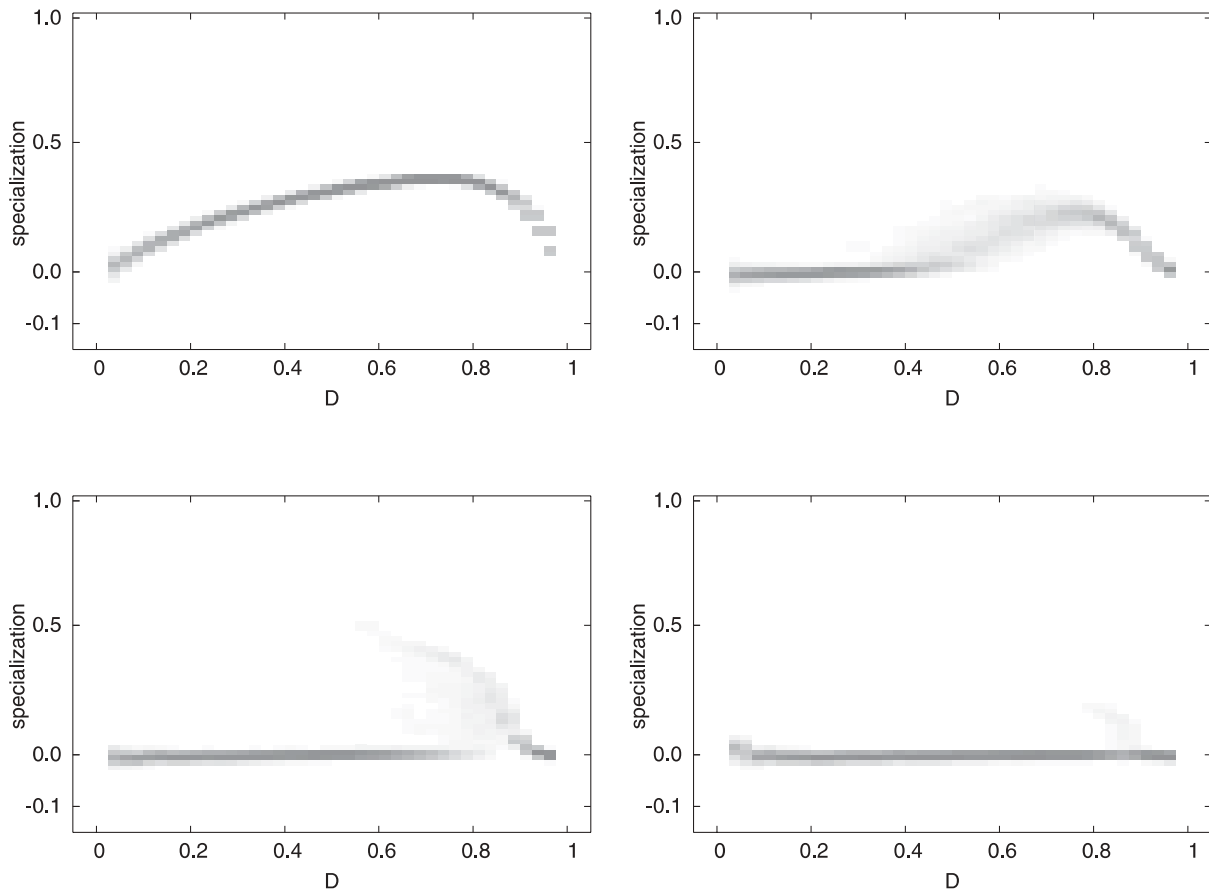


Figure 3 Infinite life span model: specialization level for different demands D ; $\Theta_{\max} \in \{20, 500, 1000, 2000\}$ (from top left to bottom right); $N = 100$; the darker the color the larger is the fraction of individuals have the corresponding specialization level.

life span. The results are shown in Figures 3 and 4. Only the results for colony size 100 are given since for other tested colony sizes from 5 to 2000 the results are very similar. For infinite life span and extreme demand values ($D \approx 0.0$ or $D \approx 1.0$) no specialization occurs. If D is very small ($D \approx 0.0$), both thresholds values of the individuals usually grow to the maximal value. If D is very large ($D \approx 1.0$) the work load is so high that both threshold values of the individuals stay close to zero. However, specialization does not occur for very high demand because a high threshold value of a specialist for one task would decrease its overall probability to work. As a consequence, the demand could then not be satisfied and the stimulus values would increase further until all individuals start to work for both tasks and their threshold values decrease. For larger Θ_{\max} values and medium to high demand (e.g., $\Theta_{\max} = 1000$, $D = 0.8$, $N = 1000$) some individuals specialize to some

extent (because they have one threshold value near zero and the other is larger). But there are also individuals that have both threshold values high. This is different for smaller Θ_{\max} values. The reason is that here the individuals usually specialize to one task for some time, but as Θ_{\max} is small, the probability of switching and specializing to the other task for some time is high. Overall, this results in a medium level of specialization.

For a system with individuals that have a finite life span the results show that for small values of Θ_{\max} the specialization level is very similar to the equivalent system with individuals of infinite lifespan. However, this is different for large values of Θ_{\max} . In this case there are no specialized individuals in the infinite life span model. But in the finite life span model highly specialized individuals occur, as they decide in the first steps in which task they specialize. As Θ_{\max} is

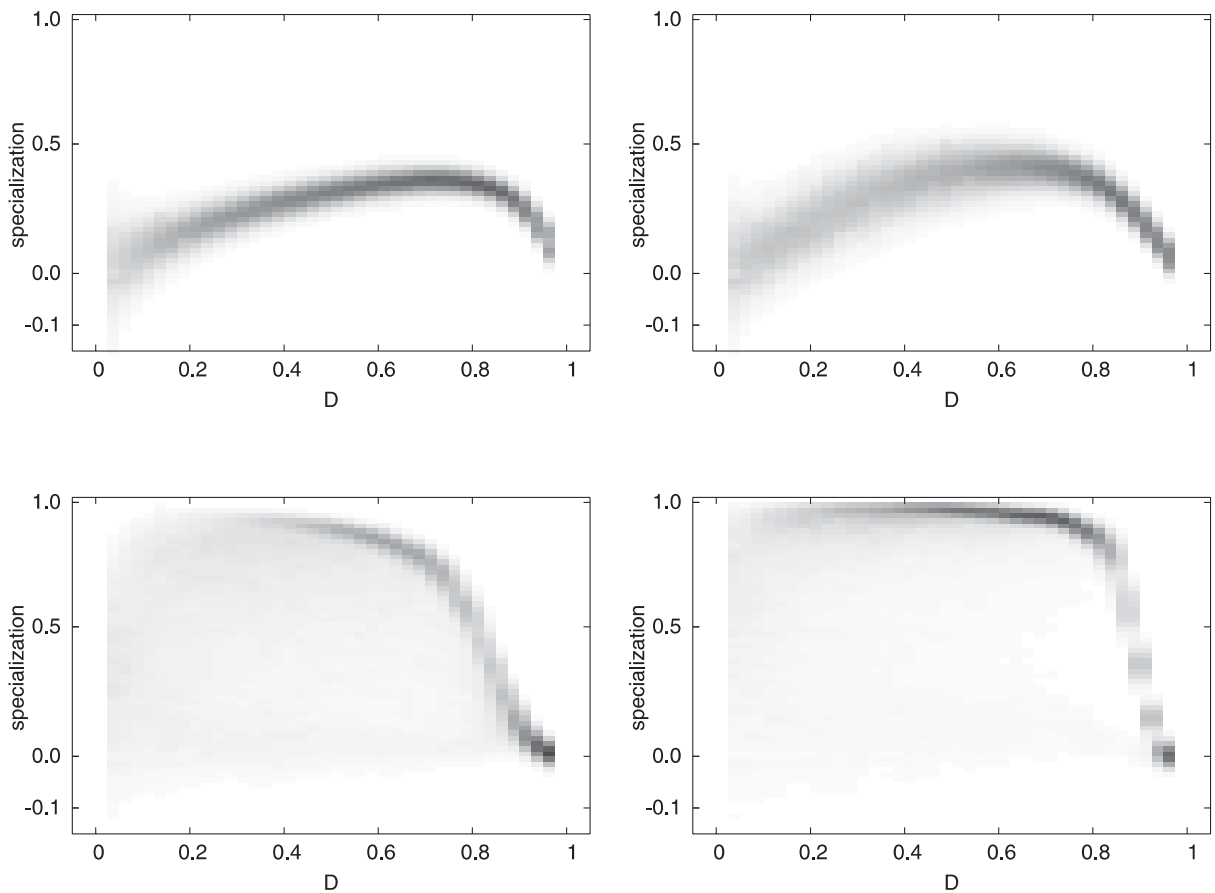


Figure 4 Finite life span model with $a_{\max} = 10000$: Specialization level for different demands D ; $\Theta_{\max} \in \{20, 100, 500, 1000\}$ (from top left to bottom right); $N = 100$, the darker the color the larger is the fraction of individuals have the corresponding specialization level.

very large, they will not switch back again to another task during their life time.

5 Age-Dependent Maximal Thresholds

In this section we introduce a mechanism for age-dependent development of individuals into the threshold reinforcement model. Then we study its influence on task division over individuals of different ages. Age-dependent task division is interesting because it occurs in many social insect societies. Examples are honey bees where young workers work mostly within the hive while older workers become foragers and work outside of the hive (e.g., Seeley, 1995). Age-dependent behavior is a complex phenomenon that is influenced by social, environmental, and genetic factors (Ben-Shahar, Robichon, Sokolowski, & Robinson, 2002;

Wakano Nakata & Yamamura, 1998). Age-dependent task division in social insects has been explained by activator-inhibitor models where activation occurs through an internal age-dependent development of behavior and inhibition works through social interactions (see Naug and Gadagkar (1999) for a corresponding model for a eusocial wasp and Beshers, Huang, Oono, and Robinson (2001) for the honey bee). Some forms of emergent task succession have been explained with non-age-dependent threshold models (e.g. Bonabeau et al., 1999a) or by models of task competition (see Sendova-Franks, Franks, & Britton, 2002). A model for age-neutral transition from hive-bee to forager which assumes an internal and an external repressor of the allatregulatory central nervous system was investigated by Amdam and Omholt (2003).

Age dependence is introduced to our model by assuming that the maximum threshold values differ

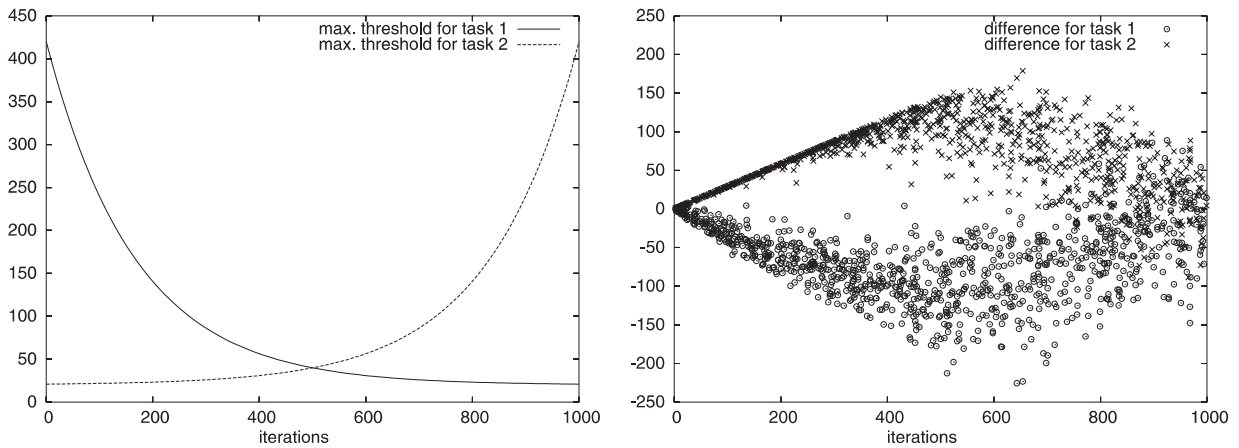


Figure 5 Age-dependent maximal thresholds Θ_{\max}^1 and Θ_{\max}^2 (left); difference between expected number of worksteps and performed number of worksteps for each individual and both tasks for $D = 0.8$, $N = 500$ (right); $\Theta_{\text{base}} = 20$, $a_{\max} = 1000$.

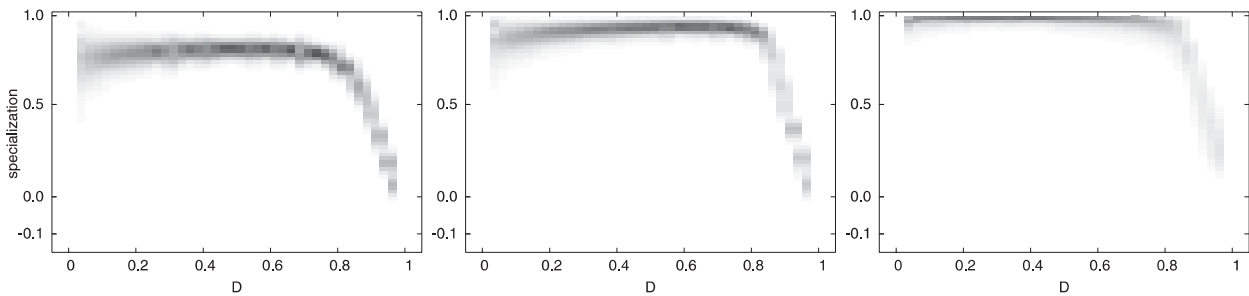


Figure 6 Age-dependent thresholds: Specialization level for different demands D ; $\Theta_{\text{base}} \in \{20, 100, 1000\}$ (from left to right), $N = 100$, $a_{\max} = 10,000$; the darker the color the larger is the fraction of individuals have the corresponding specialization level.

between the individuals depend on their age. A motivation for this assumption is that the maximum thresholds values reflect the personal minimum likelihoods of an individual to perform different tasks. Hence, they describe more the role that an individual has and not its actual tasks (an overview on the differences between the task of an individual and its role and on the factors that determine the role of individuals in insect societies is given in Blanchard, Orledge, Reynolds, and Franks (2000)). It has been shown that the temporal changes of the roles of an individual can depend on its physiological development (Huang & Robinson, 1999).

In the model we assume that the age-dependent maximum thresholds of an individual might increase or decrease exponentially with its relative age (relative with respect to the maximum age a_{\max}). It is also assumed that there exist a minimum value for each maximum threshold. For the test we assume the age-

dependent maximum thresholds Θ_{\max}^1 and Θ_{\max}^2 for task T_1 , respectively T_2 , for an individual of age a are defined by (see also left part of Figure 5) $\Theta_{\max}^1(a) = \Theta_{\text{base}}^{(2*a)/a_{\max}} + \Theta_{\text{base}}$, $\Theta_{\max}^2(a) = \Theta_{\text{base}}^{2-(2*a)/a_{\max}} + \Theta_{\text{base}}$ where Θ_{base} is the minimal maximum threshold value. We study a system with maximal age $a_{\max} = 1000$.

Figure 6 shows the distribution of specialization levels for different values of Θ_{base} . A high degree of specialization occurs even for small demands. Young individuals have a high (resp. small) maximal threshold for task T_1 (resp. task T_2). Note that, in contrast to individuals without age dependent thresholds, the threshold for task T_1 was initialized to the maximal value when the individual is born. Therefore it is very unlikely that an individual will work on task T_1 , when it is young. This can clearly be seen in the right part of Figure 5. For every individual in the colony the difference between the number of time steps the individual has worked for a task and its expected number assum-

ing that there is no age-dependent influence is shown. The expected number $E(a)$ of worksteps that an individual should have worked at a specific task at age a is defined as $E(a) = (D \cdot a)/(m \cdot (1 + p))$. Only for high demands can the individuals not specialize (to the different tasks during different age) because otherwise the high demand cannot be satisfied by the colony (see Figure 5). This shows that the colony can react flexibly to high demands even in the presence of age-dependent maximum thresholds in that individuals of all ages work on both tasks. Hence, the threshold reinforcement model with age-dependent maximum thresholds shows that the combination of age-dependent specialization and flexibility to switch between different tasks is possible (compare the discussion in Johnson (2003) which concludes that the organizational structure of honey bees colonies retains the advantages of age-dependent roles and behavioral flexibility).

6 Competition for Tasks and Colony Size Dependence

In this section we introduce an extended threshold reinforcement model that shows emergent colony size-dependent polyethism. In natural systems not all individuals that have decided to work for a task will actually be able to do so. A simple reason can be that there is not enough work for all. A simple example from honey bees can be observed in the hive section where foraging bees unload their collected nectar to food storer bees (e.g., Seeley, 1995). When there are too many food storer bees not all of them receive nectar from the incoming foraging bees. With competition for tasks we denote a situation where not all individuals that decide to work for a task can actually work for it. In social insect colonies there exist fascinating mechanisms that regulate the number of individuals that want to work for different types of tasks. For example, the numbers of foraging bees and food storer bees in a honey bee colony can be adapted very fast to the actual needs (see e.g., Seeley, 1995). But even when such regulation mechanisms can reduce the strength of competition for work (defined as the relative rate of individuals that actually can work for the task with respect to all individuals that want to work for task) it still exists.

In order to reflect such competition for task situations in the model we introduce a selection process between individuals that want to work for the same

task. We assume that success in such a competition between individuals depends on the individual thresholds for the corresponding task. An individual with a low threshold can be viewed as a highly motivated individual that has therefore better chances to be successful in the competition for a task (compare the related discussion in Bonabeau, Théraulaz, and Deneubourg (1999b) about motivation of individuals, changes of interaction rates between individuals and the establishment of dominance hierarchies in a colony). In the model we assume simply that from all individuals that have decided to work for a task at a time step only a fraction of $1 - \rho$ individuals with the lowest thresholds for the corresponding task are successful where parameter $\rho \geq 0$ defines the selection pressure. The non-successful individuals become idle for that time step. Note that on average fewer individuals will work per time step compared to the model without selection. Since we want to compare colonies with different selection pressures (i.e., different degree of competition for tasks) but where the average rate of working individuals is the same we decrease the parameter σ that determines the increase of the stimulus values and the forgetting parameter ϕ by multiplication with the factor $(1 - \rho)$ compared to the model without selection.

Figure 7 shows the observed degree of specialization for different selection pressures for individuals with infinite lifetime. It can be seen that similar as for the model without specialization there is no significant difference between the degree of specialization for different colony sizes when the selection pressure is low ($\rho = 0.5$). But for larger selection pressure there is a clear colony size-dependent degree of specialization. For $\rho = 0.9$ the small colonies with ≤ 10 individuals have a low specialization level of 0.5 whereas the large colonies with more than 500 individuals have a specialization level of about 0.9.

A reason why no strong specialists occur in small colonies (for suitable parameter values) is the larger variance in the decisions of the individuals. It happens with high probability that individuals which start to specialize slightly for one task are selected to work for the other task (because individuals with relatively low thresholds accidentally might have decided not to try to work for this other task). Hence the emerging specialization breaks down. For large colonies it is more unlikely that an individual which has a relatively low threshold for one task due to random effects is selected to work for this task. But this means that

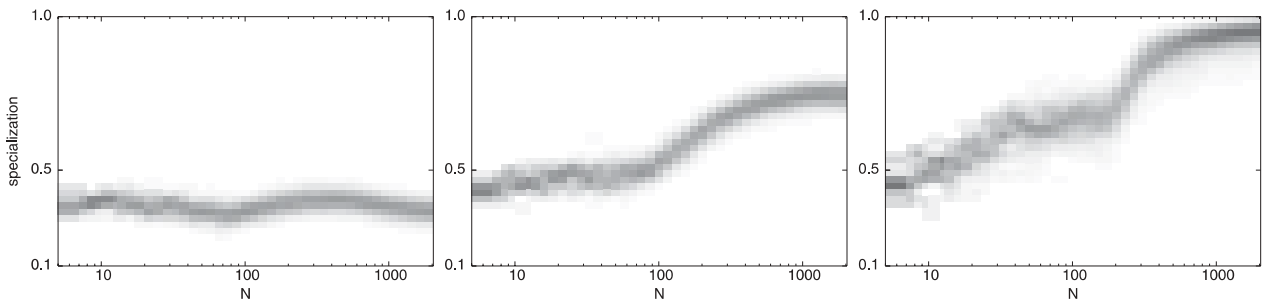


Figure 7 Influence of competition for tasks with selection parameter $\rho \in \{0.5, 0.7, 0.9\}$ (from left to right): Specialization level for different colony sizes; infinite age, $\Theta_{\max} = 20$, $D = 0.5$; the darker the color the larger is the fraction of individuals have the corresponding specialization level.

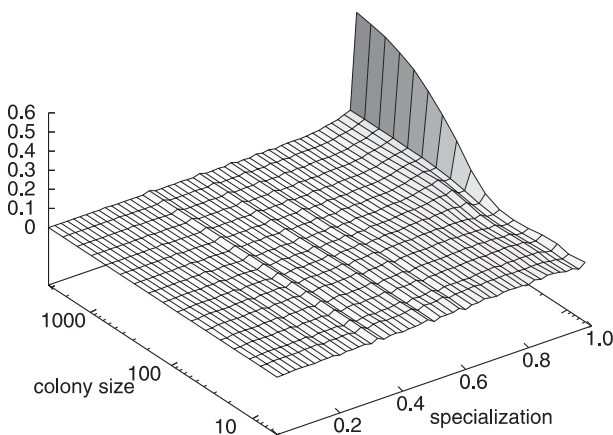


Figure 8 Influence of competition for tasks with selection parameter $\rho = 0.5$: For different colony sizes the figure shows the relative amount of individuals for the different specialization levels; finite age $a_{\max} = 500$, $\Theta_{\text{base}} = 100$, $D = 0.8$, $N = 100$.

small specialization that happens due to random effects is enforced by the selection mechanism.

For the finite age model a differentiation between the individuals can be observed. See Figure 8 for results. For small colonies with at most 50 members the specialization level of the individuals varies between 0.0 and 1.0. The number of individuals with specialization level ≥ 0.99 is not much higher than for the other levels of specialization (less than 6% of the individuals have specialization level ≥ 0.98). This is different for the larger colonies with ≥ 1000 members where most individuals (between 50% and 60%) have specialization level ≥ 0.98 .

Since our results have shown that colony size-dependent specialization and differentiation occurs in the threshold reinforcement model as an emergent phenomenon only when a selection process due to

competition for task occurs it will be interesting to study whether such competition processes can also be found in natural systems. Particularly interesting is the relation between the occurrence of specialization and differentiation to colony size and strength of competition for tasks. Moreover, the results suggest that emergent specialization and differentiation can be implemented for response threshold controlled multi-agent system and groups of robots through the introduction of a suitable competition for task mechanism.

7 Conclusion

In this paper we have simulated task division in the threshold reinforcement model of Gautrais et al. (2002). We re-examined the emergence of colony size-dependent specialization and have shown that colony-size-dependent specialization in this model is due to a colony size-dependent stimulus increase during the initialization phase and that differentiation is a (simulation) time-dependent phenomenon. To make our results more independent from some unwanted initialization effects we introduced an initialization phase for the simulations with varying demands. We have studied colonies of individuals with threshold reinforcement models where individuals have a finite life span, different maximum threshold values, and age-dependent maximal threshold values. It was argued that small (compared to the learning and forgetting rates) maximum threshold values are relevant for modeling natural systems because several learning/forgetting processes in insects are fast and show only few levels of skill. It was shown that smaller maximal threshold values change the behavior of the system because individuals can change more easily between specialization for different tasks.

We have also proposed an extension of the threshold reinforcement model with threshold-dependent competition for tasks between the individuals during task selection. It was observed for this model that the occurrence of specialists is an emergent phenomenon that depends on colony size and on the strength of competition for tasks. It will be interesting to study whether colony size-dependent phenomena of task division in nature can be explained with the help of threshold-dependent competition processes. For the design of multi-agent systems and bio-inspired robotic systems our results might be helpful in order to obtain emergent specialization and differentiation for response threshold regulated systems.

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About the Authors



Daniel Merkle received the Diploma degree in computer science at the University of Karlsruhe, Germany, in 1997. He finished his Ph.D. in applied computer science at the Institute of Applied Informatics and Formal Description Methods, University of Karlsruhe, Germany in 2002. Since then he has worked as an assistant professor with the Parallel Computing and Complex Systems Group of the Department of Computer Science in Leipzig, Germany. His research interests include algorithms from nature, parallel algorithms, social insect behaviour and phylogeny.



Martin Middendorf received the Diploma degree in mathematics and a *Dr. rer. nat.* at the University of Hannover, Germany, in 1988 and 1992, respectively. He gained his professorial Habilitation in 1998 at the University of Karlsruhe, Germany. He has worked at the University of Dortmund, Germany, and the University of Hannover, Germany, as a visiting Professor of Computer Science. He was Professor of Computer Science at the Catholic University of Eichstätt, Germany. Currently he is Professor for Parallel Computing and Complex Systems with the University of Leipzig, Germany. His research interests include reconfigurable architectures, parallel algorithms, algorithms from nature and bioinformatics. *Address:* Parallel Computing and Complex Systems Group, Department of Computer Science, University of Leipzig, Augustusplatz 10-11, D-04109 Leipzig, Germany. E-mail: middendorf@informatik.uni-leipzig.de