



A Trade-off in Task Allocation between Sensitivity to the Environment and Response Time

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(Received on 14 April 2000, Accepted in revised form on 5 October 2000)

Task allocation is the process that adjusts the number of workers in each colony task in response to the environment. There is no central coordination of task allocation; instead workers use local cues from the environment and from other workers to decide which task to perform. We examine two aspects of task allocation: the sensitivity to the environment of task distribution, and the rate of response to environmental changes. We investigate how these two aspects are influenced by: (1) colony size, and (2) behavioral rules used by workers, i.e. how a worker uses cues from the environment and from social interactions with other workers in deciding which task to perform. We show that if workers use social cues in their choice of task, response time decreases with increasing colony size. Sensitivity of task distribution to the environment may decrease or not with colony size, depending on the behavioral rules used by workers. This produces a trade-off in task allocation: short response times can be achieved by increasing colony size, but at the cost of decreased sensitivity to the environment. We show that when a worker's response to social interactions depends on the local environment, sensitivity of task distribution to the environment is not affected by colony size and the trade-off is avoided.

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1. Introduction

Animals may maximize fitness by tracking the environment. Optimal foraging theory (Houston & McNamara, 1999; Perry & Pianka, 1997; Stephens & Krebs, 1986) predicts that an animal's choice of prey should depend on the abundance of the several types of prey and on predation risk. In the ideal free distribution (Fretwell, 1972; Kacelnik *et al.*, 1992; Sutherland & Parker, 1985), the distribution of individuals among patches of the environment corresponds to the available resources in each patch. In social insects, a colony tracks the environment by adjusting the number

of workers in each task, a process called task allocation (Gordon, 1996). For example, in the harvester ant *Pogonomyrmex barbatus*, when extra food is available, more ants forage (Gordon, 1989).

The rate of response to environmental change may also affect fitness (McNamara & Houston, 1985). For example, the Argentine ant (*Linepithema humile*) is faster in locating and recruiting to food sources than native species, and this apparently contributes to its ecological success (Holway, 1999; Human & Gordon, 1996).

Here we examine how these two aspects of task allocation, sensitivity to the environment and response time, are influenced by colony size and by the behavioral rules used by workers.

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1.1. BEHAVIORAL RULES USED BY WORKERS

There is no central coordination of task allocation in a social insect colony. Instead each individual decides which task to perform based on local cues (Gordon, 1996; Gordon *et al.*, 1992; Seeley *et al.*, 1991). These local cues include information about local environmental conditions and interactions with other individuals (Gordon & Mehdiabadi, 1999).

The behavioral rules that relate local cues to the choice of task are not known. The foraging-for-work model (Bourke & Franks, 1995; Tofts, 1993) proposes that individuals use rules such as search for work in current task, and if there is no work then search for work in nearby tasks. The study of Sendova-Franks & Franks (1993) suggests that *Leptothorax unifasciatus* may use such behavioral rules.

Pacala *et al.* (1996) propose a different set of rules. In each task, individuals are successful if they have captured a unit of resource and are unsuccessful otherwise. Unsuccessful individuals switch to the task of the successful individuals they meet. Recently, Gordon & Mehdiabadi (1999) found that in *Pogonomyrmex barbatus*, a worker that interacts with midden workers is more likely to engage in midden work. Two assumptions of Pacala *et al.* (1996) remain untested: (1) the response to social interactions depends on the local environment of the worker, so that only unsuccessful workers switch tasks, and (2) individuals exchange information about the environment during social interactions, so that individuals switch tasks only after meeting a successful individual.

Here we examine theoretically the effect of these assumptions. First, we consider models with assumptions (1) and (2) dropped. In these models, workers in the same task are not distinguished with regard to success, so dynamics are described with a single state per task. Next, we consider models in which workers can be in one of two states. The two states are analogous to the successful/unsuccessful states of Pacala *et al.* (1996), but here we define the two states differently. Either the individual has found an environmental stimulus to perform its task or it has not. We assume that the response to social interactions depends on environmental cues (assumption 1),

so that only workers that have not recently found a stimulus for their task switch tasks. We consider the case when assumption (2) is met, and workers assess the state of the other worker, and the case when assumption (2) is not met.

1.2. COLONY SIZE

In ants, colony size varies among species from a few individuals to several million individuals (Hölldobler & Wilson, 1990), and within a species colony size changes during the life cycle of a colony. Colony size affects many aspects of insect societies (Bourke, 1999). Larger colonies have smaller variances in productivity (Karsai & Wenzel, 1998; Wenzel & Pickering, 1991), higher productivity per capita [Jeanne, (1999); but see Karsai & Wenzel (1998) and Michener (1964)], faster recruitment to food (Burkhardt, 1998), display more homeostatic responses to perturbations (Gordon, 1987) and rely more on communication in foraging (Beckers *et al.*, 1989). Some of these effects may be caused by differences in task allocation dynamics between small and large colonies. Here we examine how colony size affects sensitivity to the environment and response time for each type of model considered.

2. Response to Interactions does not Depend on Local Environment

In this section, we develop a model for the case in which the response of an individual to social interactions does not depend on the local environment and there is no exchange of information about the environment. The model uses a framework similar to the one proposed by Lachmann & Sella (1995).

Let $X_i(t)$ be the number of individuals doing task i at time t . We study task allocation at the scale of hours, thus colony size can be considered constant, i.e. $\sum_{i=1}^m X_i(t) = N$, where m is the number of tasks and N is the colony size.

We assume that an individual switches from one task to another when it finds an environmental stimulus to perform the new task. Let $e_{ij}\Delta t$ be the probability of finding a stimulus for task j in the neighborhood of task i , in a small

time interval Δt . This probability is directly proportional to the density of stimuli, thus we will also refer e_{ij} as the density of stimuli. The instantaneous rate at which workers switch from tasks i to j in response to environmental cues is $e_{ij}X_i(t)$.

Workers also switch tasks in response to social interactions. Let $f_i(X_j)\Delta t$ be the probability that a worker in task i meets a worker in task j in a small time interval Δt . Interaction rates increase with colony size (Beckers *et al.*, 1989; Karsai and Wenzel, 1998; Pasteels *et al.*, 1987). However, empirical (Gordon *et al.*, 1993) and theoretical work (Bonabeau *et al.*, 1998; Pacala *et al.*, 1996) suggest that this relationship is sub-linear, leveling off for large colony sizes. For simplicity, we assume a linear relation between interaction rate and colony size, $f_i(X_j) = \alpha_{ij}X_j$ where α_{ij} is a proportionality constant measuring the spatial proximity of tasks i and j (for symmetry we make $\alpha_{ij} = \alpha_{ji}$), but note the results that hold when the relation is sub-linear. Let s_{ijk} be the probability that a worker engaged in task i switches to task k after meeting a worker engaged in task j . The rate at which workers switch from task i to task k in response to social cues is $X_i(t)\sum_{j=1}^m s_{ijk}\alpha_{ij}X_j(t)$.

The task allocation dynamics are given by:

$$\begin{aligned} \frac{dX_i}{dt} = & \sum_{j=1}^m e_{ji}X_j + \sum_{k=1}^m \sum_{j=1}^m s_{kji}\alpha_{kj}X_kX_j \\ & - \sum_{j=1}^m e_{ij}X_i - \sum_{k=1}^m \sum_{j=1}^m s_{ijk}\alpha_{ij}X_iX_j \end{aligned} \quad (1)$$

for $i = 1 \dots m$.

It is important to note that in the absence of social interactions (α_{ij} 's = 0), this model is linear and has the same dynamics for any colony size. It is only when there are social interactions that the dynamics change with colony size, because the social terms are quadratic.

We start by analysing eqn (1) for two tasks, and then we move to models with three and four tasks. Our findings are summarized in Table 1.

2.1. A MODEL WITH TWO TASKS

The task allocation dynamics of a model with two tasks can be described by

$$\begin{aligned} \frac{dX_1}{dt} = & e_{21}X_2 - e_{12}X_1 + (S_{211} - S_{122})X_1X_2 \\ & + S_{221}X_2X_2 - S_{112}X_1X_1, \end{aligned}$$

$$X_2(t) = N - X_1(t), \quad (2)$$

where $S_{ijk} = s_{ijk}\alpha_{ij}$ [see Fig. 1(a)].

To illustrate the properties of this model we use a numerical example. Figure 2 shows task distribution and response time as a function of colony size in three different environments. The three environments are:

- environment 1, equal density of environmental stimuli for both tasks;
- environment 2, most stimuli (98%) are for task 1;
- environment 3, most stimuli (98%) are for task 2.

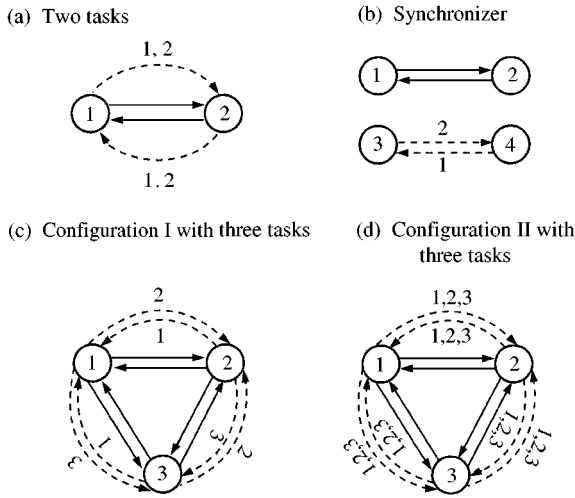
First, we will consider the sensitivity of the task distribution to the environment. Figure 2(a) shows the proportion of workers engaged in task 1 at the stable equilibrium, for colony sizes ranging from 1 to 600 workers. The task distribution of small colonies is very different in each of the three environments: the proportion of workers in task 1 approximates the proportion of environmental stimuli for task 1. As colony size grows, the differences in the task distribution among the three environments decrease. Eventually, the task distribution in all three environments approximates a static distribution determined only by the social interactions (see analytical proof in Appendix A). This is because the social terms $S_{ijk}X_iX_j$ are quadratic, increasing much faster with colony size than the linear terms $e_{ij}X_i$ of the environmental responses. Thus, interaction rates in large colonies are so high that workers respond mostly to social cues.

This decrease in sensitivity for large colony sizes is not surprising. We assumed that the parameters associated with social interactions, the

TABLE 1
Summary of results for each model studied

Response to social interactions and local environment	Section describing model	No. of tasks	Type of model	Response time with increasing colony size	Sensitivity to environment with increasing colony size	Effect of exchanging information about the environment
Response to social interactions does not depend on local environment	2.1 Fig. 1(a)	2	Any configuration of responses to social interactions possible	Decreases	Decreases: different environments tend to same response	No exchange of information about the environment assumed
	2.2.1 Fig. 1(c) and (d)	> 2	Non-zero probability of switching tasks after interaction: I—switch to task of worker met II—switch to any task	Decreases	Decreases: different environments tend to same response	
	2.2.2 Fig. 1(b)	4	Synchronizer: two pools of workers, one responding to environmental cues and the other to social cues	Delay between pool 1 and pool 2 decreases	Constant	
Only workers that have not found a stimulus for their task respond to social cues	3.1 Fig. 1(e)	≥ 2	Switch to task of worker met, environment does not depend on task distribution	Decreases	Decreases: bifurcation to two types of response	<i>Global dynamics:</i> no effect <i>Individual level:</i> fewer task switches
			Switch to task of worker met, density of stimuli decreases with number of workers in task	Decreases	Relatively constant	
	3.2 Fig. 1(f)	≥ 2 active + 1 inactive	Active tasks recruit workers from inactive pool	Decreases	Constant	<i>Global dynamics:</i> decreases linearity of response to environment <i>Individual level:</i> fewer task switches

Response to social interactions does not depend on environment



Response to social interactions depends on environment

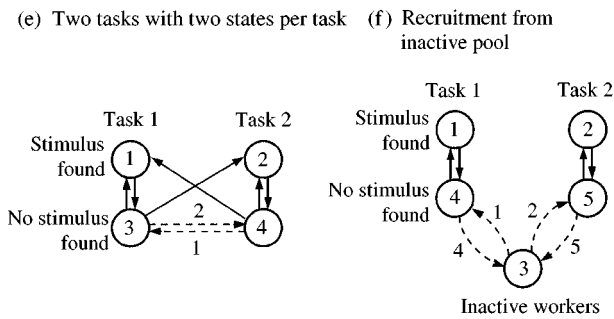


FIG. 1. Graphs of models of task allocation. Each circle in a graph represents a possible state for a worker. For example, in graph (f), state 1 represents a worker of task 1 that has found a stimulus to perform its task. State switches in response to environmental stimuli or spontaneous state switches (i.e. workers “forgetting” they found a stimulus for work) are represented by solid arrows. State switches in response to social interactions are represented by dashed arrows. The numbers above each arrow indicate which interactions cause the switch. For example, in graph F, a worker in state 3 switches to state 4 after interacting with a worker in state 1.

probabilities of switching tasks after a social interaction (s_{ijk} 's) and the interaction rate constants (α_{ij} 's) are constant and independent of the environment. Thus, the social interactions push the task distribution to an equilibrium that is independent of the environment. We made these assumptions about the s_{ijk} 's because we are studying the case in which the response to social interactions does not depend on the local environment and there is no exchange of information

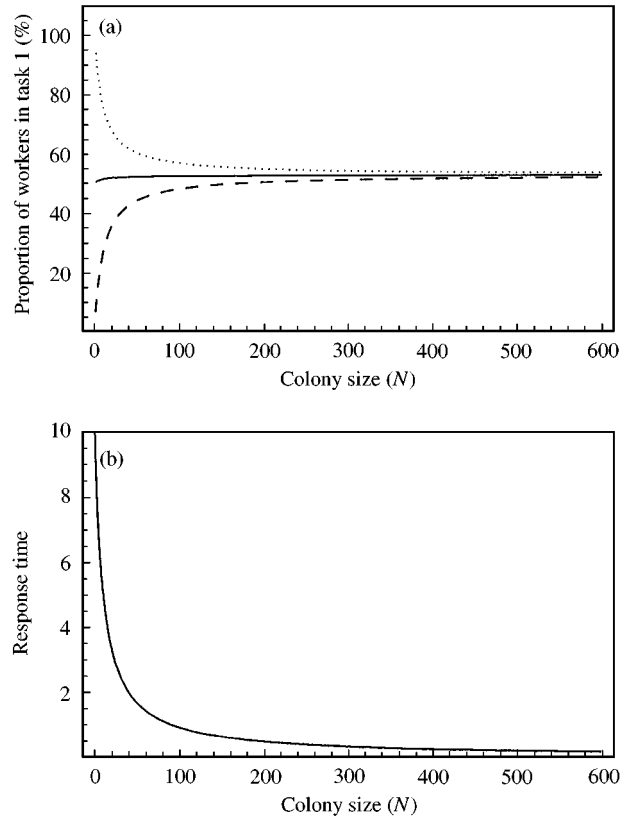


FIG. 2. A model with two tasks in which responses to social interactions do not depend on the local environment. Task distribution (a) and response time (b) as a function of colony size in three different environments. Environment 1 (—): $e_{21}/(e_{12} + e_{21}) = 50\%$. Environment 2 (···): $e_{21}/(e_{12} + e_{21}) = 98\%$. Environment 3 (- - -): $e_{21}/(e_{12} + e_{21}) = 2\%$. For all environments $e_{12} + e_{21} = 0.1$. Parameters: $S_{122} = 0.005$, $S_{211} = 0.006$, $S_{112} = 0.005$, $S_{221} = 0.005$.

about the environment. However, the interaction rate constants (α_{ij} 's) could depend on the environment if workers that had experienced a certain environment were more likely to interact with other workers. We do not consider such cases.

Figure 2(b) shows the response time of the colony as a function of size for each of the three environments. Our measure of response time is return time, the negative reciprocal of the real part of the largest eigenvalue of the task dynamics (Pimm, 1982). This measure estimates the time taken for a perturbation of the task distribution at equilibrium to decay to 37% of its initial value. This is also a measure of how long a colony takes to adjust its task distribution to a new environment. The response times in the three

environments are very similar, so all three curves overlap (see Appendix A for an analytical expression of response time). The response time decreases as the colony size increases. This is caused by the increasing rate of social interactions.

Considering Fig. 2(a) and 2(b) together, it is apparent that the decrease in response time occurs simultaneously with an increase in the importance of the social interactions in determining the task distribution at equilibrium. Thus, when the response of workers to social interactions does not depend on the local environment and no information about the environment is exchanged, there is a trade-off between how well the task distribution tracks the environment and short response times to environmental changes. Shorter response times can be obtained by increasing colony size, but this comes at the cost of a decreased sensitivity to environmental changes.

This trade-off still holds when we relax some assumptions. We assumed that workers switch tasks immediately after finding a stimulus for a different task. Instead, suppose workers are continuously gathering information about the environment and use this in their decision rule for task switching. The e_{ij} 's would still represent the mean rate at which workers switch from task i to task j in the absence of social interactions, but would not be directly proportional to stimuli density. For instance, if workers switched tasks only when the density of stimuli for a different task was above a certain threshold, the e_{ij} 's would be a sigmoidal function of stimuli density (e.g. Theraulaz *et al.*, 1998). Nonetheless, task allocation would still be described by eqn (2) and the trade-off would still occur.

The trade-off also occurs for sub-linear interaction rates of the form $f_i(X_j) = \alpha_{ij} X_j/N^z$ with $0 \leq z < 1$ (the linear case corresponds to $z = 0$), because the corresponding social terms $s_{ijk}\alpha_{ij}X_iX_j/N^z$ increase with colony size faster than the environmental terms $e_{ij}X_i$. When $z = 1$, the response time does not decrease with colony size, and thus it is not an interesting case.

We have implicitly assumed that the density of environmental stimuli (the e_{ij} 's) are independent of colony size and independent of the number of workers in each task. This may be more realistic for some tasks than others. For example, the

density of food items may be inversely related to the number of foragers. In this case, it can be shown that the trade-off between sensitivity to the environment and response time still holds. The density of stimuli for brood care may increase with colony size if the per capita productivity of the colony increases with colony size (Jeanne, 1999). In this case the trade-off will hold as long as the increase in the density of stimuli $e_{ij}(N)$ with colony size is slower than the increase in interaction rates $\alpha_{ij} X_j/N^z$.

2.2. MORE THAN TWO TASKS

We now consider whether the decreased sensitivity of large colonies to the environment persists when there are more than two tasks. We show that when there is a non-zero probability of switching tasks after a social interaction with a worker in a different task, task distribution for large colonies is determined by social interactions and does not depend on the environment (Table 1). We then present an example of a model in which the response to social cues is organized in such a way that task distribution always depends on the environment (Table 1).

2.2.1. Non-zero Probability of Switching Tasks after a Social Interaction

We consider two configurations of the social parameters S_{ijk} , configurations I and II. In configuration I, when a worker in task i meets a worker in task j , it can switch only to task j , $S_{ijj} > 0$ and $S_{ijk} = 0$ if $j \neq k$ [see Fig. 1(c)]. In configuration II, a worker can switch to any other task, $S_{ijk} > 0$ for any i, j and k [see Fig. 1(d)]. For each configuration, we consider colonies with three and four tasks. Note that in both configurations, there is a non-zero probability of switching tasks after a social interaction with a worker in a different task ($\sum_{k \neq i} S_{ijk} > 0$ for any i, j). These two configurations are particular cases of eqn (1) and thus our study of models with more than two tasks is not as general as our study of the two-task model in Section 2.1 (see Table 1).

We could not find general analytical solutions for stable equilibria for models with more than two tasks, so we used a numerical approach. The algorithm is described in detail in Appendix B. For a model with a given set of numerical

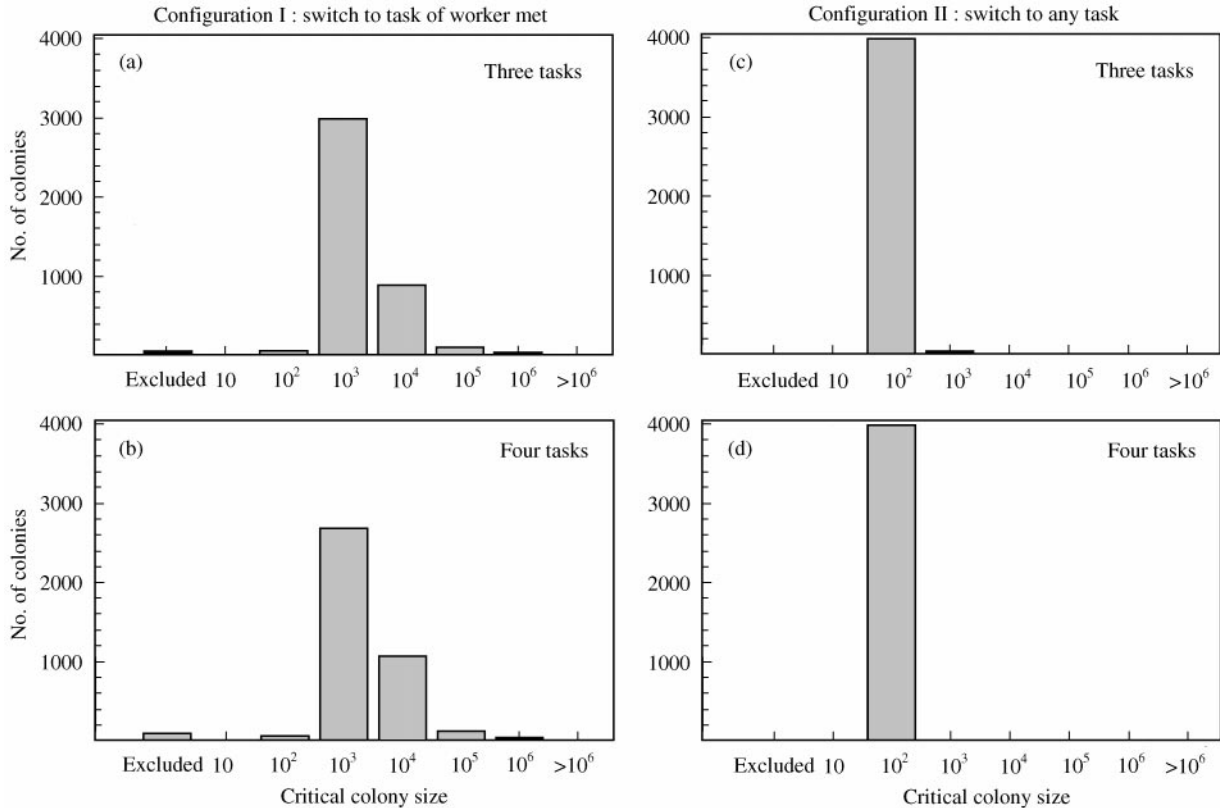


FIG. 3. Models with three and four tasks in which response to social interactions does not depend on the local environment. Histograms of colony sizes at which task distribution does not depend on the environment. See text for explanation of configurations I & II.

parameters (a model replicate), the algorithm checks for the existence of a critical colony size, i.e. a colony size above which the task distribution does not respond to the environment. This is done by studying the task distribution for increasing colony sizes, starting with ten workers and then in increasing powers of ten to a maximum of 1 million workers. If found, the critical colony size is recorded.

For each configuration and for each number of tasks, 4000 model replicates were generated with social parameters S_{ijk} randomly drawn from a uniform distribution between 0 and 1. The histograms in Fig. 3 show the number of replicates at each critical size.

Configuration I: Switch to task of worker met. We were able to find a critical size for 99.7% of the three-task replicates and 97.9% of the four-task replicates [sum of the bars to the right of the

excluded category in Fig. 3(a) and 3(b)]. Some of the replicates were excluded from our search for a critical size (excluded bar), because no stable equilibria were found, or in a very small proportion of replicates from the four-task model (0.1%), because multiple stable equilibria existed for a single environment. No replicates were found where the search for a critical size stopped because the maximum colony size was reached (0% of cases with critical size $>10^6$).

Configuration II: Switch to any task. The dominance of social interactions in determining the task distribution at equilibrium is even more marked in configuration II. We always found a critical size [Fig. 3(c) and (d)]. Furthermore, the critical colony sizes were smaller compared to configuration I critical sizes. Most configuration II replicates had critical sizes of 100 workers, with a small proportion having critical sizes of 1000

workers, while most configuration I replicates had critical sizes of 1000 workers, and some had critical sizes as large as one million workers. This happens because workers in the replicates with configuration II are more responsive to social interactions: all social parameters S_{ijk} are non-zero, in contrast with configuration I where the majority of social parameters are zero. Thus, the probability of switching tasks after a social interaction is higher in configuration II, and social interactions dominate at even smaller colony sizes.

Numerical analysis shows that in general, response time decreases with colony size for any number of tasks (not shown). Thus, these results suggest that, when there is a non-zero probability of switching tasks after a social interaction, a trade-off exists between response time and the ability to track environmental changes for any number of tasks. We note that this trade-off will also be present when interaction rates are sub-linear of the form, $f_i(X_j) = \alpha_{ij} X_j / N^z$ with $0 \leq z < 1$.

2.2.2. The Synchronizer Model

Suppose there are two pools of workers. Workers in the first pool perform tasks 1 and 2 and respond to environmental cues. Workers in the second pool respond to social interactions with workers in the first pool: workers switch from task 3 to 4 when they meet a worker in task 2 and workers switch from task 4 to 3 when they meet a worker in task 1 [see Fig. 1(b)]. The task allocation dynamics are

$$\begin{aligned} \frac{dX_1}{dt} &= e_{21}X_2 - e_{12}X_1, \\ X_2(t) &= N_1 - X_1(t), \\ \frac{dX_3}{dt} &= X_1X_4S_{413} - X_2X_3S_{324}, \\ X_4(t) &= N_2 - X_2(t), \end{aligned} \quad (3)$$

where N_1 is the total number of workers in the first pool and N_2 is the total number of workers in the second pool. The stable equilibrium of

eqn (3) is

$$\begin{aligned} X_1^* &= \frac{e_{21}}{e_{12} + e_{21}} N_1, \\ X_2^* &= \frac{e_{12}}{e_{12} + e_{21}} N_1, \\ X_3^* &= \frac{e_{21}S_{413}}{e_{12}S_{324} + e_{21}S_{413}} N_2, \\ X_4^* &= \frac{e_{12}S_{324}}{e_{12}S_{324} + e_{21}S_{413}} N_2. \end{aligned} \quad (4)$$

Workers in the first pool are distributed between tasks 1 and 2 in direct proportion to the amount of environmental stimuli for each task. Workers in the second pool are distributed between tasks 3 and 4 in a weighted proportion of the amount of environmental stimuli for tasks 1 and 2. Rewriting the task distribution as ratios between the first and second pools we have:

$$\frac{X_3^*}{X_4^*} = \frac{S_{413}}{S_{324}} \frac{X_1^*}{X_2^*}. \quad (5)$$

The ratio of tasks 3 to 4 workers is directly proportional to the ratio of tasks 1 to 2 workers. This model synchronizes tasks 3 and 4 with tasks 1 and 2.

In this model, task distribution tracks the environment for any colony size. This differs from the models studied in Section 2.2.1 (see Table 1). Here, responses to social interactions and responses to environmental cues are partitioned between two groups of tasks: the quadratic terms appear only in tasks 3 and 4 while the linear terms appear only in tasks 1 and 2 [see eqn (3) and Fig. 1(b)]. Consequently, one type of term never dominates over the other type in a given task. This model has the restriction that workers never switch between the two pools, so this model is not as general as the models in Section 2.2.1 in which there are task switches between every pair of tasks. However, there may be scenarios where task allocation may resemble this model. For instance, in harvester ants (*Pogonomyrmex barbatus*), foragers are less likely to go outside when environmental stimuli increase the activity of

nest maintenance workers (Gordon, 1987). It may be that an interaction between an inactive forager and an active nest maintenance worker increases the probability that the forager will remain in the nest. Another example is harvester ant patrollers, whose return to the nest affects the activity of foragers (Gordon, 1999).

We finish this section by noting some characteristics of response time. The response time of workers in the first pool is

$$\text{Response time}_{X_1, X_2} = \frac{1}{e_{12} + e_{21}}. \quad (6)$$

Workers in the first pool respond faster when there are more stimuli in the environment, i.e. when e_{12} and e_{21} increase. The response time is independent of colony size because these workers do not use social cues.

The response time of workers in the second pool is given by

$$\text{Response time}_{X_3, X_4} = \frac{e_{12} + e_{21}}{N_1(e_{12}S_{324} + e_{21}S_{413})}. \quad (7)$$

Interestingly, the response time of workers in the second pool depends on the total number of workers in the first pool, but not on the number of workers in the second pool. The higher the number of workers in the first pool, the faster the workers in the second pool respond. Note that when the environment changes, first the distribution of workers in tasks 1 and 2 changes, and only then does the distribution of workers in the second pool start to change. So the response time in eqn (7) measures the delay between the response of workers in the first and second pools.

3. Response to Interactions depends on Local Environment

In this section, we analyse models in which the response of individuals to social interactions depends on the local environment. We assume that an individual can be in one of two states: either it recently found a stimulus for its task (stimulus-found state) or not (no-stimulus-found state). Only individuals that have not recently found a stimulus respond to social interactions.

In the models in Section 2 the state variables were the number of workers in each task. In contrast, for the models developed in this section, we need two state variables for each task, one for the workers in the stimulus-found state and other for the workers in the no-stimulus-found state. Eqn (1) could be used to describe a general framework for this section, with $i = 1 \dots 2 \times m$, and a broader interpretation of e_{ij} as the rate of switching from state i to state j in the absence of social interactions. Nevertheless, for simplicity's sake, we will use a slightly different notation.

We study two different models. The first is a two-task model [Fig. 1(e)] which is the counterpart to the model studied in Section 2.1. In the second model [Fig. 1(f)], workers are recruited to tasks from a common pool of inactive individuals. For both models, we start by assuming that during social interactions individuals exchange information about their environments, i.e. about finding or not finding stimulus for their tasks. We then drop this assumption and investigate whether this affects the task dynamics. Our findings are summarized in Table 1.

3.1. A MODEL WITH TWO TASKS AND TWO STATES PER TASK

We assume that a worker that has not recently found a stimulus for its task switches tasks when it finds stimulus for a different task, or after meeting a worker in a different task that has found a stimulus for work. Workers that have recently found a stimulus for work do not switch tasks. Let $X_i(t)$ and $Y_i(t)$ denote, respectively, the number of workers in task i that have found and have not found a stimulus for work. The task dynamics are given by [see Fig. 1(e)]:

$$\begin{aligned} \frac{dX_1}{dt} &= e_1 Y_1 - qX_1 + \delta \cdot e_1 Y_2, \\ \frac{dX_2}{dt} &= e_2 Y_2 - qX_2 + \delta \cdot e_2 Y_1, \\ \frac{dY_1}{dt} &= qX_1 - e_1 Y_1 - \delta \cdot e_2 Y_1 - \alpha Y_1 X_2 + \alpha Y_2 X_1, \\ \frac{dY_2}{dt} &= qX_2 - e_2 Y_2 - \delta \cdot e_1 Y_2 + \alpha Y_1 X_2 - \alpha Y_2 X_1, \end{aligned} \quad (8)$$

where e_i is the density of stimuli for task i in the neighborhood of that task, $\delta \cdot e_i$ is the density of stimuli for task i in the neighborhood of the opposite task, q is the rate at which individuals forget they have found a stimulus for work and α is the interaction rate constant. We assume that tasks are spatially separated. Consequently, the density of stimuli for a given task is likely to be higher in the neighborhood of that task than in the neighborhood of any other task, and δ is assumed to be small ($\delta \ll 1$). The stimulus-found/no-stimulus-found states could alternatively represent employed/unemployed states, as in the foraging-for-work model (Sendova-Franks and Franks, 1993), and in that case q would be the mean rate of execution of a single unit of work.

One way of interpreting this model is that the probabilities S_{ijk} in eqn (2) now depend on the environment. For instance, the probability that a worker in task 1 switches tasks after meeting a worker in task 2 is $[Y_1/(Y_1 + X_1)] \times [X_2/(X_2 + Y_2)]$, and each of these ratios depends on the environment.

Figure 4 shows a numerical study of this model (see Appendix C for methods). Figure 4(a) shows the task distribution at the stable equilibrium as a function of the environment for two different colony sizes, $N = 10$ and 10000. The total density of environmental stimuli, $e_1 + e_2$, is left constant, while the proportion of environmental stimuli for task 1, $e_1/(e_1 + e_2)$, varies from 0 to 100%. Note that there is only one stable equilibrium for each environment. Two results are important here. First, for any colony size the task distribution depends on the environment (see Appendix C). Figure 4(a) shows that at the two extreme environments, the task distribution of a small colony ($N = 10$) is identical to the task distribution of a large colony ($N = 10000$): for 0% of stimuli for task 1 both colonies have no workers in task 1, and for 100% of stimuli for task 1 both colonies have all workers in task 1. In contrast, if we were to plot the task distribution from the model in Section 2.1 (response to social interactions does not depend on the environment), the task distribution at the two extreme environments would be very different in a large and in a small colony. A large colony would have the same task distribution in both environments

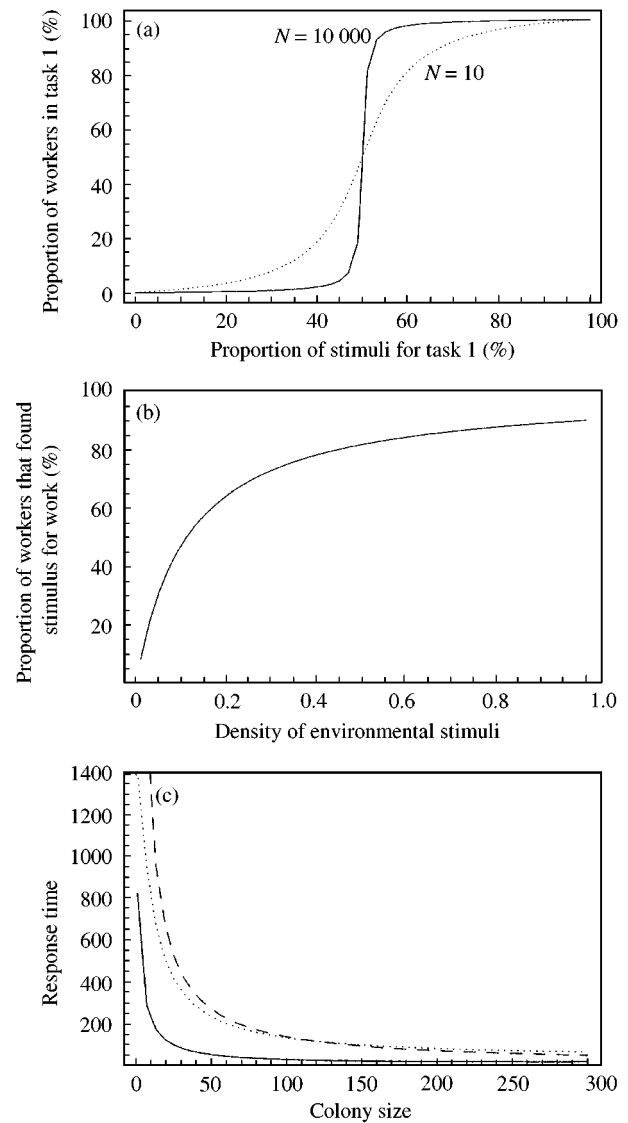


FIG. 4. A model with two tasks, in which workers respond to social interactions only when they have not recently found a stimulus for work. Parameters: $\alpha = 0.001$, $q = 0.1$, $\delta = 0.01$. (a): Task distribution as a function of the environment ($e_1 + e_2 = 0.1$, $e_1/(e_1 + e_2)$ varying from 0 to 100%), for two colony sizes $N = 10$ (\cdots) and $N = 10000$ (—). (b): Proportion of workers that recently found a stimulus for work as a function of stimulus density ($e_1/(e_1 + e_2) = 10\%$, $e_1 + e_2$ varying from 0.01 to 1, $N = 100$). (c): Response time as a function of colony size in three different environments. Environment 1 (—): $e_1/(e_1 + e_2) = 10\%$, $e_1 + e_2 = 0.1$. Environment 2 (\cdots): $e_1/(e_1 + e_2) = 40\%$, $e_1 + e_2 = 0.1$. Environment 3 (---): $e_1/(e_1 + e_2) = 10\%$, $e_1 + e_2 = 0.01$.

(and thus a flat response to the environment), while a small colony would have more workers in task 1 for 100% than for 0% of stimuli for task 1. Second, the relationship between the proportion of workers in task 1 and the proportion of stimuli

for that task is nonlinear, following a sigmoidal relationship [Fig. 4(a)]. In the absence of social interactions, this relationship would be linear. Not surprisingly, the sigmoid curve gets steeper with increasing colony size: the large colony has almost all workers allocated to the task with a higher proportion of stimuli.

Figure 4(b) illustrates the relationship between the number of individuals in the found-stimulus state and the density of environmental stimuli. The proportion of individuals that have recently found stimuli for work increases with the density of environmental stimuli, $e_1 + e_2$.

Figure 4(c) shows response time as a function of colony size in three different environments. Environments 1 and 2 have a high density of environmental stimuli ($e_1 + e_2 = 0.1$), but in environment 1 the proportion of stimuli for task 1 is only 10% while in environment 2 it is 40%. Environment 3 has a low density of environmental stimuli ($e_1 + e_2 = 0.01$) and the proportion of stimuli for task 1 is the same as in environment 1. In all three environments the response time decreases with colony size. Response time is slower when the density of stimuli is similar for both tasks (environment 2) than when most environmental stimuli is for a single task (environment 1). This happens because when the density of stimuli is similar for both tasks, workers switch tasks in both directions, so task switches cancel out and change in task distribution is slow. For the same proportion of stimuli for task 1, response time is faster when the density of environmental stimuli is high (environment 1) than when the density of environmental stimuli is low (environment 3).

If the spatial separation of the tasks is reduced [by making δ larger, not shown in Fig. 4(c)] then small colonies have shorter response times and the decrease in response time with colony size would be less steep than shown in Fig. 4(c). This happens because the information relayed by social cues adds little if the spatial separation of the tasks is small (a worker near the environmental stimulus can discover the stimulus itself). Note that because the density of stimuli in the neighborhood of the opposite task is 100 times lower here than in the model of Section 2.1, the response times for small colony sizes in Fig. 4(c) are much longer than the response times in Fig. 2(b).

In this model, response time decreases with colony size while the task distribution always depends on the environment. Nevertheless, it can be argued that there is still a trade-off between environmental sensitivity and response time, due to the sigmoidal relationship between task distribution and environment [Fig. 4(a)]. As colony size increases, the colony distinguishes fewer and fewer environments because the response to the environment tends to bifurcate: most workers engage in task 1 when there are more stimuli for task 1 than for task 2, and vice versa. Thus, sensitivity to the environment decreases in the sense that a very large colony distinguishes mainly two environments. Pacala *et al.* (1996) found a similar phenomenon, and showed that in their model it was a consequence of assuming that the environment was not affected by task distribution. We have made the same assumption so far. In many cases, however, it might be more realistic for the density of stimuli to decrease with the number of individuals in the task (e.g. foraging). This can be expressed as

$$e_i(X_i) = \frac{e_i^0}{1 + k X_i/N} \quad (9)$$

where $e_i(X_i)$ is the density of stimuli for task i as a function of the workforce, e_i^0 is the base stimuli density for task i , i.e. the density of stimuli when no individuals are engaged in task i , and k is a normalizing constant.

In Fig. 5, we plot the task distribution at the stable equilibrium for a large colony ($N = 10\,000$) as a function of the environment, comparing the case in which the environment is not affected by task distribution with the case in which stimulus density decreases with the number of workers (see Appendix C for methods). In the latter case, there is a range of environments where the colony responds in an almost linear fashion (in Fig. 5 from 20 to 80% stimuli for task 1): when the base stimulus density for a task increases, the number of workers allocated to that task increases correspondingly. Outside this range the colony allocates the vast majority of workers to the task with more environmental stimuli, as it does when the environment is not affected by the task distribution. It can be shown that within the linear

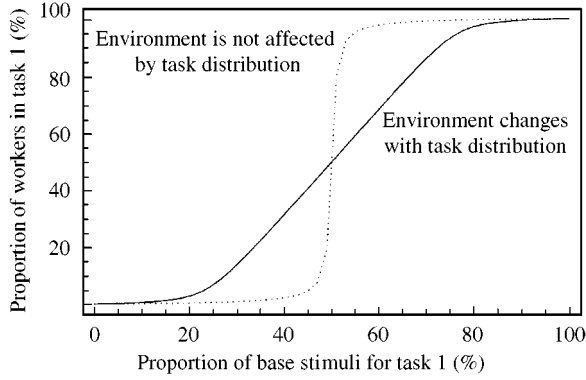


FIG. 5. Comparison of task distributions in an environment that is not affected by task distribution (\cdots) and an environment where the stimulus density for a task decreases with the number of workers ($-$), in a model with two tasks where workers respond to social interactions only when they have not recently found a stimulus for work. Parameters: $N = 10\,000$, $\alpha = 0.001$, $q = 0.1$, $\delta = 0.01$. Environment: $e_1^0 + e_2^0 = 1$, $e_1^0/(e_1^0 + e_2^0)$ varying from 0 to 100%, $k = 3$. When the environment is not affected by task distribution $e_i = e_i^0$, otherwise we use eqn (9).

range, the densities of stimuli for the two tasks are equalized by the task distribution, i.e. $e_1(X_1) \approx e_2(X_2)$. Outside the linear range, the difference between the base stimulus densities e_1^0 and e_2^0 is too large to be equalized by task distribution. Thus, when the response of workers to social interactions depends on the local environment and the environmental stimuli decrease with the number of workers, there is a range of environments where the trade-off between environmental sensitivity and response time disappears.

So far, we have assumed that workers exchange information about the environment during social interactions: individuals switch tasks only when they meet an individual that has recently found a stimulus for work in a different task. We now show that our results would be the same if individuals would not exchange information about the environment. In this case, two workers in different tasks that had not found stimulus for work, would switch tasks when they meet. These two task switches would cancel each other out. Therefore, despite many more task switches, the colony task dynamics would still be as in eqn (8). Thus, in the model presented here there is no apparent advantage of exchanging information about the environment. However,

costs of task switching might make such information worthwhile.

3.2. A MODEL WITH RECRUITMENT FROM AN INACTIVE POOL OF WORKERS

In some species, foragers come back to the nest to recruit inactive workers to food resources (Beckers *et al.*, 1989). In this section, we develop a task allocation model inspired by this type of social recruitment. We consider two active tasks outside the nest, tasks 1 and 2, and one inactive pool of workers inside the nest. Workers in the active tasks can be in the stimulus-found or no-stimulus-found state. When two individuals that have not recently found a stimulus meet, they join the inactive pool of individuals inside the nest. When an inactive individual meets an individual in task i that has recently found a stimulus for work, it switches to the no-stimulus-found state of task i . This assumes that individuals that have recently found a stimulus for work will interact regularly with inactive individuals, for instance by coming to the nest. Let X_0 denote the number of inactive individuals. The task allocation dynamics are [see Fig. 1(f)]:

$$\begin{aligned} \frac{dX_0}{dt} &= \alpha_2 Y_1 Y_1 + \alpha_2 Y_2 Y_2 \\ &\quad - \alpha_1 X_0 X_1 - \alpha_1 X_0 X_2, \\ \frac{dX_1}{dt} &= e_1 Y_1 - q X_1, \\ \frac{dX_2}{dt} &= e_2 Y_2 - q X_2, \\ \frac{dY_1}{dt} &= q X_1 - e_1 Y_1 - \alpha_2 Y_1 Y_1 + \alpha_1 X_0 X_1, \\ \frac{dY_2}{dt} &= q X_2 - e_2 Y_2 - \alpha_2 Y_2 Y_2 + \alpha_1 X_0 X_2, \end{aligned} \tag{10}$$

where e_i is the density of stimuli for task i in the neighborhood of that task, q is the rate at which individuals “forget” they have found a stimulus for work, α_1 is the interaction rate constant between workers in outside tasks and inactive

workers, and α_2 is the interaction rate constant for workers in the same task. Note that we are assuming that outside tasks are performed in different areas of the environment, so there is a negligible chance of finding stimuli for a different task or meeting a worker in a different task.

Figure 6 shows a numerical study of this model at the stable equilibrium (see Appendix D for methods). Figure 6(a) shows the proportion of workers in each task as a function of the proportion of stimuli for task 1, keeping the total density of environmental stimuli constant. The proportion of workers in the active tasks follows almost linearly the proportion of environmental stimuli for those tasks [compare with the sigmoidal response in the two-task model in Fig. 4(a)]. The number of inactive workers is relatively constant.

Figure 6(b) shows the proportion of individuals in the stimulus-found state, no-stimulus-found state, and inactive individuals as a function of the total density of environmental stimuli. For very low densities of environmental stimuli all workers are inactive. As the stimulus density increases some workers become active, but in the no-stimulus-found state, and then as the stimulus density continues to increase, all workers become active, mostly in the stimulus-found state.

It is important to note that the proportion of workers in each task does not depend on colony size (see Appendix D). Thus, Fig. 6(a) and (b) are the same for any colony size, and the sensitivity to the environment of the task distribution is not affected by colony size.

What is the relationship between response time and colony size? Numerical simulations show that usually, response time decreases strongly with colony size. Figure 7 illustrates this in a biologically inspired scenario. We plot an imaginary day for two different colony sizes, 25 and 1000 workers. During the night there are few environmental stimuli. In the early morning ($t = 6$ a.m.) there are some stimuli for task 1. Later in the day ($t = 10$ a.m.), there are many environmental stimuli for task 2 and the stimuli for task 1 decrease, $e_1 = 0.01$, $e_2 = 0.5$. Finally, at the end of the day ($t = 6$ p.m.), environmental stimuli for task 2 decrease to the night time level.

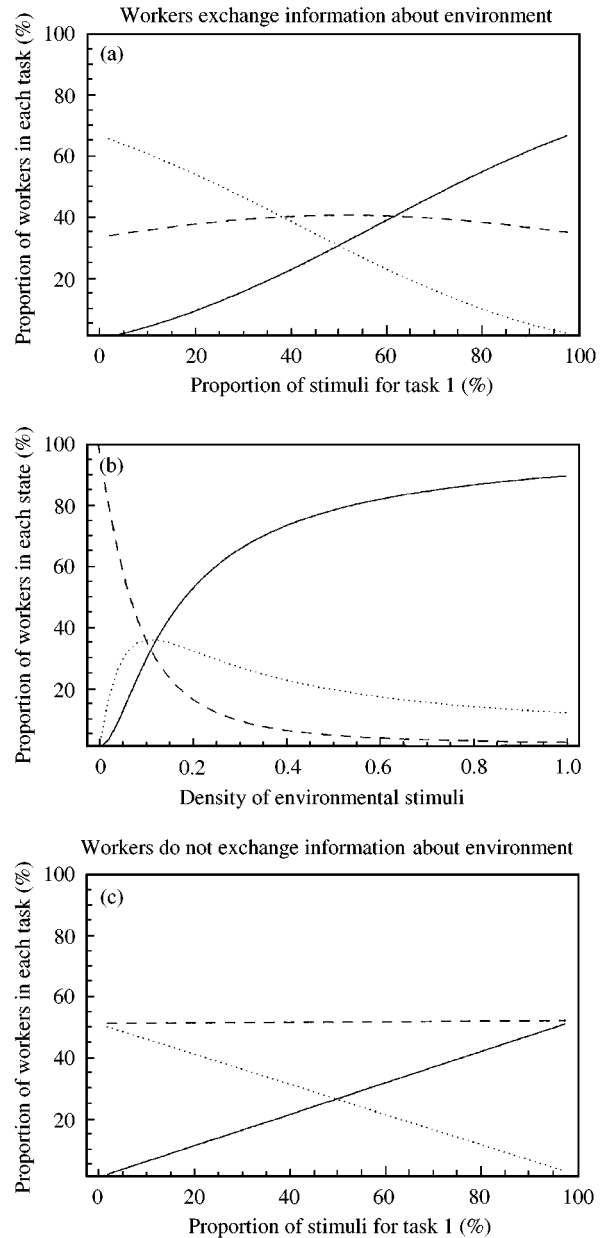


FIG. 6. A model with recruitment from an inactive pool of workers, in which the response to social interactions depends on the environment. Parameters: $\alpha_1 = \alpha_2 = 0.001$, $q = 0.1$, $N = 100$. (a): Task distribution as a function of the environment when workers do not exchange information about the environment ($e_1 + e_2 = 0.1$, $e_1/(e_1 + e_2)$ varies from 0 to 100%). Task 1, (—); task 2, (·····); inactive, (---). (b) Proportion of workers that are inactive, that have found a stimulus for work, and that have not found a stimulus for work as a function of total stimulus density ($e_1/(e_1 + e_2) = 10\%$, $e_1 + e_2$ varies from 0.01 to 1): Stimulus found, (—); no stimulus found, (·····); inactive, (---). (c): Task distribution as a function of the environment when workers exchange information about the environment ($e_1 + e_2 = 0.1$, $e_1/(e_1 + e_2)$ varies from 0 to 100%). (—), task 1; (·····), task 2; (---), inactive.

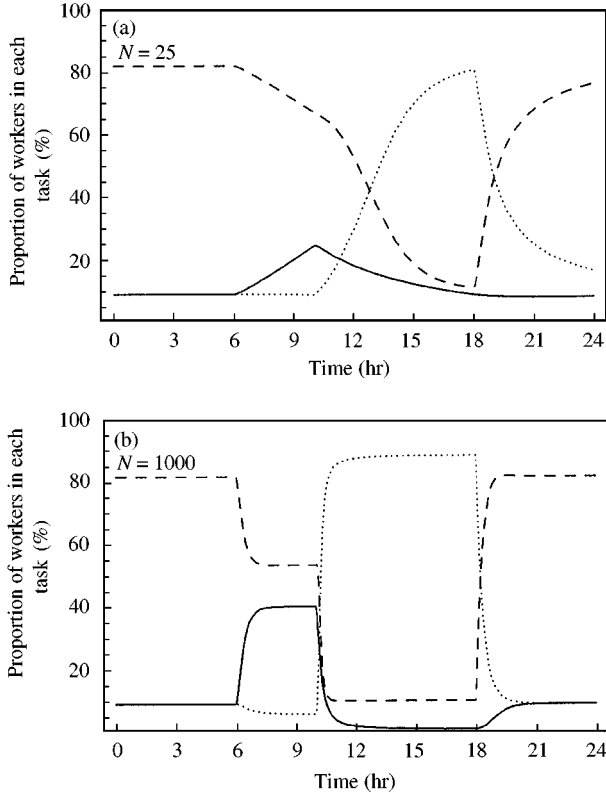


FIG. 7. Simulation of a 24-hr cycle of a colony with recruitment from an inactive pool of workers, for two different colony sizes: 25 workers (a) and 1000 workers (b). Parameters: $\alpha_1 = \alpha_2 = 0.001$, $q = 0.1$. Environment: before 6 hr - $e_1 = 0.01$, $e_2 = 0.01$; between 6 and 10 hr - $e_1 = 0.05$, $e_2 = 0.01$; between 10 and 18 hr - $e_1 = 0.01$, $e_2 = 0.25$; after 18 hr - $e_1 = 0.01$, $e_2 = 0.01$. Task 1, (—); task 2, (····); inactive, (---).

For both colony sizes the task distribution tracks the environment. During the night, most of the workers are inactive. In the beginning of the day, one-third of the inactive workers switch to task 1. At 10 a.m., workers start switching from inactivity and from tasks 1 to 2, reaching an equilibrium task distribution with almost 90% of the workers in task 2. Finally, at the end of the day, workers switch back to inactivity. The only difference between the two colonies is that the larger one responds much faster to the environment. For example, colony emergence at 6 a.m. takes 4 hr for the colony with 25 workers, and only 20 min for the colony with 1000 workers.

In this model we have again assumed that individuals exchange information about the environment during social interactions. We now look at what happens when individuals assess only the

task of the individuals they interact with. We need to make two changes to the task allocation dynamics:

- (1) Individuals that have not found a stimulus switch to inactivity after meeting an individual in the same task, both if the met individual had not found a stimulus (already in the model), or had found a stimulus (new term) for its task.
- (2) When an inactive individual interacts with an individual in task i it switches to the no-stimulus-found state of task i , both if the met individual had found a stimulus (already in the model), or had not found a stimulus (new term) for its task.

If individuals are able to recognize inactive individuals, the second change can be avoided by assuming that active workers that have not found a stimulus switch to inactivity after meeting an inactive worker (however, as in the model of Section 3.1, this implies that many more task switching will be happening than if they were exchanging information about the environment—see Table 1). So we need to make only the first change in the dynamics of eqn (10):

$$\begin{aligned}
 \frac{dX_0}{dt} &= \alpha_2 Y_1 (Y_1 + X_1) + \alpha_2 Y_2 (Y_2 + X_2) \\
 &\quad - \alpha_1 X_0 X_1 - \alpha_1 X_0 X_2, \\
 \frac{dX_1}{dt} &= e_1 Y_1 - q X_1, \\
 \frac{dX_2}{dt} &= e_2 Y_2 - q X_2, \\
 \frac{dY_1}{dt} &= q X_1 - e_1 Y_1 - \alpha_2 Y_1 (Y_1 + X_1) \\
 &\quad + \alpha_1 X_0 X_1, \\
 \frac{dY_2}{dt} &= q X_2 - e_2 Y_2 - \alpha_2 Y_2 (Y_2 + X_2) \\
 &\quad + \alpha_1 X_0 X_2.
 \end{aligned} \tag{11}$$

Remember that in the model of Section 3.1, the equations describing task allocation were identical both when individuals did and did not exchange information about the environment. That happened because there was a perfect symmetry between tasks 1 and 2. Here, however, there is an inactive pool of individuals, bringing an asymmetry to the task switching.

The question now is how much difference the change from eqns (10) to (11) makes. Figure 6(c) shows a numerical study of the equilibrium task distribution of eqn (11). Surprisingly, the task distribution changes very little when workers do not exchange information about the environment [compare with Fig. 6(a)]. The number of individuals in each task is still proportional to the density of environmental stimuli, and the linearity of this relationship is even improved. It can also be shown that the task distribution at equilibrium does not depend on colony size. Furthermore, numerical examples suggest that the response time does not change significantly with this new term.

In summary, when a worker's response to interactions depends on the local environment and there is recruitment from an inactive pool of workers there is no trade-off between response time and sensitivity to the environment. This suggests that the existence of an inactive state increases the sensitivity of the task distribution to the environment [compare Fig. 6(a) with Fig. 4(a) for $N = 10\,000$], even when the environment is not affected by task distribution (see Table 1). We note that the main results for this model and the model described in Section 3.1 (see Table 1) can be extended to more than two tasks.

4. Discussion

Response time to environmental changes decreases with increasing colony size (Table 1). Pacala et al. (1996) found the same result, but here we show this decrease persists when we alter the assumptions about the behavioral rules of the workers. Response time decreases with colony size whether or not a worker's response to social interactions depends on the local environment [Figs. 4(c) and 2(b), respectively]. When a worker's response to social interactions does depend on the local environment, response time

decreases with colony size whether or not workers exchange information about the environment (Table 1). The decrease in response time with colony size occurs only when individuals use social interactions as cues for task switching. In the absence of social interactions a large colony tracks the environment as fast as a single individual. This suggests that an ecological advantage of colonies over single individuals is the use of social cues to respond more quickly to the environment. This complements other advantages of colony living suggested by theoretical work, such as redundancy (Oster & Wilson, 1978), being able to exploit a larger portion of the environment (Seeley *et al.*, 1991), smaller queuing delays in task partitioning (Anderson & Ratnieks, 1999) and the ability of simple individuals to produce complex colony-level responses to the environment (Bonabeau *et al.*, 1997; Deneubourg and Goss, 1989; Lachmann and Sella, 1995). Some of the differences in behavior and productivity between large and small colonies (see Section 1.2) may be due to differences in response times in task allocation.

The sensitivity of task distribution to the environment may decrease with colony size, depending on the behavioral rules used by the workers and on the type of environment (Table 1). When the response of workers to social interactions does not depend on the local environment and no information about the environment is exchanged, sensitivity to the environment decreases with colony size for most models (see Table 1): large colonies show a single task distribution, independent of the environment [Fig. 2(a)]. If workers respond to social interactions only when they have not recently found a stimulus for their task, sensitivity to the environment does not decrease with colony size [Fig. 6(a)], or the task distribution tends to a bifurcated response [Fig. 4(a)], in which the colony distinguishes at least two types of environment.

Our models show differences in sensitivity to the environment because of two factors. First, our models differ in the partitioning of social and environmental cues. In most models in which the response to social interactions does not depend on the local environment [Fig. 1(a), (c) and (d)], workers switch between any pair of states in response both to environmental cues and social

cues. In large colonies, interaction rates are very high and workers tend to respond mostly to social cues. In contrast, in the synchronizer model [Fig. 1(b)] and in the models where the response to social interactions depends on the local environment [Fig. 1(e) and 1(f)], workers switch between each pair of states either through environmental or social cues, but not both, so social cues never dominate over environmental cues in the net flux of workers between two states. Second, in these latter models, the social cues depend indirectly on the environment. For instance, in the synchronizer model, workers switch from tasks 4 to 3 after meeting a worker in task 2. The number of workers in task 2 is determined by the environment, so the number of workers that switch from task 4 to task 3 in response to social cues depends on the environment.

Our findings suggest that: (1) there is a trade-off between response time and sensitivity to the environment. Large colonies have shorter response times at the cost of decreased sensitivity to the environment. (2) In certain conditions this trade-off can be avoided. Trade-offs related to colony size have been found in other studies. Bonabeau *et al.* (1998) found that as colony size increases, exploitation of food sources by mass recruitment becomes more efficient (workers are able to focus in a single food source) but flexibility (the ability to shift to the richest food source) is decreased. Pacala *et al.* (1996) found that large colonies have short response times but exhibit numbers of active workers that are higher than predicted by the ESS. Both studies suggest that large colonies may regulate their interaction rates to limit these trade-offs. Here, we show that the trade-off between response time and sensitivity to the environment is a consequence of the assumptions about the behavioral rules of the workers: this trade-off is attenuated or disappears when workers respond to social interactions only when they have not found a stimulus for their task. It would be interesting to test empirically whether workers respond differently to social interactions depending on their recent experience of the local environment. The foraging-for-work model (Bourke & Franks, 1995), like our models in Section 3, supposes that task decision depends on the recent experience of the worker.

There may be many behavioral rules that avoid the trade-off between environmental sensitivity and response time. The models of Sections 2 and 3 differ in that the former have only one state per task, while the latter have two states per task that are related to the local environment. We explored only a subset of the possible behavioral rules for the models with two states per task. For example, we did not study the case in which the response of workers does not depend on the local environment but there is exchange of information about the environment (see Table 1).

Surprisingly, we found that when workers respond to social interactions only when they have not found a stimulus for their task, exchanging information about the environment has little effect on the dynamics of task allocation (Table 1). However, when workers do not exchange information about the environment there are many more task switches, which may have costs.

Our models assumed that only the last social interaction determined the probability of task switching. It would be interesting to extend our models to make the decision rule more complex, making the probability of task switching dependent on the last few interactions with other workers.

We wish to acknowledge Paul Armsworth, Ben Kerr, Guy Sella and Joan Roughgarden for numerous discussions during the development of this work. We thank Carl Anderson, Marc Feldman, Brian McGill, Aaron Hirsh, Susan Ptak, and Nathan Sanders for valuable comments on this manuscript. Henrique Pereira was supported by a PRAXIS fellowship BD/11203/97. This work was supported by NSF grant IBN 960639 to Deborah Gordon.

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APPENDIX A

Expression (2) has a single stable equilibrium:

$$X_1^* = \frac{-B - \sqrt{B^2 - 4AC}}{2A}$$

$$X_2^* = 1 - X_1^*$$

where

$$A = S_{122} - S_{112} + S_{221} - S_{211}$$

$$B = -e_{12} - e_{21} + (S_{211} - S_{122} - 2S_{221})N$$

$$C = e_{21}N + S_{221}N^2$$

and (A.3) as

$$\text{Response Time} = \frac{1}{\sqrt{B^2 - 4AC}} \quad (\text{A.1})$$

For a very large colony size ($N \rightarrow \infty$), the stable equilibrium is

$$X_1^* = N \frac{S_{122} - S_{211} + 2S_{221} - \sqrt{(S_{122} - S_{211})^2 + 4S_{112}S_{221}}}{2(S_{122} - S_{112} + S_{221} - S_{211})},$$

$$X_2^* = N - X_1^* \quad (\text{A.2})$$

Thus, for a very large colony the equilibrium depends only on the social parameters S_{ijk} and is independent of the environment (parameters e_{12} and e_{21}).

The response time is:

Response time

$$\frac{1}{\sqrt{B^2 - 4AC}} \quad (\text{A.3})$$

APPENDIX B

For each random replicate (i.e. set of S_{ijk} 's drawn from a random distribution) we tested whether there was a critical colony size as follows. First, the stable equilibrium in the absence of environmental stimuli (i.e. all $e_{ij} = 0$) was calculated and recorded in vector $\mathbf{X}^{*,0}$. At this equilibrium, the proportion of workers in each task $\mathbf{X}^{*,0}/N$ does not depend on colony size and is determined only by the social parameters S_{ijk} . Next, the stable equilibrium was determined for two environments, starting with a colony size of ten workers, and then in increasing powers of 10, until one of the criteria for the critical colony size was met (see below) or colony size exceeded 10^6 . The two environments were chosen so that the task distributions in the absence of social interactions (i.e. all $S_{ijk} = 0$) were very different:

- environment *A*: equal density of environmental stimuli for all tasks, stimulus density is the same everywhere, $e_{ij} = 1$; in the absence of social interactions workers are allocated homogeneously among tasks, $X_1^{*,A} = \dots = X_m^{*,A} = N/m$
- environment *B*: there exists only environmental stimuli for task 1 and stimulus density

is the same everywhere, i.e. $e_{i1} = 1$ and $e_{ij \neq 1} = 0$; in the absence of social interactions all workers engage in task 1, $X_1^{*,B} = N$ and $X_{i \neq 1}^{*,B} = 0$.

If for a given colony size in one of these environments no stable equilibria were found, or multiple stable equilibria existed, the replicate was not considered further but it was accounted for in the excluded category. Note that in replicates where this happened, the social parameters were strongly modifying the task allocation at equilibrium. Nonetheless, the replicate could still have distinct task distributions in different environments, and since this differs from our original definition of critical colony size (task distributions converging in all environments to a single equilibrium determined by social interactions), we chose to designate these cases as a different category.

The primary criterion for the critical colony size was that the maximum distance between the equilibria in any environment and the equilibrium in the absence of environmental stimuli be smaller than 2.5% of the colony size:

$$\text{Max}(\|\mathbf{X}^{*,A} - \mathbf{X}^{*,0}\|, \|\mathbf{X}^{*,B} - \mathbf{X}^{*,0}\|) \leq 0.025N. \quad (\text{B.1})$$

Note that if $\mathbf{X}^{*,A}$ and $\mathbf{X}^{*,B}$ were calculated in the absence of social interactions (or in a very small colony) this distance would be at least 41% of the colony size for three tasks and at least 43% for four tasks. Therefore, if the distance is smaller than 2.5%, task sensitivity to the environment has substantially decreased.

In some cases, no stable equilibria or multiple stable equilibria were found in the absence of environmental stimuli, and then the criterion used was that the distance between equilibria in the two environments be smaller than 2.5% of the colony size:

$$\|\mathbf{X}^{*,A} - \mathbf{X}^{*,B}\| \leq 0.025N. \quad (\text{B.2})$$

In the absence of social interactions this distance would be 82 and 87% of the colony size for 3 and 4 tasks, respectively.

Stable equilibria were found by numerically solving eqn (1) for all positive equilibria. For models with three tasks this was done using the Jenkins–Traub algorithm (Wolfram, 1996). For models with four tasks we used the damped Newton’s method (Wolfram, 1996) with 140 initial guesses, homogeneously distributed in the solution space. Positive equilibria were then tested for stability using the Jacobian of eqn (1).

APPENDIX C

For our parameter values the stable equilibrium of eqn (8) when $\delta > 0$ is

$$\begin{aligned} X_1^* &= e_1 \frac{Y_1 + \delta Y_2}{q}, \\ X_2^* &= e_2 \frac{\delta Y_1 + Y_2}{q}, \\ Y_1^* &= \frac{-B - \sqrt{B^2 - 4AC}}{2A}, \\ Y_2^* &= N - X_1^* - X_2^* - Y_1^*, \end{aligned} \quad (C.1)$$

where

$$\begin{aligned} A &= \alpha(\delta - 1)(e_1 - e_2)[q(q + e_2) \\ &\quad + e_1(q - e_2(\delta^2 - 1))], \\ B &= -q[\delta^2 e_1^3 + e_2(q + e_2)(N\alpha + \delta + \delta e_2) \\ &\quad + \delta e_1^2(q + N\alpha + q\delta + e_2(2\delta^2 + 1)) \\ &\quad + e_1(q(q\delta + N\alpha(2\delta - 1)) + e_2(q\delta(1 + 3\delta) \\ &\quad + N\alpha(2\delta^2 + \delta - 1) + 3e_2\delta^2)], \\ C &= Nq^2\delta e_1(q + N\alpha + \delta e_1 + e_2). \end{aligned} \quad (C.2)$$

When $\delta = 0$ the stable equilibrium is:

$$\begin{aligned} X_1^* &= \frac{e_1}{q + e_1}N \\ Y_1^* &= \frac{q}{q + e_1}N \quad \text{if } e_1 > e_2 \\ X_2^* &= Y_2^* = 0 \\ X_1^* &= Y_1^* = 0 \\ X_2^* &= \frac{e_2}{q + e_2}N \quad \text{if } e_1 < e_2 \\ Y_2^* &= \frac{q}{q + e_2}N \end{aligned} \quad (C.3)$$

and the relationship between workers engaged in task 1 and proportion of stimuli for task 1 becomes a step function; there is a bifurcation of the response to the environment. For positive δ , when $N \rightarrow \infty$ there is also a tendency for bifurcation [see Figure 4(a)], but a perfect bifurcation as in eqn (C.3) is never reached. Response time was calculated using the Jacobian of eqn (8).

For an environment where the stimuli density decreases with the number of workers in the task, no analytical solutions were found for the equilibria. We performed a numerical search for equilibria using the damped Newton’s method (Wolfram, 1996) with 140 initial guesses. Positive equilibria were tested for stability using the Jacobian of eqn (8). Only one stable equilibrium was found for each environment.

APPENDIX D

For our parameter values the stable equilibrium of eqn (10) is

$$\begin{aligned} X_0^* &= \frac{\alpha_2 q^2}{\alpha_2 q^2 + \alpha_1(qe_1 + e_1^2 + qe_2 + e_2^2)}N, \\ X_1^* &= \frac{\alpha_1 e_1^2}{\alpha_2 q^2 + \alpha_1(qe_1 + e_1^2 + qe_2 + e_2^2)}N, \\ X_2^* &= \frac{\alpha_1 e_2^2}{\alpha_2 q^2 + \alpha_1(qe_1 + e_1^2 + qe_2 + e_2^2)}N, \\ Y_1^* &= \frac{\alpha_1 qe_1}{\alpha_2 q^2 + \alpha_1(qe_1 + e_1^2 + qe_2 + e_2^2)}N, \\ Y_2^* &= \frac{\alpha_1 qe_2}{\alpha_2 q^2 + \alpha_1(qe_1 + e_1^2 + qe_2 + e_2^2)}N. \end{aligned} \quad (D.1)$$

We did not find analytical solutions for the equilibria of eqn (11). We performed a numerical search for equilibria using the damped Newton's method (Wolfram, 1996) with 630

initial guesses. Positive equilibria were tested for stability using the Jacobian of eqn (11). Only one stable equilibrium was found for each environment.