



Fixed Response Thresholds and the Regulation of Division of Labor in Insect Societies

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We introduce a simple mathematical model of regulation of division of labor in insect societies based on fixed-response thresholds. Individuals with different thresholds respond differently to task-associated stimuli. Low-threshold individuals become involved at a lower level of stimulus than high-threshold individuals. We show that this simple model can account for experimental observations of Wilson (1984), extend the model to more complicated situations, explore its properties, and study under what conditions it can account for temporal polyethism.

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1. INTRODUCTION

A key factor contributing to the impressive ecological success of social insects is their social organization, and particularly their division of labor (Oster and Wilson, 1978; Robinson, 1992). It is widely accepted that dividing tasks among members of a colony, so that individuals tend to become specialized in certain roles, enhances colony efficiency (here, reproductive output), either because workers develop task-specific skills through practice, or because spatial fidelity, whereby individuals become more and more spatially localized to perform specific tasks, reduces the need for time- and energy-consuming movements between different locations

(Wilson, 1976; Oster and Wilson, 1978; Seeley, 1982; Jeanne, 1986; Sendova-Franks and Franks, 1993). Genotype, physiology, morphology, age, experience, social and external environments have been shown to influence patterns of task allocation (Lenoir, 1987; Jeanne, 1991) in such a way that division of labor is not only efficient (i.e., allows more work to be done for the same energy expense), but also flexible. A colony can, in many cases, respond to internal needs and external perturbations in a flexible and robust way. Colony-level flexibility is attained over short time scales [see, for example, Wilson (1984)] mostly through the workers' behavioral flexibility. Over longer time scales, the colony may, for example, adjust caste ratios in response to a threatening environment (Passera *et al.*, 1996), but this appears to be relatively uncommon (Wilson and Hölldobler, 1988).

How are colony-level robustness and individual flexibility connected? In a previous work (Bonabeau *et al.*, 1996), we have shown that a simple response threshold model (Wilson, 1985; Robinson, 1987a, 1987b, 1992; Robinson and Page, 1988; Calabi, 1988; Detrain *et al.*, 1988; Detrain and Pasteels, 1991, 1992; Page and Robinson, 1991) can account for the workers' behavioral flexibility. The model assumes that workers are able to assess needs through particular stimuli triggering task performance (the nature of these stimuli and how they are perceived are issues not addressed by the model), and that response thresholds do not vary over time. This model is able to account for experimental observations by Wilson (1984), who artificially varied the ratio of majors to minors in several polymorphic ant species (*Pheidole*) and observed a dramatic increase in task performance by previously inactive majors as the ratio exceeded some value; the involvement of majors occurred within an hour of the removal of the minors. When individuals that are characterized by low response thresholds with respect to stimuli related to a given task are withdrawn (for example, minors), the associated demand increases, as does the intensity of the stimulus, until it eventually reaches the higher characteristic response thresholds of the remaining individuals that are not initially specialized into that task (for example, majors); the increase of stimulus intensity beyond threshold has the effect of stimulating these individuals into performing the task (Calabi, 1988).

Two aspects of division of labor can be discussed: (1) How is information gathered by workers? (2) How are decisions made on the basis of such information? Although these two aspects are certainly not unrelated, they should not be confused in the modeling process. Some models of flexible task allocation are aimed at describing either one of the two aspects, and make simplifying assumptions about the other. For example, in the threshold model, it is assumed that each task to be performed is associated with a demand expressed under the form of a stimulus. The focus of the model is not the nature of such stimuli, but rather how an individual engages in task performance, given exposure to the associated stimulus (here, when the level of the stimulus exceeds the individual's threshold). Another example is the foraging-for-work (FFW) model, introduced by Tofts and Franks (1992); Tofts (1993); Franks and Tofts (1994); Franks *et al.* (1997), where individuals seek work and engage in task performance when they encounter a stimulus. How tasks are

allocated is modeled by FFW, using the basis of perceived stimuli and not that of the detailed nature of the evaluation of colony needs, which could rely on interactions among individuals as well as on nest patrolling, or any other relevant mechanism. The relation of our model to the FFW model will be discussed in detail in Section 5.1.1.

We shall not address the first question in this paper, and assume that each task is associated with a stimulus or set of stimuli (signals and cues strongly and reliably correlated with specific labor requirements). The respective intensities of these various stimuli that individual insects can sense, contain enough information. Individuals can therefore 'evaluate' the demand for one particular task when they are in contact with the associated stimulus. We assume that each insect encounters all stimuli with some probability within some period of time, and can in principle respond to these stimuli. For simplicity, we shall first neglect the fact that performing a given task may promote contacts with specific stimuli, and prevent other stimuli from being encountered, but this aspect will be dealt with in Section 4. Let us give a simple example: if the task is larval feeding, the associated demand is larval demand, which is expressed, for instance, through the emission of pheromones. The nature of task-related stimuli may vary greatly from one task to another, and so can information sampling techniques, which may involve direct interactions among workers (trophallaxis, antennation, etc.) (Gordon, 1996; Huang and Robinson, 1992), nest 'patrolling' (Lindauer, 1952), or more or less random exposure to task-related stimuli. Another way of obtaining information is through waiting times, when a complex task requires the coordination of several task groups. For example, Seeley (1989) showed that the time it takes for a forager to unload her nectar to a storer bee depends on the availability of such bees in the unloading area, which itself depends on whether or not more nectar is needed. Jeanne (1996) showed that the same type of process is taking place in the regulation of nest construction in the tropical wasp *Polybia occidentalis*, where three different groups of workers, pulp foragers, water foragers and builders, are involved and interdependent. The time taken to unload water or pulp to a builder gives an indication about whether foragers are needed or not, or if more foragers are needed, while the stimulus that initially triggers foraging can be the number of waiting builders in the unloading area.

The focus of the present paper is the second question, which can be studied with the help of the fixed-threshold model (Robinson, 1987a, 1987b, 1992; Calabi, 1988; Bonabeau *et al.*, 1996), where it is assumed that individuals are characterized by (genetically determined) fixed-response thresholds to the various stimuli. A mathematical framework is presented for this model, some exact results are given, and the behavior of the model is explored in detail. The model is also extended to include spatial 'fidelity' or specialization by workers, so that task-associated stimuli are encountered with differential probabilities. An explicit age dependence of the probabilities of encountering task-associated stimuli leads to a strong pattern of age polyethism. If, instead of being explicitly age based, differential probabilities of encountering the various task-associated stimuli are combined with an inflow

of newly born individuals emerging in the nest and an outflow of older individuals driven out of the nest, the model can generate temporal polyethism [in a way similar to Tofts and Franks (1992) and Tofts (1993)], but in a weaker and more unstable form. Finally, the influence of genetic diversity on temporal polyethism, colony efficiency and colony flexibility is studied. In the present context, genetic diversity is represented by distributions of response thresholds (corresponding, for example, to patrines).

2. EXPERIMENTAL EVIDENCE FOR THE THRESHOLD MODEL

The first question that we have to answer is: What is a response threshold? Let s be the intensity of a stimulus associated with a particular task; s can be a number of encounters, a chemical concentration, or any quantitative cue sensed by individuals. A response threshold θ , expressed in units of stimulus intensity, is an internal variable that determines the tendency of an individual to respond to the stimulus s and perform the associated task. More precisely, θ is such that the probability of response is low for $s \ll \theta$ and high for $s \gg \theta$. One family of response functions $T_\theta(s)$ that can be parametrized with thresholds that satisfy this requirement is given by

$$T_\theta(s) = \frac{s^n}{s^n + \theta^n}, \quad (1)$$

where $n > 1$ determines the steepness of the threshold. In the rest of the paper we will be concerned with the case $n = 2$, but similar results can be obtained with other values of $n > 1$. Figure 1(a) shows several such response curves, with $n = 2$, for different values of θ . The meaning of θ is clear: for $s \ll \theta$, the probability of engaging task performance is close to 0, and for $s \gg \theta$, this probability is close to 1; at $s = \theta$, this probability is exactly $\frac{1}{2}$. Therefore, individuals with a lower value of θ are likely to respond to a lower level of stimulus. The notion of a threshold is often associated with a change in concavity in the response curve, as is the case, for example, for response curves given by equation (1) with $n > 1$, where the inflection point is given by $s = \theta((n-1)/(n+1))^{1/n}$. But the definition of a threshold given above does not require a change in concavity. One example is when $n = 1$. Another important example is when the response function is exponential, rather than given by equation (1). [Plowright and Plowright (1988) use this type of response function in their model of the emergence of specialization.] In that case,

$$T_\theta(s) = 1 - e^{-s/\theta} \quad (2)$$

Figure 1(b) shows $T_\theta(s)$ given by equation (2) for different values of θ . We see, here again, that the probability of engaging task performance is small for $s \ll \theta$, and is close to 1 for $s \gg \theta$. Although there is no change in concavity in the curve, this response function produces behaviors which are comparable to those produced

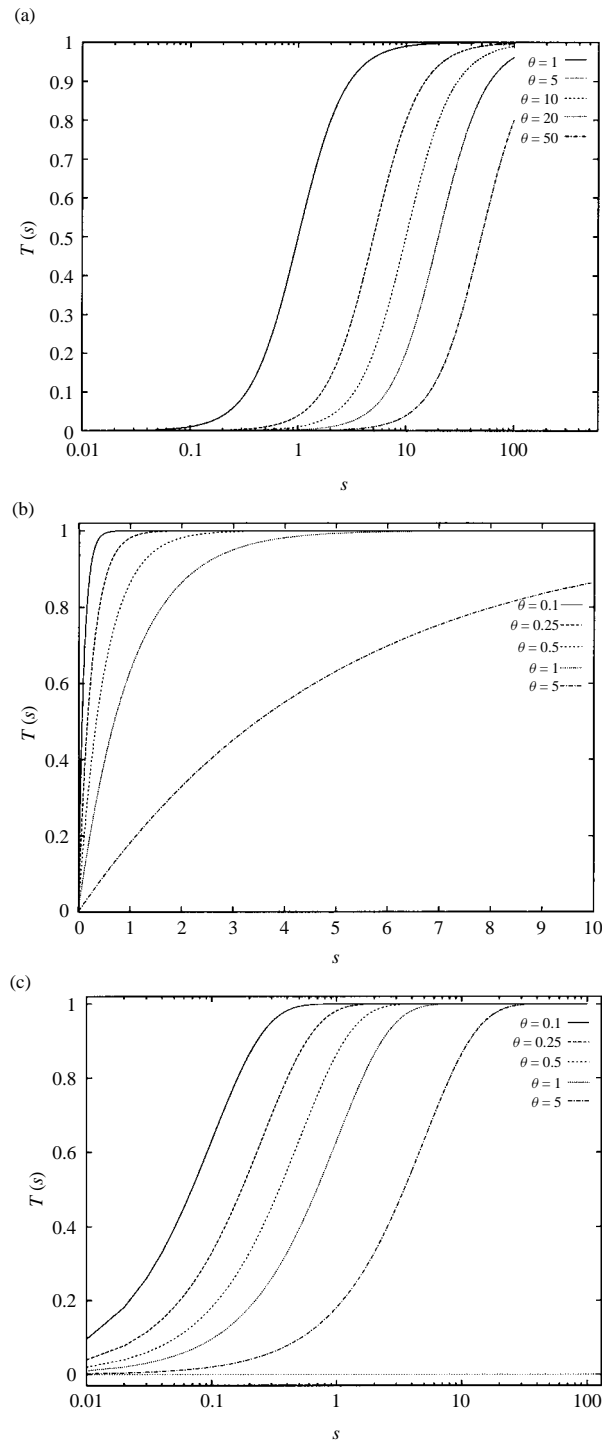


Figure 1. (a) Semi-logarithmic plot of threshold response curves ($n = 2$) with different thresholds ($\theta = 1, 5, 10, 20, 50$). (b) Exponential response curves with different thresholds ($\theta = 0.1, 0.25, 0.5, 1, 5$). (c) Semi-logarithmic plot of exponential response curves with different thresholds ($\theta = 0.1, 0.25, 0.5, 1, 5$).

by response functions based on equation (1) (see, for example, Fig. 4 below). Figure 1(c) also shows that a semilogarithmic plot of $T_\theta(s)$ given by equation (2) exhibits a change in concavity, and Fig. 1(c) is actually very similar to Fig. 1(a). In most of this paper, we make use of equation (1) with $n = 2$ rather than equation (2), simply because analytical results are possible for equation (1) with $n = 2$. But it is important to emphasize that threshold models encompass exponential response functions: the important ingredient is the existence of a characteristic θ . Exponential response functions are particularly important because they may be encountered quite frequently (although, as discussed below, there are not many experiments studying response functions in social insects). For example, imagine a stimulus that consists of a series of encounters with, say, items to process. If, at each encounter with an item, an individual has a fixed probability of processing the item, then the probability that the individual will not respond to the first N encountered items is given by $(1 - \rho)^N$. Therefore, the probability $P(N)$ that there will be a response within the N encounters is given by $P(N) = 1 - (1 - \rho)^N = 1 - e^{N \ln(1 - \rho)}$, which is exactly equation (2) with $s = N$ and $\theta = -1 / \ln(1 - \rho)$. For example, the organization of cemeteries in ants provides a good illustration of this process. The probability of dropping a dead body (or a dead item, i.e., a thorax or an abdomen) has been studied experimentally by Chrétien (1996) in the ant *Lasius niger*: the probability that a laden ant drops an item next to an N cluster can be approximated by $P(N) = 1 - (1 - p)^N = 1 - e^{N \ln(1 - p)}$, for N up to 30, where $p \approx 0.2$ [Fig. 2(a)]. Here, the intensity of the stimulus is the number of encountered dead bodies, and the associated response is dropping an item. Another situation in which exponential response functions may be observed is when there are waiting times involved, although it may not always be the case. Let us assume that Tasks A and B are causally related in the sense that a worker performing Task A has to wait for a worker performing Task B to unload nectar or pulp, say, or any kind of material. If a Task A worker has a fixed probability p per unit waiting time of giving up Task A performance, the probability that this worker will still be waiting after t time units is given by $P(t) = 1 - (1 - p)^t = 1 - e^{t \ln(1 - p)}$. In conclusion, threshold response functions, such as the one given by equation (1), or exponential response functions, such as the one given by equation (2), can be encountered in various situations, and, as will be shown below, yield similar results.

Viewed from the perspective of response thresholds, castes may correspond to possible physical differences, but also to innate differences in response thresholds without any visible physical difference. Note that differences in response thresholds may either reflect actual differences in behavioral responses, or differences in the way task-related stimuli are perceived.

Let us further discuss the experimental basis of the model. Only a few experimental results support the idea of thresholds, but very few experiments have been aimed at showing the existence of response thresholds in social insects. Such experiments require controlling (or at least being able to vary and measure) the intensity of the stimuli workers are responsive to, a task that can be very difficult. Most experi-

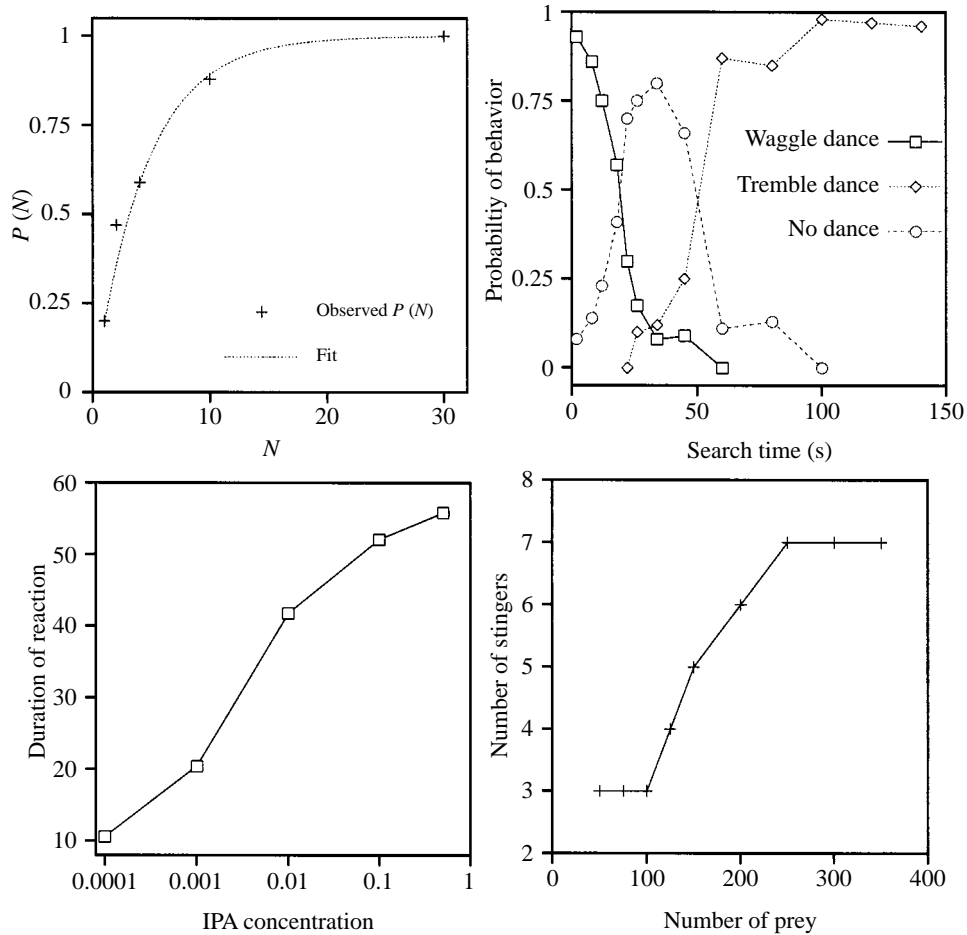


Figure 2. (a) Probability $P(N)$ of dropping a dead body next to an N -cluster as a function of N (after Chrétien, 1996). Fit $P(N) = 1 - (1 - p)^N$ with $p = 0.2$ is shown. (b) Probabilities of performing a waggle dance and a tremble dance as a function of in-hive search time for foragers visiting a rich nectar source (after Seeley, 1992). (c) Duration of reaction to isopentyl acetate (IPA) as a function of IPA concentration (after Collins and Rothenbuler, 1978). (d) Number of stingers involved in prey retrieval as a function of the number of prey in the ant *Ectatomma ruidum*, for a nest comprised of 130 workers (after Schatz, 1996).

mental curves show the probability of response of an individual as a function of its size, or weight, etc., at *fixed stimulus* intensity. Although these curves can teach a lot, they cannot prove the existence or lack of response thresholds.

Robinson (1987a, 1992) and Breed *et al.* (1990) showed the existence of hormonally regulated behavioral response thresholds to alarm pheromones in honeybees (*Apis mellifera*). Treatment of young worker honeybees with a juvenile hormone (JH) analog increases their sensitivity to alarm pheromones, which play a role in nest defense. The corpora allata glands produce JH, and are known to grow with age. Robinson (1987a) also showed that JH treatment of bees stimulates their production of alarm pheromone. He further noted that isolated JH-treated bees do not respond to presented alarm pheromones, but do respond when in a group. This may be due to the fact that increased production of alarm pheromones by treated bees allows a threshold to be reached when several such bees are put together. Robinson and Page (1988) and Page and Robinson (1991) have shown that honeybee workers belonging to different Patriline may have different response thresholds. For example, assume for simplicity that workers of Patriline A engage in nest guarding as soon as there are less than 20 guards, whereas workers of Patriline B start performing this task when there are less than 10 workers guarding the hive's entrance: workers of Patriline B have a higher response threshold to perform this task. More generally, in a series of papers, these authors have shown that response thresholds are partly determined by genes.

We mentioned Seeley's (1989) work in the previous section. If it takes a forager too long to unload her nectar to a storer bee, she gives up foraging with a probability that depends on her search time in the unloading area. She will then start a 'tremble dance' (Seeley, 1992) to recruit storer bees (the tremble dance also inhibits waggle dancing). If, on the other hand, her in-hive waiting or search time is very small, she starts recruiting other foragers with a waggle dance. If her in-hive waiting or search time lies within a given window, she is likely not to dance at all and return to the food source. If one plots the probability of either waggle or tremble dancing as a function of search time, a clear threshold function can be observed [Fig. 2(b)]. It is also interesting to note that search time is correlated with the spatial distribution of nectar unloadings: nectar foragers have to go deeper into the hive in order to find an available storer bee when the influx of foragers is high than when it is low. This means that nectar foragers may use spatial (location of unloading) as well as temporal (search time) information to make decisions.

Collins and Rothenbuler (1978) performed laboratory experiments on *Apis mellifera* to measure the duration of reactions to a particular chemical, isopentyl acetate, (IPA), the major component of the sting alarm pheromone (Boch *et al.*, 1962). Using paraffin oil IPA diluted in volume, and reactions were tested for different dilutions. Figure 2(c) shows the duration of the reaction as a function of IPA concentration. We can see that the response function is an exponential-like response function.

A series of experiments by Detrain *et al.* (1988) and Detrain and Pasteels (1991, 1992) clearly indicate the existence of differential response thresholds in the ant

Pheidole pallidula in at least two activities, foraging and nest defense. The intensity of behavioral stimuli (measured by trail concentration and the number of tactile invitations in the case of foraging, supplemented by the number of intruders in the case of defense) required to induce the effective recruitment of majors is greater than for minors for both tasks, indicating that majors have higher response thresholds. An interesting discussion of the adaptive significance of these findings is given by Detrain and Pasteels (1991, 1992). They also hypothesize that JH titers (Wheeler and Nijhout, 1981) or the volume and number of cells of corpora allata could affect behavioral thresholds.

Finally, Schatz (1997) presents convincing evidence of response thresholds in the ant *Ectatomma ruidum*. When presented with an increasing number of prey, specialized ‘stinger ants’ (or killer ants) start to become involved in the retrieval process (in addition to transporters, to which dead prey are transferred), the number of such ants being dependent on the number of prey in a characteristic sigmoid-like manner [Fig. 2(d)]. This suggests that within-caste specialization among hunters is indeed based on response thresholds.

3. EQUIPROBABLE EXPOSURE TO TASK-ASSOCIATED STIMULI

3.1. One task. Let us assume for the moment that one task only has to be performed, and that this task is associated with a stimulus or demand, the level of which increases if it is not satisfied (because the task is not performed by enough individuals, or not performed with enough efficiency). We first consider two types of workers, Types 1 and 2, or Groups 1 and 2. In what follows, we may sometimes call workers of Type 1 ‘majors’ and workers of Type 2 ‘minors’ in reference to physical castes, but Types 1 and 2 workers could as well represent different behavioral or age castes, or individuals belonging to different patriline. Majors often (but not always) are characterized by a lower probability of becoming active than minors. Let n_1 and n_2 be the respective numbers of workers of Types 1 and 2 in the colony, N the total number of workers in the colony ($n_1 + n_2 = N$), $f = n_1/N$ the fraction of workers of Type 1 in the colony, N_1 and N_2 the respective numbers of workers of Types 1 and 2 engaged in task performance, and x_1 and x_2 the corresponding fractions ($x_i = N_i/n_i$). The average deterministic equations describing the dynamics of x_1 and x_2 are given by:

$$\partial_t x_1 = T_{\theta_1}(s)(1 - x_1) - px_1, \quad (3)$$

$$\partial_t x_2 = T_{\theta_2}(s)(1 - x_2) - px_2, \quad (4)$$

where θ_i is the response threshold of Type i workers, and s the integrated intensity of task-associated stimuli. The first term on the rhs of equations (3) and (4) describes how the $(1 - x_i)$ fraction of inactive Type i workers responds to the stimulus intensity

or demand s , with a threshold function $T_{\theta_i}(s)$

$$T_{\theta_i}(s) = \frac{s^2}{s^2 + \theta_i^2}. \quad (5)$$

We assume that individuals can assess the demand for a particular task when they are in contact with the associated stimulus. A critical assumption of this section is that each insect encounters all stimuli with equal probability per time unit, and can respond to these stimuli. Let us define $z = \theta_1^2/\theta_2^2$: here, $z > 1$, i.e., workers of Type 1 are less responsive than workers of Type 2 to task-associated stimuli. The second rhs term in equations (3) and (4) expresses the fact that an active individual gives up task performance and becomes inactive with probability p per unit time (that we take identical for both types of workers). The average time spent by an individual in task performance before giving up this task is $1/p$. It is assumed that p is fixed, and independent of any stimulus. Therefore, individuals involved in task performance spend $1/p$ time units working even if their work is no longer necessary. Such a behavior has been reported in several cases [e.g., building behavior; see Deneubourg and Franks (1995)]. Individuals give up task performance after $1/p$, but may become engaged again immediately if the stimulus is still large. The dynamics of the demand is described by:

$$\partial_t s = \delta - \frac{\alpha}{N}(N_1 + N_2), \quad (6)$$

i.e., since $(N_1 + N_2)/N = fx_1 + (1 - f)x_2$,

$$\partial_t s = \delta - \alpha fx_1 - \alpha(1 - f)x_2, \quad (7)$$

where δ is the (fixed) increase in stimulus intensity per unit time, and α is a scale factor measuring the efficiency of task performance. Identical efficiencies in task performance are assumed for Types 1 and 2 individuals. That efficiencies do not vary significantly is a plausible assumption provided the time scales of experiments are sufficiently short, whereas learning may take place over longer time scales. The amount of work performed by active individuals is scaled by N , as can be seen by equation (6), to reflect the idea that the demand is an increasing function of N , that we take to be linear here. For example, the brood should be divided by 2 when colony size is divided by 2 [see experiments by Wilson (1984)]. In other words, colony requirements scale (more or less) linearly with colony size. Under this assumption, our results should be independent of colony size. In the stationary state, where all $\partial_t s$ are equal to 0, one has:

$$\frac{p\theta_1^2 x_1}{1 - (p + 1)x_1} = \frac{p\theta_2^2 x_2}{1 - (p + 1)x_2}, \quad (8)$$

$$x_2 = \frac{1}{1 - f} \left(\frac{\delta}{\alpha} - fx_1 \right). \quad (9)$$

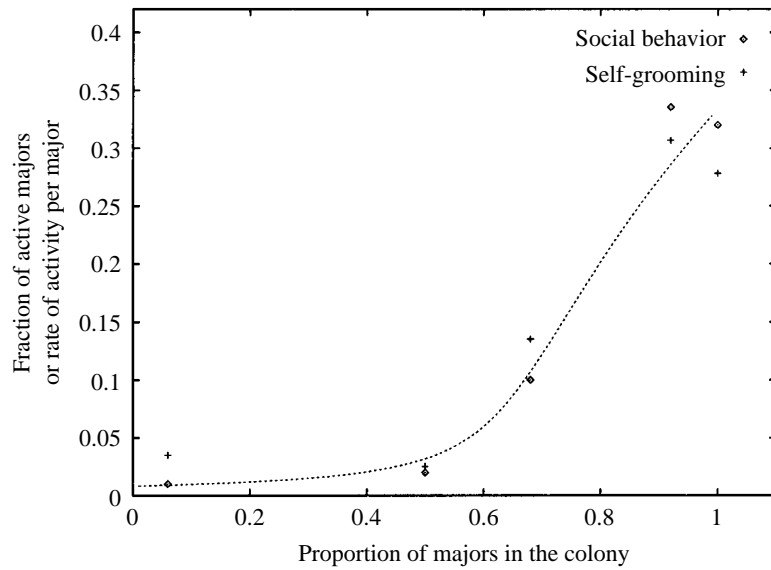


Figure 3. Fraction of active majors given by equation (11) as a function of the proportion f of majors in the colony, for $\theta_1 = 8$, $\theta_2 = 1$, $\alpha = 3$, $\delta = 1$, $p = 0.2$. Comparison with the results of Wilson (1984) (scaled so that curves of the model and the experiments lie within the same range): number of acts of social behavior and self-grooming per major within the time of experiments in *Pheidole guilelmimuelleri*.

The stationary value x_1^s of x_1 can then be easily found. Let us define for convenience

$$\chi = (z - 1) \left(f + (p + 1) \frac{\delta}{\alpha} \right) - z \tag{10}$$

Then,

$$x_1^s = \frac{\chi + (\chi^2 + 4f(p + 1)(z - 1)(\delta/\alpha))^{1/2}}{2f(p + 1)(z - 1)}. \tag{11}$$

Numerical integration of equations (3) and (4) and Monte Carlo simulations (Bonabeau *et al.*, 1996) are in very good agreement with this expression of x_1^s . Moreover, values of x_1^s obtained in simulations are independent of initial conditions, indicating that x_1^s given by equation (11) is a global attractor of the dynamics. Figure 3 shows how x_1^s varies as a function of f , for $z = 64$, $p = 0.2$, $\delta = 1$, and $\alpha = 3$, and are comparable with Wilson's (1984) results (who measured, among other things, the number of acts of social behavior and self grooming per major in *Pheidole guilelmimuelleri*). When individuals performing a given task are withdrawn (they have low response thresholds with respect to stimuli related to this task)—here, Type 1 workers—the associated demand increases until it eventually reaches the higher characteristic response thresholds of the remaining individuals—here Type 2 workers—that are not initially specialized into that task. The increase of stimulus intensity beyond threshold has the effect of stimulating Type 2 workers into performing the task. Figure 4 illustrates the fact that it is possible to find

appropriate parameters (here, $\theta_1 = 0.1$, $\theta_2 = 1$, $\alpha = 3$, $\delta = 1$, $p = 0.2$) with an exponential response function ($T_\theta(s) = 1 - e^{-s/\theta}$) such that it reproduces the same results as the threshold response function. As can be seen from equations (10) and (11), there are only three parameters influencing the shape of $x_1^s(f)$: δ/α , z , and p . Figures 5–7 show how the $x_1^s(f)$ relationship varies with these parameters. When individuals are very efficient at performing the task (δ/α small), the value of f above which an important fraction of majors is performing the task is larger and the crossover becomes smoother; conversely, a decrease in efficiency leads to an earlier and more abrupt modification of the number of majors engaged in task performance (Fig. 5: $\delta = 1$, α varying). This result is relatively natural, as more efficient task performances by individuals which have a low response threshold prevent task-related stimuli from growing large, and therefore from eliciting task performances by individuals that have larger response thresholds. The crossover becomes more abrupt as z increases, and the point at which the crossover is observed decreases; when z is close to 1, the proportion of majors engaged in task performance starts from a larger value (Fig. 6). When the probability of giving up task performance becomes small, the involvement of majors in task performance becomes less progressive, and starts at a larger value of f (Fig. 7). This is due to the fact that task performers, mostly minors for low values of f , spend more time on average in task performance, so that less majors are required. However, when majors have to engage in task performance, they must do so more massively because missing minors were performing a lot of work. Finally, it is important to note that in Figs 5–7, there is always a fraction of active majors as f comes close to 0 [this property may be difficult to see directly in equation (11)].

Besides the nine species of *Pheidole* studied by Wilson (1984), there are other examples of flexibility, whereby individuals perform tasks that do not belong to the normal repertoire of their physical or age caste, that the threshold model can certainly explain (Calabi, 1988). Wilson (1980, 1983a, 1983b) studied flexibility in the ants *Atta cephalotes* and *A. sexdens*, in which there is a continuum of size classes rather than simply two physical castes, as is the case in *Pheidole*. He showed that the experimental removal of a size class stimulates individuals belonging to adjacent size classes into performing the tasks of the missing size class. Lenoir (1979) found that young workers of the ant *Tapinoma erraticum* tend to be stimulated into foraging activities when the ratio of old to young workers < 1 . Calabi (1986) found that young workers of the ant *Pheidole dentata*, when raised in the absence of older minors, forage significantly earlier than when older minors are present; conversely, old minors in colonies without young minors perform brood care, a behavior that is not observed when young minors are present. Carlin and Hölldobler (1983), cited in Calabi (1988), found interesting interspecific differences, possibly related to differences in response thresholds, in mixed-species colonies of *Camponotus* ants. *Camponotus pennsylvanicus* performs brood care and works inside the nest when raised with *C. americanus* or *C. noveboracensis*, but works outside the nest when raised with *C. ferrugineus*. This suggests, within the context of the threshold

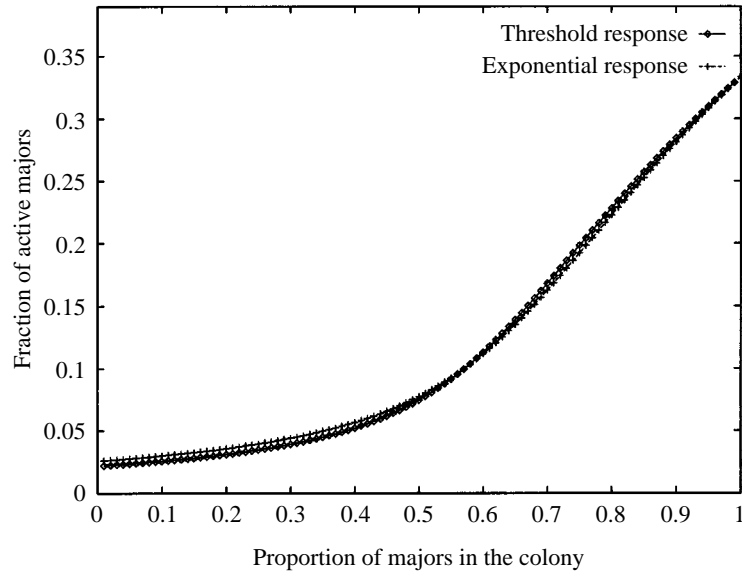


Figure 4. Comparison between the fraction of active majors as a function of the proportion of majors in the colony obtained with an exponential response function ($\theta_1 = 0.1, \theta_2 = 1, \alpha = 3, \delta = 1, p = 0.2$) and a threshold response function ($\theta_1 = 8, \theta_2 = 1, \alpha = 3, \delta = 1, p = 0.2$).

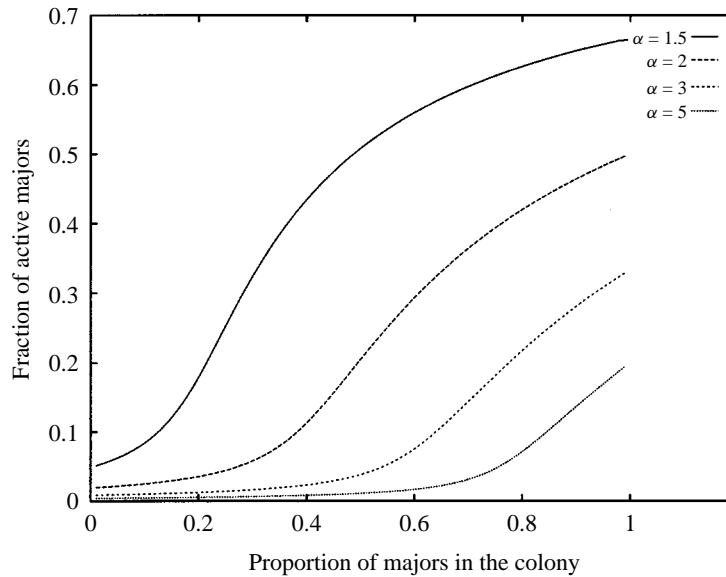


Figure 5. Fraction of active majors given by equation (11) as a function of the proportion f of majors in the colony, for $z = 64, \delta = 1, p = 0.2, \alpha = 1.5, 2, 3, 5$.

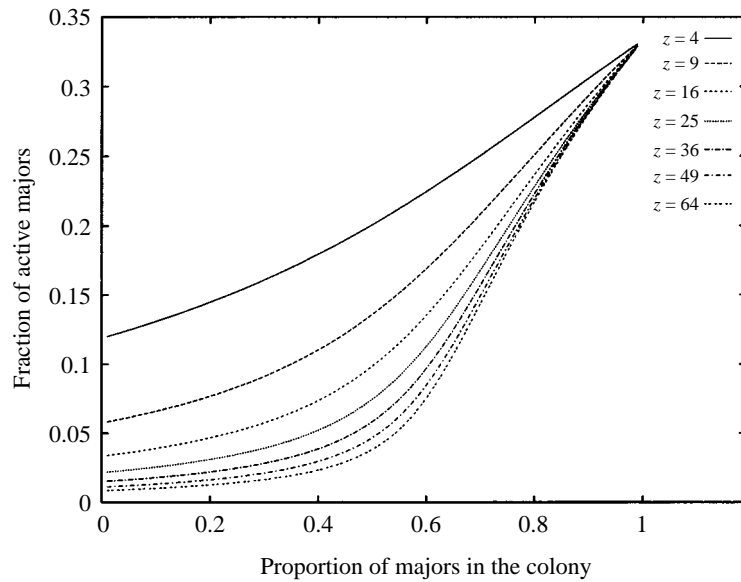


Figure 6. Fraction of active majors given by equation (11) as a function of the proportion f of majors in the colony, for $\alpha = 3$, $\delta = 1$, $p = 0.2$, $z = 4, 9, 16, 25, 36, 49$ and 64 .

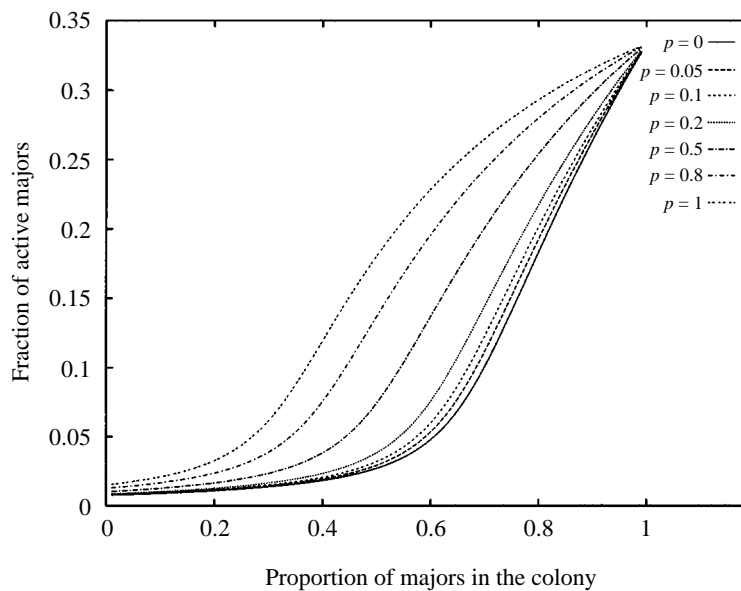


Figure 7. Fraction of active majors given by equation (11) as a function of the proportion f of majors in the colony, for $\alpha = 3$, $\delta = 1$, $z = 64$, and $p = 0, 0.05, 0.1, 0.2, 0.5, 0.8$ and 1 .

model, that *C. pennsylvanicus* has a lower response threshold to brood care than *C. americanus* or *C. noveboracensis*, but higher than *C. ferrugineus*. More studies would be welcome, however, since other factors could play a role in this unusual example of interspecific task allocation.

3.2. A note on between-caste aversion. In order to explain the increased involvement of majors in minor-related tasks when the fraction of majors in the colony increases (Wilson, 1984), Wilson (1985) introduced the notion of between-caste aversion, a phenomenon that he apparently observed in *Pheidole pubiventris*. He studied the case of brood care, and noticed that majors pay a greater attention to the brood when less minors are present, which is due, according to him, to the fact that majors actively avoid minors while in the vicinity of the immature stages. He further noticed that majors did not avoid minors in any other part of the nest (which in passing casts doubt on the generality of between-caste aversion as a basis for division of labor). Wilson (1985) presented this hypothesis as an alternative to response thresholds, which had rarely been evidenced (but a good reason for this situation, is discussed in Section 2). However, all of Wilson's (1985) observations can be explained by a threshold model. Moreover, making the assumption that response thresholds exist does not make any further assumption about the associated stimuli: in particular, majors could use contacts with minors or *with other majors* in the vicinity of the brood as a stimulus to assess indirectly the degree of satisfaction of the brood. It is hard to determine whether majors *avoid* minors, or respond to a brood-specific chemical (or other) cues carried by minors. Indeed, Wilson (1985) reports that majors showed the clearest responses after making direct antennal contacts with minors: this suggests that instead of identifying minors, they may be sensitive to cues carried by minors from the brood area. It is also perfectly possible that majors have higher response thresholds to brood stimuli, so that brood care by minors maintains larval demand below threshold. In summary, the response-threshold approach explains Wilson's (1985) observations qualitatively and quantitatively, and does not raise the same issues as between-caste aversion. In effect, between-caste aversion does not seem to be an efficient way of dividing labor among workers (notwithstanding its lack of generality): if larvae are satiated, less minors will take care of the brood, so that more majors will access the brood area and take over brood care, which is not necessary; if larvae are hungry, many minors are present, preventing majors from reaching the brood, where they could be useful. All these remarks make the threshold hypothesis far more likely.

3.3. Several tasks. Let us now proceed to the case of m tasks. By analogy with the previous case, let us define N_{ij} the number of workers of Type i engaged in Task j performance, x_{ij} the corresponding fraction ($x_{ij} = N_{ij}/n_i$), and θ_{ij} the associated response threshold. Alternatively, x_{ij} can be interpreted as the probability of finding a worker of Group i performing Task j . The average deterministic

equations describing the dynamics of the x_{ij} s are given by:

$$\partial_t x_{ij} = \frac{(q_{ij}s_j)^2}{(q_{ij}s_j)^2 + \theta_{ij}^2} \left(1 - \sum_{k=1}^m x_{ik} \right) - px_{ij}, \quad (12)$$

where q_{ij} is the probability that workers of Type i encounter stimuli associated with Task j ($\forall i, \sum_{j=1}^m q_{ij} = 1$), and s_j the integrated intensity of Task j -associated stimuli. Again, we here assume that $q_{ij} = q = 1/m$, i.e., stimuli associated with all tasks are equally likely to be encountered by all types of workers. Finally, let us assume for simplicity that $m = 2$ and $i = 1, 2$. Results for other cases can readily be inferred from those obtained with these parameters. The dynamics of the demand s_j associated with Task j is given by:

$$\partial_t s_j = \delta - \alpha f x_{1j} - \alpha(1 - f)x_{2j}. \quad (13)$$

Here again, we assume that efficiency in task performance, measured by α , is identical for workers of both types. Furthermore, α is the same for all tasks. Let us now distinguish two cases.

CASE 1. $\theta_{11} > \theta_{21}$ and $\theta_{12} > \theta_{22}$: workers of Type 2 are more responsive to task-associated stimuli for both tasks. Introducing $z_j = \theta_{1j}^2/\theta_{2j}^2$, we can study, without loss of generality, the case where, for example, $z_1 > z_2$.

CASE 2. $\theta_{11} > \theta_{21}$ but $\theta_{12} < \theta_{22}$: workers of Type 1 (respectively, Type 2) are more responsive than workers of Type 2 (respectively, Type 1) to stimuli associated with Task 1 (respectively, Task 2). We can study the symmetric case, i.e., where $z_1 z_2 = 1$.

The stationary state of equation (13) cannot be easily calculated: numerical integration has been used to find the stationary values of x_{ij} as a function of f . Figures 8 and 9 show the x_{ij} vs. f relationships in Case 1 [x_{ij} vs. f ($j = 1, 2$), $z_1 = 64$ and $z_2 = 25$] and Case 2 [x_{ij} vs. f ($i = 1, 2$ and $j = 1, 2$), $z_1 = 64 = 1/z_2$] for $p = 0.2$, $\delta = 1$, and $\alpha = 3$. In Case 1, when workers of Type 1 have lower response thresholds to both tasks, we obtain two x_{ij} vs. f curves that are qualitatively similar to those observed on Fig. 3. The x_{11} vs. f and x_{12} vs. f curves are, however, quantitatively different because z_1 and z_2 are different. Wilson (1984) measured the number of acts per major for social behavior and self grooming in *Pheidole megacephala*. There is a reasonably good agreement between Wilson's observations and the curves of the model. In Case 2, when a caste is specialized in one of the two tasks, and the other caste in the other task, behavioral flexibility is observed on both sides: workers of Type 1 can replace workers of Type 2, and vice versa (Fig. 9). Since minors cannot always be induced to perform major-specific tasks (while majors can always be induced to perform tasks usually performed by minors) [e.g., Wilson (1984)], this example may not apply to the case of physical castes, but can certainly apply to less rigid castes, or to intracaste behavioral flexibility. One can model such an observation by assuming that minors have very large

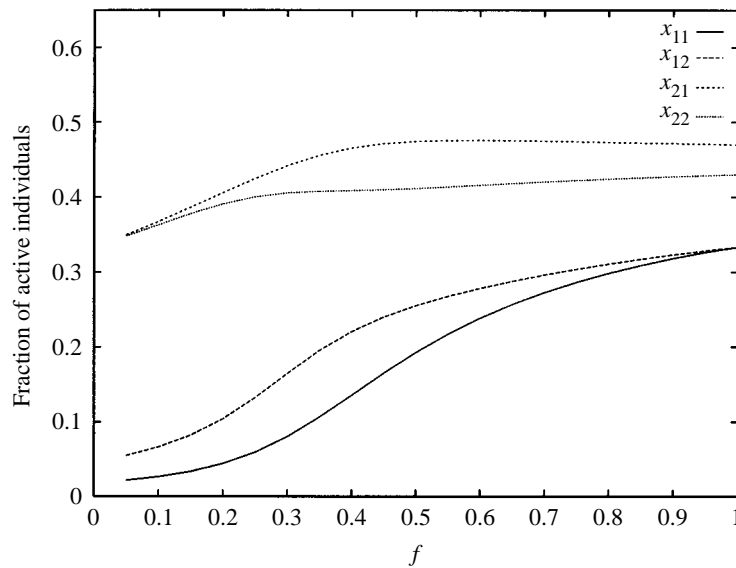


Figure 8. Fractions of minors and majors performing Tasks 1 and 2 as a function of the proportion f of majors in the colony, obtained by numerical integration of equations (12) and (13). $q_{ij} = \frac{1}{2}$, $\theta_{11} = 5$, $\theta_{12} = 10$, $\theta_{21} = 1$, $\theta_{22} = 1$, $\alpha_1 = 1$, $\alpha_2 = 3$, $\delta_1 = \delta_2 = 1$, $p_1 = p_2 = 0.2$.

(virtually infinite) response thresholds for stimuli associated with majors' tasks, although in principle any finite threshold will elicit task performance once stimulus intensity becomes large enough. But if minors lack perceptual tools for stimuli associated with tasks usually performed by majors, we are in the case where, indeed, the response threshold is infinite, since differences in response thresholds may either reflect actual differences in behavioral responses, or differences in the way task-related stimuli are perceived.

3.4. Succession of tasks. It is possible, with fixed response thresholds, to observe a simulated colony perform some tasks in succession in situations that are not uncommon. There are two possible models. Model 1 assumes that individuals all have identical response thresholds, but these thresholds are different for the various tasks to be performed, and, moreover, the success rate in task performance also varies with the task. This model can describe the dynamics of brood sorting in *Leptothorax* ants (Franks and Sendova-Franks, 1992) or seed piling in harvester ants. Model 2 assumes that performing a given task increases the demand for another task. For example, excavation, by creating a refuse pile just at the entrance of the nest, generates a need for cleaning (Chrétien, 1996). Both models will give the impression that individuals have decided to perform the tasks in sequence.

MODEL 1. Let us assume that m different types of items have to be processed. Let L_i be the number of workers loaded with item type i , U the number of unloaded workers, s_i the number of items that still need to be processed, r_i the number of

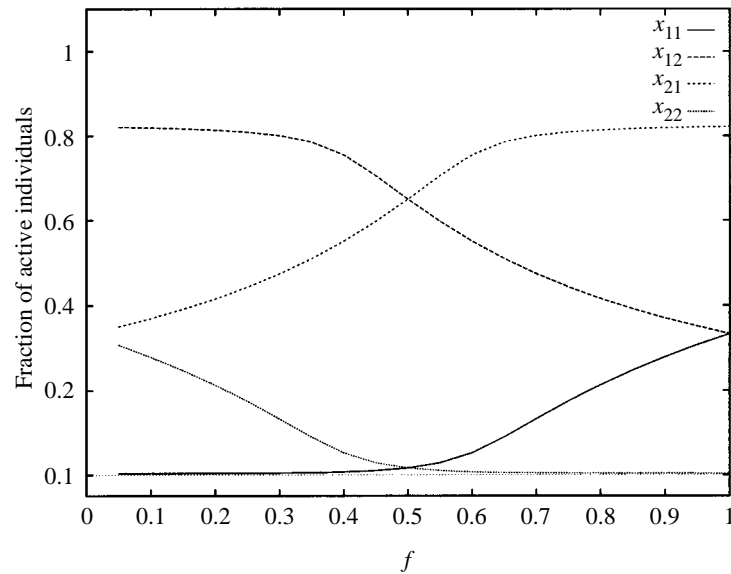


Figure 9. Fractions of minors and majors performing Tasks 1 and 2 as a function of the proportion f of majors in the colony, obtained by numerical integration of equations (12) and (13). $q_{ij} = \frac{1}{2}$, $\theta_{11} = 8$, $\theta_{12} = 1$, $\theta_{21} = 1$, $\theta_{22} = 8$, $\alpha_1 = \alpha_2 = 3$, $\delta_1 = \delta_2 = 1$, $p_1 = p_2 = 0.2$.

items that have been successfully processed, and τ_i the time it takes to process an item of Type i (for example, to carry a larva or seed to the appropriate location), and $f_i = e^{-\tau_i/\tau}$, where τ is a characteristic time, the probability of success of the task (the longer it takes to carry a larva or seed to the appropriate location, the less likely the individual is to succeed). The idea behind this model is that, for example, heavier items or items that are harder to work with will be processed after lighter or easier items have been processed. Heavier items are naturally associated with a lower probability of success. The dynamics of U and L_i are given by

$$\partial_t U = \sum_{i=1}^m \left(\frac{L_i}{\tau_i} - \alpha_i U s_i \right), \quad (14)$$

$$\partial_t L_i = \alpha_i U s_i - \frac{L_i}{\tau_i} \quad (15)$$

where α_i is a threshold function

$$\alpha_i = p_i \frac{s_i^2}{\theta_i^2 + s_i^2} \quad (16)$$

weighted by the probability p_i of finding an item of Type i , that we approximate simply by

$$P_i = \frac{s_i}{\sum_{j=1}^m s_j} \quad (17)$$

Equation (14) expresses the fact that laden individuals deposit their loads every τ_i (either successfully or not) and that unloaded workers pick up items with a probability that combines the probability of encountering an item of Type i (which is proportional to $p_i s_i$) and that of responding to such an item [equation (16)]. Equation (15) also expresses how laden workers become unladen, and vice versa, but with signs opposite to those of equation (14), as it describes the dynamics of the number of laden workers. The threshold θ_i in equation (16) is such that if $s_i \ll \theta_i$, few workers will be stimulated to carry an item of Type i , and, in contrast, if $s_i \gg \theta_i$, workers will be stimulated to process items of Type i . The dynamics of r_i and s_i are given by

$$\partial_t s_i = -\alpha_i U s_i + (1 - f_i) \frac{L_i}{\tau_i}, \quad (18)$$

$$\partial_t r_i = f_i \frac{L_i}{\tau_i}. \quad (19)$$

Equation (18) expresses that the number of items that can be processed decreases when an item is picked up, but increases when a laden worker deposits an item at a wrong location (unsuccessful deposition), which happens with probability $1 - f_i$. Equations (14)–(19) have been integrated numerically for three types of items. Figure 10(a) shows the respective numbers of workers performing Tasks 1, 2 and 3 as a function of time. Figure 10(b) shows the fraction of processed items of Types 1, 2 and 3 as a function of time. Clearly, workers tend to process items of Type 1, then items of Type 2, and eventually items of Type 3.

MODEL 2. Let us now assume that there are m potential tasks to be performed by the workers. Let x_i be the fraction of workers engaged in performing Task i , s_i be the demand (stimulus intensity) associated with Task i , θ_i be the threshold associated with Task i (similar to Model 1), p_i be the probability of encountering stimuli associated with Task i , p be the probability of stopping performing Task i (the average time spent performing a task before task switching or before becoming inactive is given by $1/p$), and α be the efficiency of task performance, which we also take to be the rate of stimulus production per unit working time for the next task. The dynamics of x_i and s_i are described by

$$\partial_t x_i = p_i \frac{s_i^2}{\theta_i^2 + s_i^2} \left(1 - \sum_{k=1}^m x_k \right) - p x_i, \quad (20)$$

$$\partial_t s_i = \alpha (x_{i-1} - x_i) \quad \text{with } x_{i-1} = 0 \text{ if } i = 1. \quad (21)$$

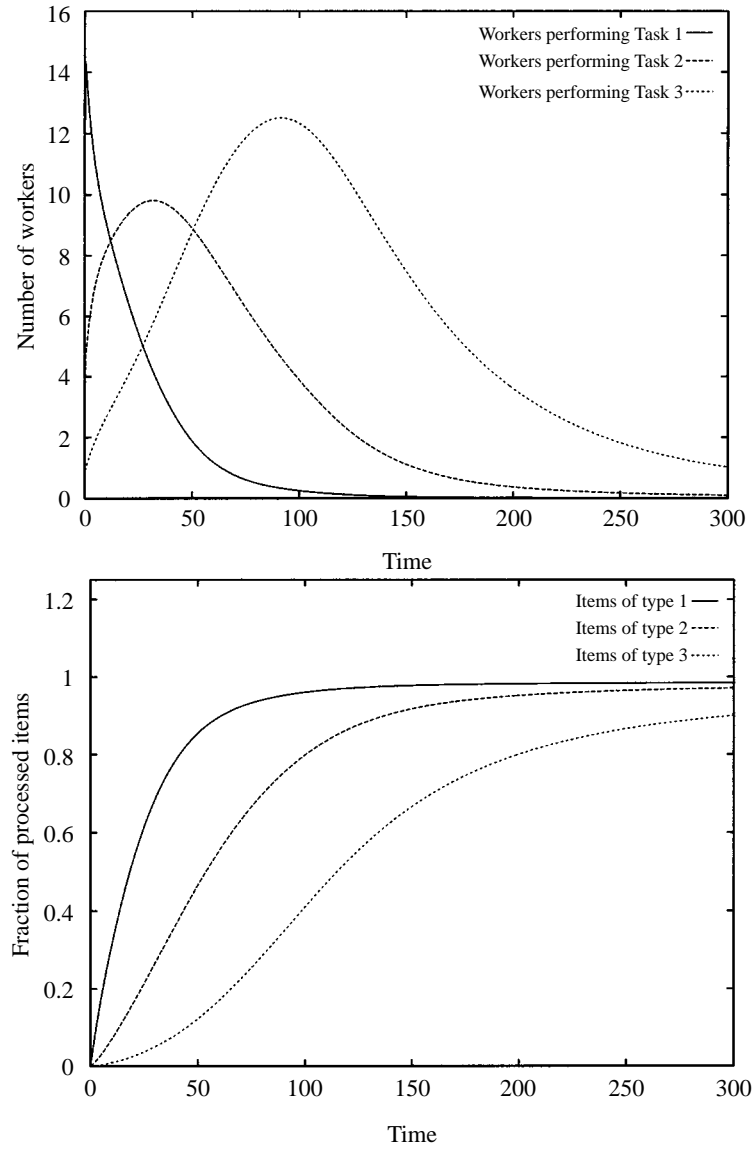


Figure 10. (a) Respective numbers of workers performing Tasks 1, 2 and 3 as a function of time. Dynamics given by equations (14)–(19), with three types of items. $\theta_1 = 10$, $\theta_2 = 40$, $\theta_3 = 80$, $\tau = 5$, $\tau_1 = 2$, $\tau_2 = 5$, $\tau_3 = 8$, $T_1(t = 0) = 120$, $T_2(t = 0) = 70$, $T_3(t = 0) = 50$. (b) Respective fractions of processed items of Types 1, 2 and 3 as a function of time for the same simulation as (a).

Equation (20) is similar to equation (12), and equation (21) expresses the fact that performing Task $i - 1$ increases s_i , which in turn decreases when Task i is being performed. Numerical integration of equations (20) and (21) has been performed for three tasks ($i = 1, 2, 3$). Figure 11(a) shows the respective numbers of workers performing Tasks 1, 2 and 3 as a function of time. Figure 11(b) shows the dynamics of stimulus intensities associated with Tasks 1, 2 and 3, respectively. It can be seen that workers first tend to perform Task 1, then Task 2 and finally Task 3. If performing Task 3 increased the demand associated with Task 1, a cyclical activity would be observed.

4. EXPOSURE TO TASK-ASSOCIATED STIMULI DEPENDS ON THE CURRENT TASK

4.1. Introduction. Until now, we have been able to observe a global flexibility obtained at the colony level with fixed response thresholds. One question that arises is: Can we also observe specialization with the same model? For example, as we allow no learning, it seems difficult under the form of a reinforcement of response thresholds (Deneubourg *et al.*, 1987; Plowright and Plowright, 1988; Theraulaz *et al.*, 1991). However, with fixed response thresholds, another type of specialization is possible in this model if stimulus perception is allowed to vary as a function of the probability of task performance. Introducing this assumption will allow us to introduce an additional type of specialization by workers, such as, for instance, spatial specialization, where workers of a certain type are more likely to encounter stimuli associated with tasks of a certain kind. For example, in some species foragers are more likely to respond to alarm signals and start to defend the colony, although defensive behavior can also be induced in non-foragers [see, for instance, Jeanne *et al.* (1992) on the tropical social wasp *Polybia occidentalis*]. We can imagine that this correlation between foraging and probability of response to alarm signals is due to the fact that foragers are more easily in contact with potential sources of danger and alarm signals. More generally, performing a task may either promote or reduce direct exposure to stimuli associated with other tasks, or may promote or prevent encounters with workers performing other tasks (antennations, trophallaxis, etc.). Such encounters can be stimulatory (recruitment) or inhibitory. Gordon (1996) advocates that encounter rates may be regulated to allow workers to assess how many workers are performing a task. In the absence of regulation, as too many encounters with individuals performing a task inhibit task performance by other individuals, the number of task performers would be fixed regardless of colony size.

Further support of this idea that exposure to stimuli depends on what task is being performed comes from experiments showing that tasks are sometimes spatially organized (not only in the absolute sense, but also relative to each other) (Wilson, 1976; Seeley, 1982; Sendova-Franks and Franks, 1994, 1995a, 1995b;

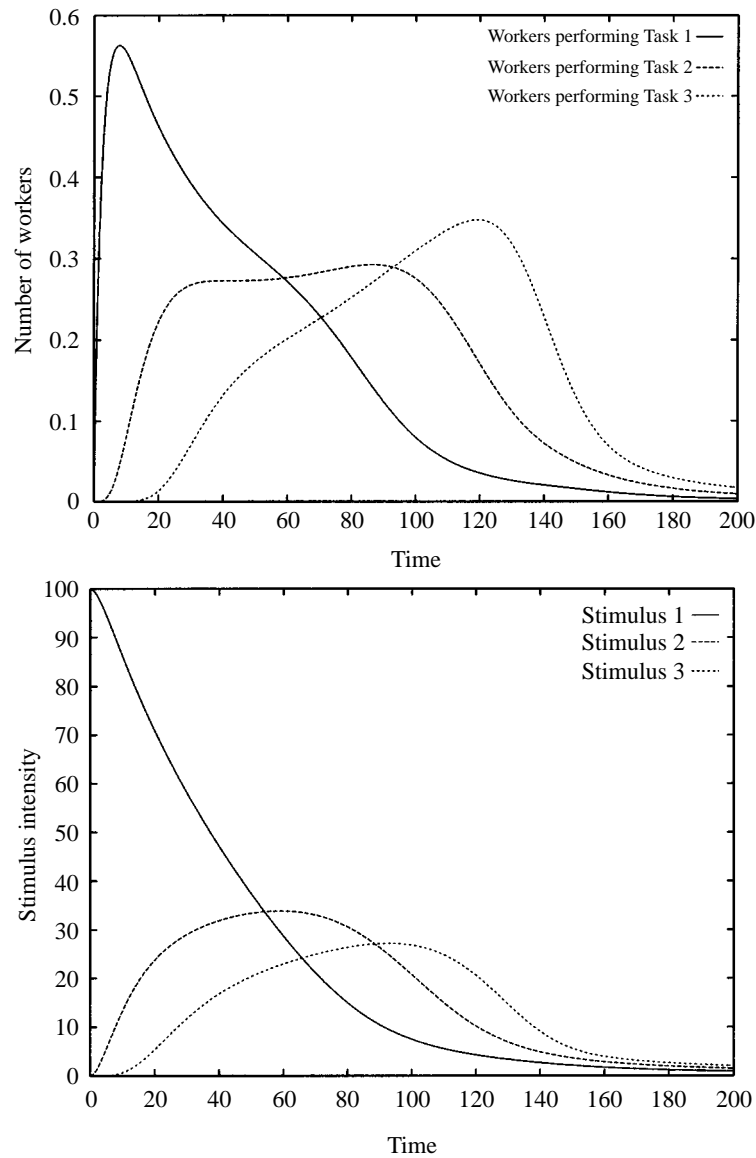


Figure 11. (a) Respective numbers of workers performing Tasks 1, 2 and 3 as a function of time. Dynamics given by equations (20) and (21) with three tasks. $D_1(t=0) = 100$, $D_2(t=0) = D_3(t=0) = 0$, $D_1 \rightarrow D_2 \rightarrow D_3$, $\alpha = 3$, $\theta_1 = \theta_2 = \theta_3 = 20$, $p_1 = p_2 = p_3 = 0.3$, $p = 0.2$. (b) Respective stimulus intensities associated with Tasks 1, 2 and 3 as a function of time for the same simulation as (a).

Franks and Sendova-Franks, 1992). When this is the case, it is clear that the probability of being exposed to stimuli (either directly or through worker interactions) associated with Task B when performing Task A depends on the spatial relationships between both tasks. Interesting quantitative information reported by Sendova-Franks and Franks (1995a), who have shown the existence of individual-specific ‘spatial fidelity zones’ (SFZ) in the ant *Leptothorax unifasciatus*, is that the frequency of brood care by a given worker is directly related to the amount of overlap between her SFZ and the spatial distribution of the brood: this suggests that the probability of responding to a particular stimulus depends on the perceived intensity of that stimulus; stimulus perception is influenced by the individual’s SFZ.

Spatial relationships among tasks is usually thought to be a factor of efficiency, if workers tend to perform a set of spatially localized tasks, so that mean free paths between tasks are minimized and tasks are more easily located (Wilson, 1976; Seeley, 1982). In cases where temporal polyethism has been evidenced, age and spatial location are often correlated [see, for example, Seeley (1982); Sendova-Franks and Franks (1995a) did not observe any significant correlation between age and spatial location]. Roughly speaking, in such cases younger individuals tend to be located within the nest, close to its centre, whereas older individuals are more likely to perform tasks outside the nest, such as nest defense or foraging. The prevailing ultimate explanation for this age-location correlation is West-Eberhard’s (1981) hypothesis of centrifugal polyethism: younger workers, because they can reproduce, tend to stay in the nest where they can lay eggs, while older workers are less likely to be able to reproduce and can therefore perform more dangerous tasks outside the nest.

The idea that task-associated stimuli are encountered differentially can be generalized to tasks which are not simply spatially related, but are causally connected or logically close. For example, in honeybees, foragers are in contact with food storers, to whom they deliver nectar, which is then stored in the combs by the food-storer bees (Seeley, 1989). It has been observed that food-storer bees (12–18 days old) are older than nurses but younger than foragers; food-storer bees then become foragers, an observation which is consistent with the notion of task connectivity. Tofts and Franks (1992) and Tofts (1993) often use a one-dimensional array of logically/spatially connected tasks because it is easy to visualize, but more complex arrays or graphs can also be used as a substrate for their model. In summary, the set of ‘topological’ relationships among tasks, which can be relatively complicated as it includes spatial, causal and other links, defines the conditional probabilities of being exposed to specific stimuli when performing a given task. We will show that, within the fixed-response threshold model, differential exposure to task-associated stimuli is sufficient to induce specialization and, under specific conditions, temporal polyethism.

4.2. Specialization. The simplest and most natural choice is to consider $q_{ij} = x_{ij}$, i.e., the probability of Group i to perceive stimuli associated with Task j directly

depends on the involvement of Group i in Task j . But then, the null state, where no worker of Group i performs Task j may be a stable attractor of the dynamics if the intensity s_j of the stimuli associated with j is too low (in effect, assuming a constant stationary level s for s_j , a necessary condition for the stationary value of x_{ij} to be different from 0 is $s^2 > 4p(p+1)\theta_{ij}$). If x_{ij} reaches 0, workers of Group i will no longer be performing Task j , no matter how large s_j may grow. We would therefore observe specialization (a specialist of Task j being defined by x_{ij} close to 1), but also a complete loss of flexibility in certain cases, when specialization becomes exclusive. This result may explain in part why minors do not do some of the majors' tasks: they do not perceive the corresponding stimuli, not necessarily for lack of the appropriate sensors, but because they do not encounter the stimuli. One way of restoring flexibility is to allow workers performing a given Task k to encounter stimuli associated with another Task j , even if they currently have a probability equal to zero of performing Task j . Of course, one would still like to retain the idea that performing Task j enhances the probability of encountering stimuli associated with Task j . If we define

$$q_{ij} = p_e x_{ij} + [(1 - p_e)/(m - 1)] \sum_{k=1, k \neq j}^m x_{ik} \quad (22)$$

(so that normalization is satisfied), where p_e is the probability of encountering stimuli associated with Task j while performing Task j , and $(1 - p_e)/(m - 1)$ is the probability of encountering stimuli associated with Task j while performing any other task, we obtain the desired property, provided that $p_e \gg (1 - p_e)/(m - 1) > 0$. We assume here that p_e is task-independent, and that the probability of encountering stimuli associated with Task j while performing another task is identical for any task different from j , which are obviously oversimplifications. However, we still have the main ingredients to generate a colony of flexible specialists. The generalization of the model to N individuals and m tasks requires a description of how task-associated demands vary. We generalize equation (6):

$$\partial_t s_j = \delta - \frac{\alpha}{N} \left(\sum_{i=1}^N x_{ij} \right). \quad (23)$$

Note that here again, s_j is scaled by N . Figure 12 shows an example of specialization (with two tasks), starting with groups of individuals with identical thresholds: although the thresholds do not vary in time, the probability of task performance evolves to match task-associated demands [x_{ik} ($k = \text{Task 1, Task 2}$) shown for two Groups i and j out of 10]. Figure 13 shows the evolution of the demand associated with Task 1: it oscillates before stabilizing above the individuals' threshold ($\theta = 5$), at $s_j = 8$. That the stationary value of s_j lies well above θ is not surprising, for individuals are not stimulated if s_j lies at or below their response thresholds.

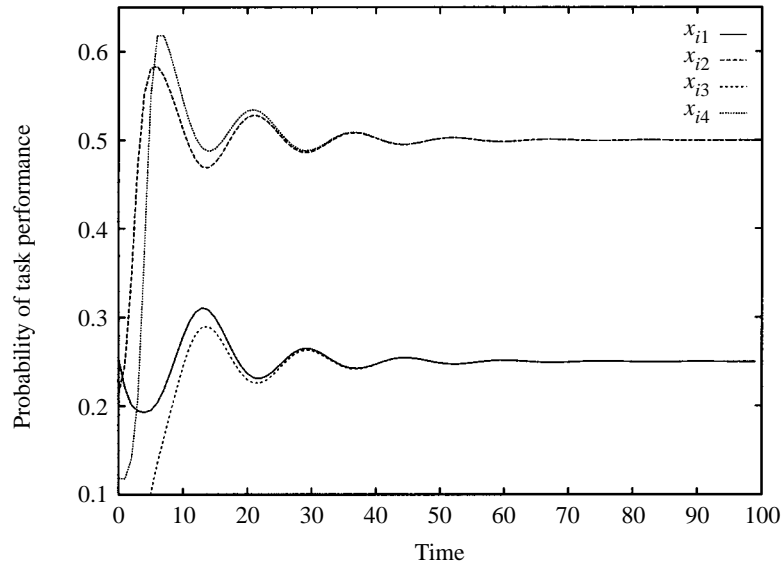


Figure 12. Frequency of task performance x_{ik} for two Tasks 1 and 2, and two individuals randomly selected out of 10, obtained by numerical integration of equations (12) and (15), with q_{ij} given by equation (14). $\theta = 5$ for both tasks and all individuals, $\alpha_1 = \alpha_2 = 3$, $\delta_1 = \delta_2 = 1$, $p_1 = p_2 = 0.2$.

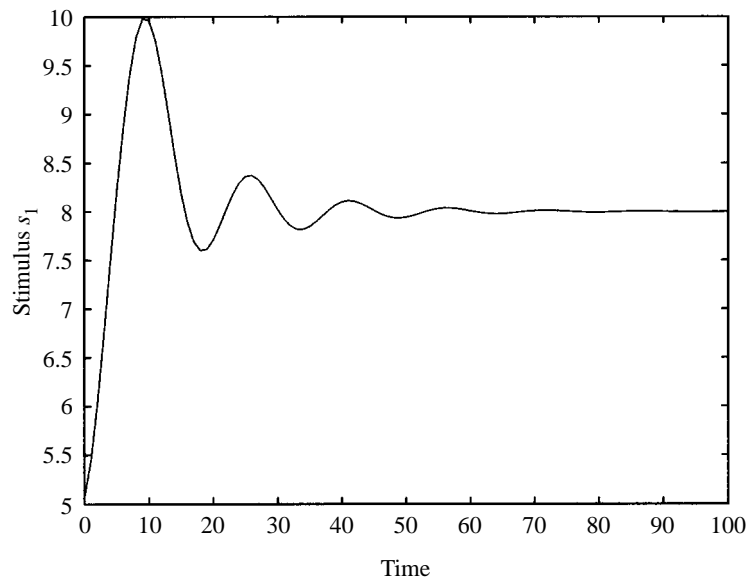


Figure 13. Dynamics of the demand associated with Task 1 for the example of Fig. 12.

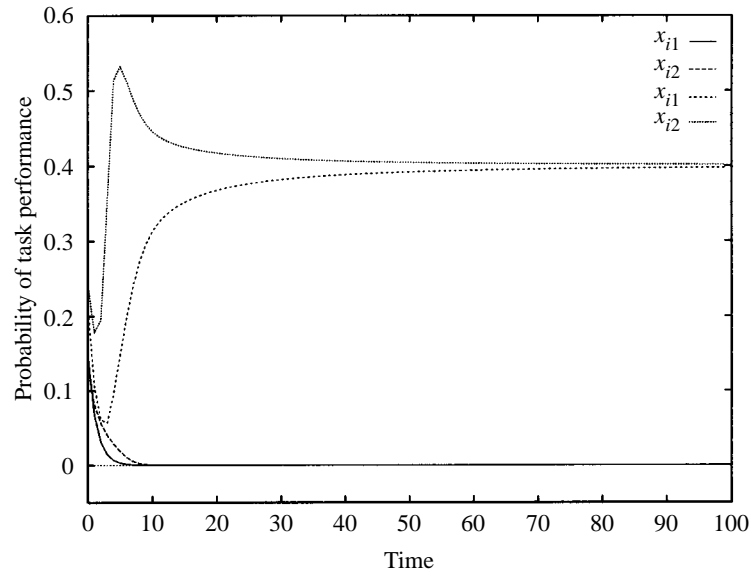


Figure 14. Same as Fig. 12 for $p_1 = p_2 = 0.5$.

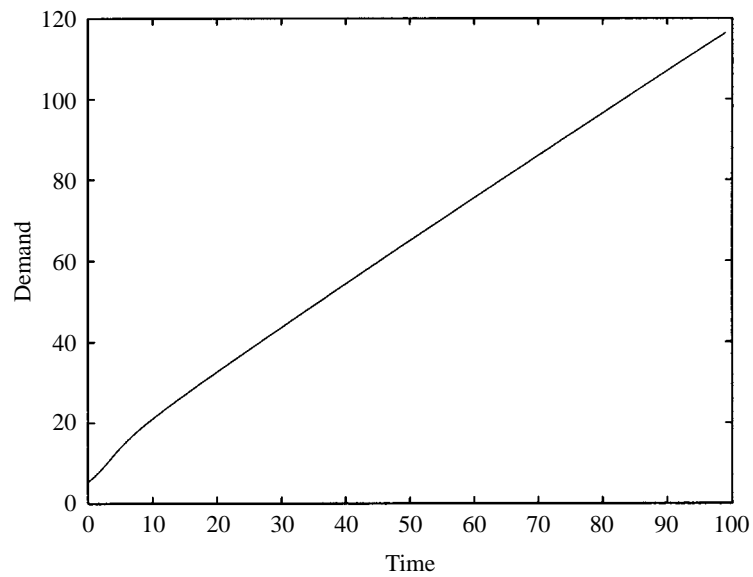


Figure 15. Dynamics of the demand associated with Task 1 for the example of Fig. 14.

Expression (12) for q_{ij} , neglecting the probability of an individual of Group i ‘spontaneously’ (i.e., while performing no task in particular) encountering a stimulus associated with Task j , can lead to another null state: one where there exists a Group i characterized by $x_{ij} = 0$ for all Tasks j , i.e., a completely idle group. This situation occurs frequently when p is large, or in other words, when the time spent performing a task before giving it up is small. Figure 14 shows a typical case, where Group i becomes completely inactive with respect to all tasks, while the other group spends 40% of its time performing each task, the rest of the time being lost in task switching (remember that p is large here: $p = 0.5$). Once, again, this state is an attractor of the dynamics. The demand associated with Task 1 is shown by Fig. 15, and can be seen to be divergent; despite this divergence, workers of Group i do not become active. It seems necessary, therefore, to introduce the probability p_s (that we take to be identical for all tasks and groups) of an individual to find a stimulus even when performing no task. Equation (14) is then transformed into

$$q_{ij} = (1 + p_s)^{-1} \left\{ p_s + p_e x_{ij} + [(1 - p_e)/(m - 1)] \sum_{k=1, k \neq j}^m x_{ik} \right\}. \quad (24)$$

Expression (22) satisfies the normalization condition of the q_{ij} . As can be seen in Fig. 16 ($p = 0.5$, $p_s = 0.001$), the null state for a group is no longer an absorbing state: Group i first becomes completely lazy, and then becomes involved in task performance again, because the demands have increased. This indicates that the specialization is weak (which permits it to be flexible), in the sense that a decrease in s_j can induce j specialists to perform other tasks or becoming lazy, and an increase in s_j can induce non- j specialists to perform j . Figure 17 shows that non-specialists of a task can become specialists when colony requirements with respect to that task increase ($p = 0.2$, $p_s = 0.0001$, at $t = 75$, task performance efficiency α changes from 4 to 2). We see that the two groups of workers switch from $x = 0.25$ to $x = 0.45$ (frequency of Task 1 performance).

4.3. Temporal polyethism. If we now add time to the previous model with specialization, for example by defining

$$q_{ij} = q_{ij}(t) = g_j(t)(1 + p_s)^{-1} \left\{ p_s + p_e x_{ij} + [(1 - p_e)/(m - 1)] \sum_{k=1, k \neq j}^m x_{ik} \right\}, \quad (25)$$

where t is the age of an individual, $g_j(t)$ ($0 \leq g_j(t) \leq 1$) is a function that defines how the probability of encountering stimuli associated with Task j varies in time, we can account for temporal polyethism, with specific sets $\{g_j(t)\}$. Here, we can include implicitly the outward motion of individuals as they age by (1) assuming that task-associated stimuli are more likely to be found in specific locations, and (2) by using $g_j(t)$ to explicitly describe in what general order locations will be visited and stimuli be encountered. Such a model is certainly less ‘emergent’ than the

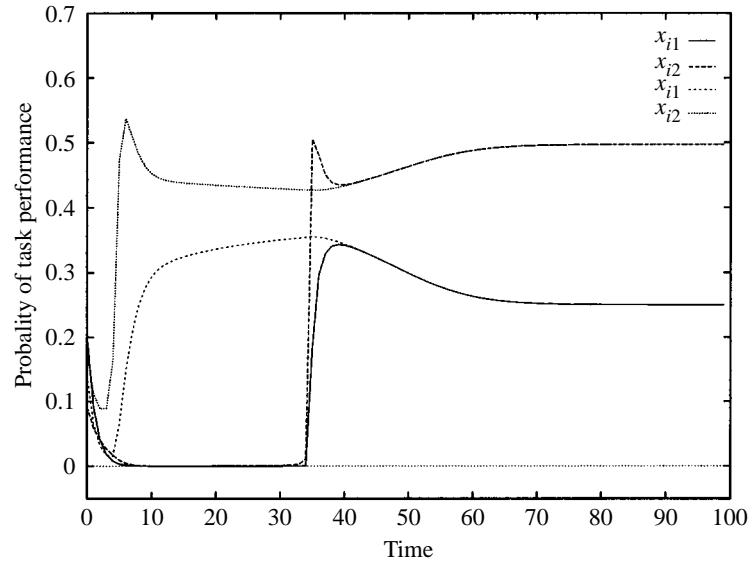


Figure 16. Same as Fig. 14, with $p_s = 0.001$.

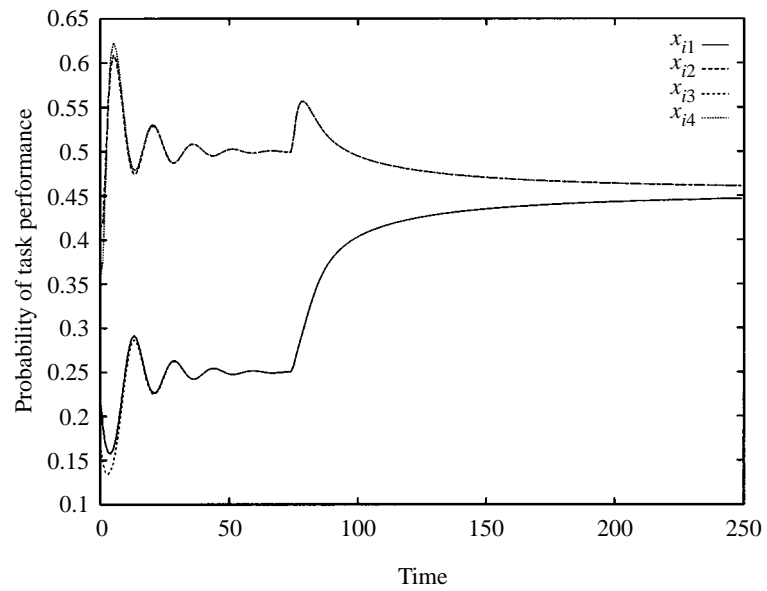


Figure 17. Same as Fig. 16, with $p = 0.2$, $p_s = 0.0001$. At $t = 75$, task performance efficiency α changes from 4 to 2.

FFW model (Tofts and Franks, 1992; Tofts, 1993), but is also more robust and more stable, and still flexible. *Our model does not assume time-varying thresholds but does assume an explicit time dependence of the probability of becoming engaged in performing a task.* The functions $g_j(t)$ could represent or include physiological ageing, although it is not exactly in the spirit of the model. We rather assume that $g_j(t)$ expresses an age-location correlation. For example, it could be physiologically necessary for newly emerged individuals to stay in the center of the nest for a certain amount of time, or alternatively, physiology again could stimulate older workers to exit the nest more often. Robinson (1987a) showed that JH is involved in the transition from intranidal to extranidal activities in honeybees, and that the onset of foraging is characterized by a rise in JH titers, but it is still not clear whether this feature is a cause or an effect of behavior. We have performed simulations with three tasks, characterized by three functions $g_j(t)$:

$$g_j(t) = e^{(t-t_j/T)^2} \quad (26)$$

where t_j is the time when stimuli associated with j are most likely to be encountered, and T is the duration of the ‘Task j period’. From now on, we consider the case where $m = 3$ (m is the number of tasks). Figure 18 shows the three functions $g_j(t)$. We now assume that each Group i is in fact limited to one individual: a colony of N individuals is described by N equations similar to equation (12), and x_{ij} describes the frequency of Task j performance by an individual i . The lifespan of an individual is $2T$, and $t_1 = 0$, $t_2 = T$ and $t_3 = 2T$. There is an inflow of $N/2T$ newly born individuals per time unit, so that colony size C is stable at N individuals (in the simulations reported below, $T = 50$, $N = 100$):

$$\partial_t C = \frac{1}{2T}(N - C). \quad (27)$$

Figure 19 shows the age- x_{ij} relationship for an individual taken at random in the colony, from $t = 5000$ to $t = 5100$. Figure 20 shows the age- x_{ij} relationship for a snapshot of the whole colony taken at $t = 5000$. The simulation started with N individuals having identical thresholds ($\theta_{ij} = \theta = 5$) and an initially random probability of performing each task $\{x_{ij}(t = 0)$ distributed uniformly in $[0, 1/m]$. New individuals are generated with the same thresholds but random initial frequencies of task performance (again, distributed uniformly in $[0, 1/m]$). We see that there is a strong correlation between age and probability of performing certain tasks: younger individuals perform mostly Task 1, intermediate individuals perform mostly Task 2 and older individuals perform mostly Task 3. There is also a striking similarity between the lifetime evolution of one individual and snapshots of the colony age-task distribution, except for young individuals, where the random initial distribution of x_{ij} induces fluctuations.

Behavioral reversion (Seeley, 1982; Lenoir, 1987; Robinson, 1992) can also be obtained in the same model if younger individuals are removed. Figures 21 and 22

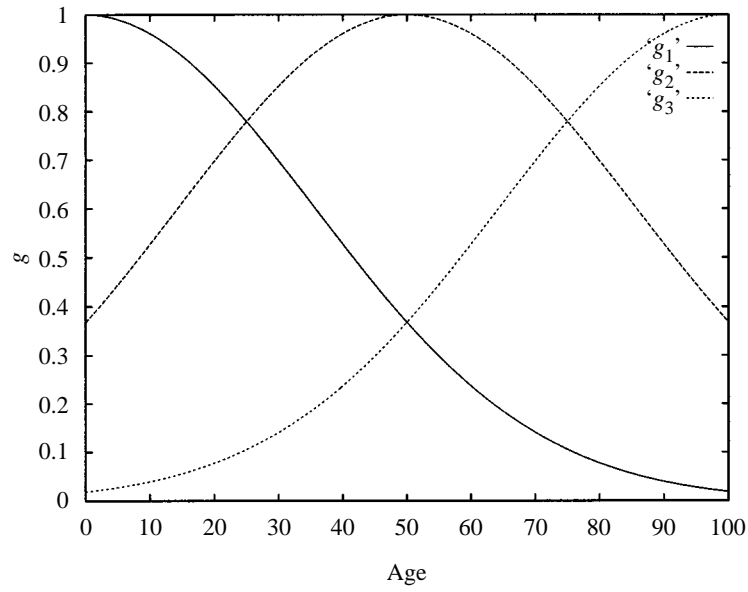


Figure 18. $g_j(t) = e^{-(t-t_j/T)^2}$, $j = 1, 2, 3$. $t_1 = 0, t_2 = T, t_3 = 2T, T = 50$.

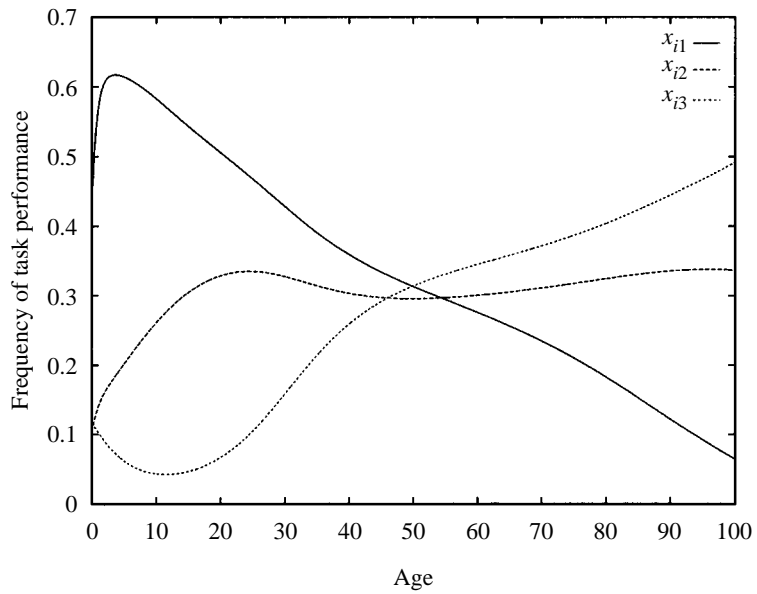


Figure 19. Frequencies of Task j performance for one individual i as a function of age. One hundred individuals with identical thresholds $\theta_{ij} = \theta = 5$ for all tasks. Initially random probability of performing each task ($x_{ij}(t = 0)$ distributed uniformly in $[0, 1/m]$). New individuals are generated with the same thresholds but random initial frequencies of task performance (again, distributed uniformly in $[0, 1/m]$).

show how older individuals increase their probability of performing tasks usually performed by younger individuals, when the latter are removed. Figure 21 shows the age- x_{ij} curve of one individual before the removal of young individuals, and Fig. 22 shows the same curve for another typical individual after the removal of young individuals (all individuals of age less than 30 time units are removed; the individual represented in Fig. 22 was 40 time units old when the removal took place). This simulation can apply, for example, to the case of swarm-founded colonies in honeybees (Robinson, 1992), where over-aged nurses can be observed caring for the brood and the queen, as no young individuals are available to perform that task. The same mechanism can induce younger individuals to perform tasks usually performed by older individuals if those are removed (as can occur naturally because of predation, competition, or other factors that tend to increase the death rate of older workers). Seeley's (1982) observation that the probability of behavioral reversion from foraging to nursing in honeybees depends on the amount of time spent foraging, cannot be explained in a robust way with this model. It would require the inclusion of a learning or task-fixation process (the probability of behavioral reversion in the present model depends weakly on the time spent performing the task, because specialization is weak). Note, however, that because the probability of reversion indirectly depends on x_{ij} , older individuals strongly involved in Task 3 are less likely to revert to Tasks 2 or 1.

This model can account not only for the maintenance of temporal polyethism, but also for its genesis: the simulation starts with one individual, and N/T individuals are added per time unit, until the colony reaches its stationary size N . The equations describing the dynamics of the various demands must also be rewritten as

$$\partial_t s_j = \delta - \frac{\alpha}{C(t)} \left(\sum_{i=1}^{C(t)} x_{ij} \right) \quad (28)$$

Figures 23 and 24 show two snapshots of the colony, respectively before and after maturity. We can see how temporal polyethism evolved from an initially loose pattern to a firm pattern of temporal polyethism (in this simulation, all thresholds are identical: $\theta_{ij} = \theta = 5$).

Finally, if one imposes that newly emerged workers remain at the nest for a certain amount of time, T' , and if tasks are coupled[†], we can obtain a pattern of temporal polyethism for some values of the parameters *without resorting to the explicit age functions* $g_j(t)$ of equation (26). Figure 25 shows an example where $T' = 5$ (in the simulations, workers younger than 5 have their q_{ij} s fixed: $q_{i1} = 0.95$, $q_{i2} = 0.04$, $q_{i3} = 0.01$, and individuals emerge with $x_{i1} = 0.8$, $x_{i2} = 0.05$, $x_{i3} = 0.05$).

[†]A worker performing Task 1 has a higher probability of encountering stimuli associated with Tasks 1 or 2 than with Task 3, a worker performing Task 2 has a higher probability of encountering stimuli associated with Task 2, but equal probabilities of encountering stimuli associated with either Tasks 1 or 3, and a worker performing Task 3 has a high probability of encountering stimuli associated with Tasks 2 and 3, but is unlikely to be stimulated to perform Task 1

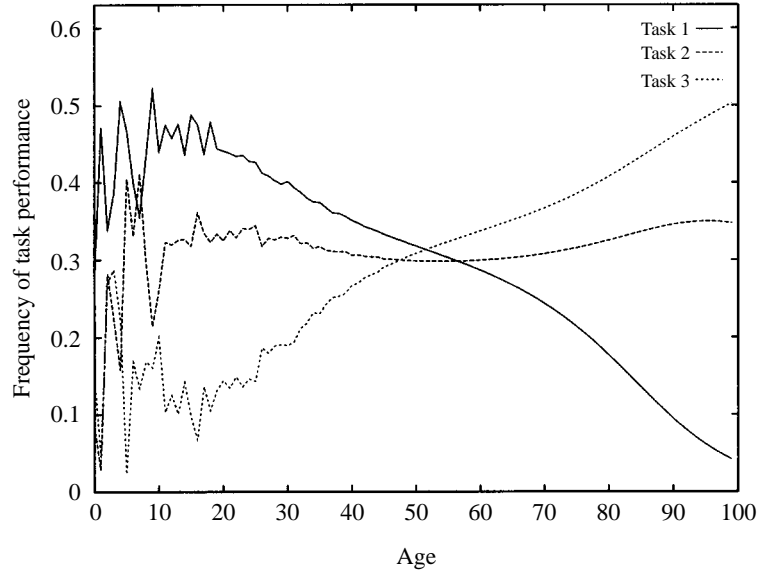


Figure 20. Snapshot of the whole colony taken at $t = 5000$ for the same simulation as in Fig. 19.

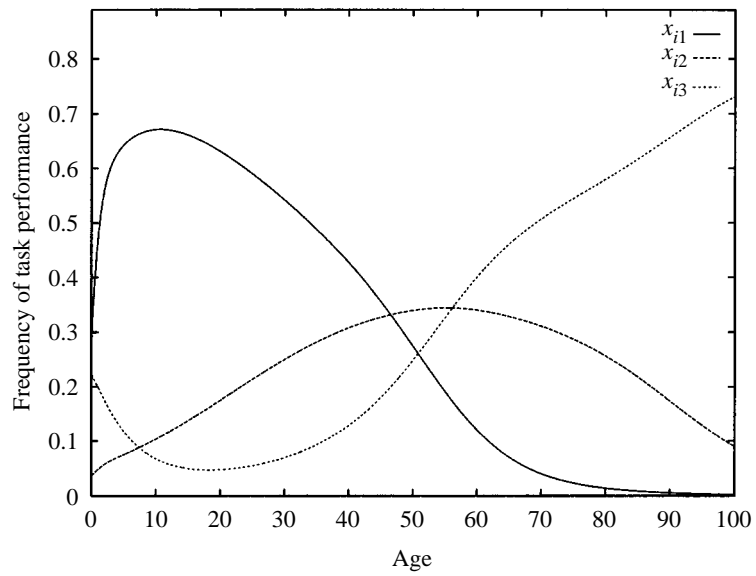


Figure 21. Age- x_{ij} curve of one individual before the removal of young individuals. Same parameters as in Fig. 19.

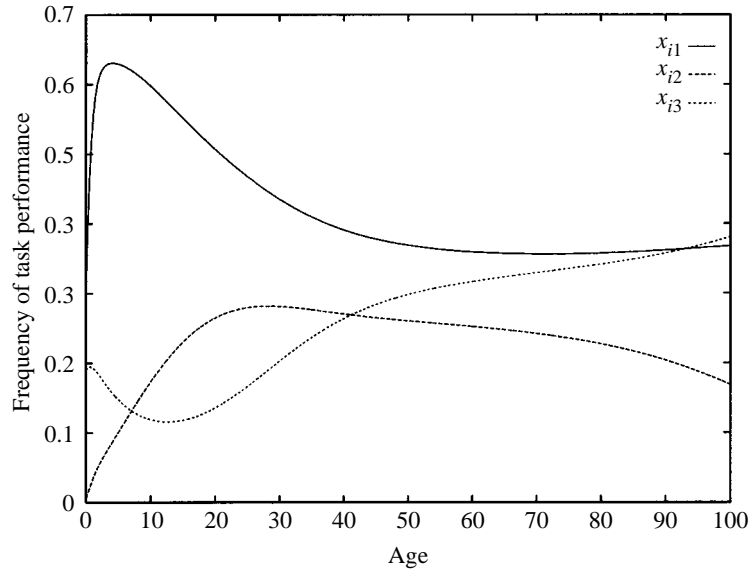


Figure 22. Same as Fig. 21 after the removal of individuals of age less than 30 time units. The individual represented in Fig. 18 was 40 time units old at the time of removal.

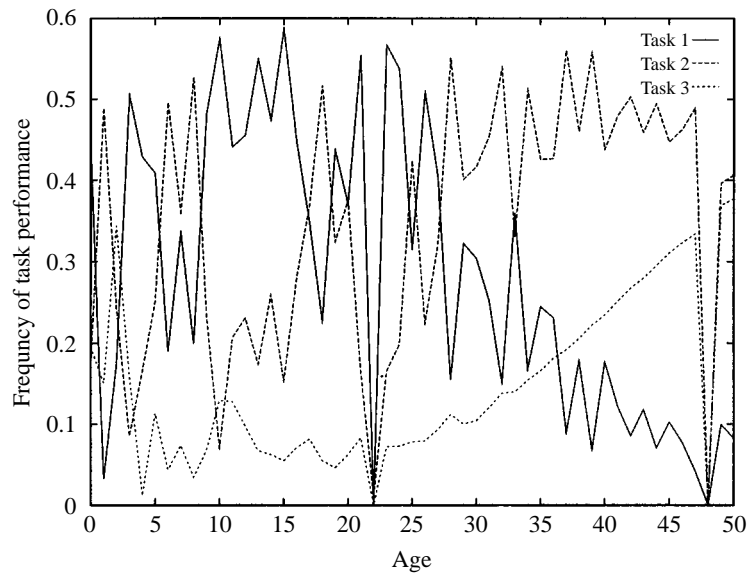


Figure 23. Snapshot of the age-task distribution in a simulated colony at half its time of maturity (the colony contains only individuals of age less than 50 time units). All individuals have identical thresholds $\theta_{ij} = \theta = 5$ for all tasks.

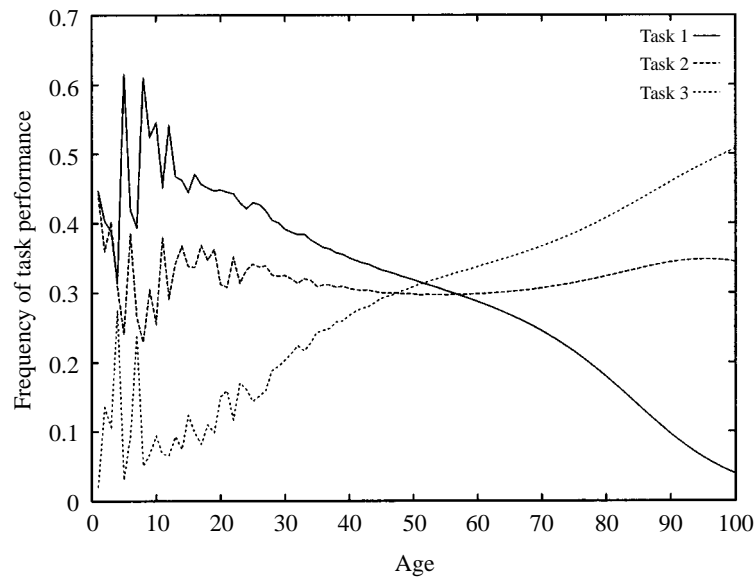


Figure 24. Same as Fig. 23, but after the colony has reached its stationary size.

This period of time spent in the nest by newly emerged individuals drastically lowers the demand for Task 1 and stimulates older workers to perform other tasks, the demands of which increase. From the snapshot presented by Fig. 25, we see that workers aged 0–30 perform mostly Task 1, workers aged 30–50 perform mostly Task 2 and workers aged 50–100 perform mostly Task 3. Notice that this more-emergent pattern of temporal polyethism can be obtained only for specific values of the parameters, and does not appear to be robust with respect to parameter variations. In particular, T' has to be sufficiently large, and new individuals have to be initialized with specific values of q_{ij} and x_{ij} .

4.4. Genotypic diversity (1): temporal polyethism. We have treated the case of identical thresholds, but it might be interesting to study the effect of genetic diversity, i.e., of distributions of thresholds. The fact that some individuals have low thresholds and others high thresholds means that there exist intrinsic specialists of a given task. Individuals with close genotypic characteristics (for example, belonging to the same patriline) may have similar response thresholds and are therefore predisposed to perform the same tasks. There is now convincing evidence that there is a genetic component to division of labor in honeybees and ants (Calderone and Page, 1988; Frumhoff and Baker, 1988; Robinson and Page, 1988; Breed *et al.*, 1990; Page and Robinson, 1991; Stuart and Page, 1991). It is generally believed (Jeanne, 1986) that the existence of specialists in a colony is a favorable trait, underlying most evolutionary explanations of division of labor: this is due to the fact specialists may be more efficient, either because they are better at performing the task, or because they do not waste time switching tasks. If specialization is a good thing,

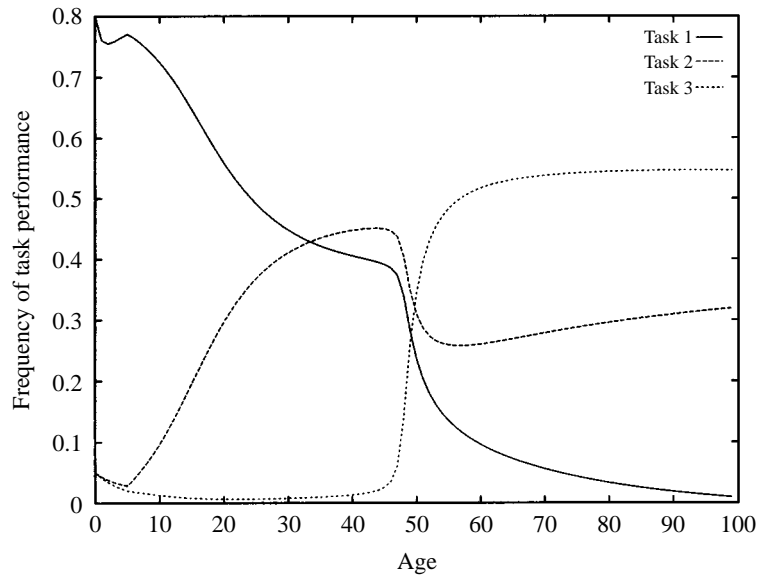


Figure 25. Snapshot of the age–task distribution in a simulated colony at $t = 10\,000$. Workers younger than 5 have their q_{ij} s fixed: $q_{i1} = 0.95$, $q_{i2} = 0.04$, $q_{i3} = 0.01$, and individuals emerge with $x_{i1} = 0.8$, $x_{i2} = 0.05$, $x_{i3} = 0.05$. q_{ij} s for older individuals are given by: $q_{i1} = 0.97x_1 + (0.03/(m-1))(1.95x_2 + 0.05x_3)$; $q_{i2} = 0.9x_2 + (0.1/(m-1))(1.8x_2 + 0.2x_3)$; $q_{i3} = 0.97x_3 + (0.03/(m-1))(0.05x_2 + 1.95x_3)$. All individuals have identical thresholds $\theta_{ij} = \theta = 5$ for all tasks, $p = 0.2$, $p_s = 0.0001$, $\alpha = 4$, $\delta = 1$.

and if genotypic variability provides a basis for behavioral differentiation, then, for example, high levels of polyandry may be favoured, as is the case in honeybees. The same reasoning applies to polygyny: it is striking that there is a strong negative correlation between polygyny and physical polymorphism among workers in ants (Keller, 1995); if genetic diversity, due for example to the presence of workers produced by different queens, endows the colony with a variety of response thresholds, and therefore specialization, physical polymorphism may not be necessary.

We study here how genotypic variability influences patterns of temporal polyethism in the context of the fixed-threshold model. Response thresholds constitute only one possible difference between individuals from different genotypes. Notice that genetic diversity can induce a bias not only in the pattern of temporal polyethism, but more fundamentally in the probabilities that individuals perform tasks, leading to patterns of genetically based specialization.

In a genetically diverse colony, some individuals may have an ‘accelerated development’ because they have a lower threshold with respect to tasks that are usually performed by older individuals, and other individuals may exhibit ‘retarded development’, as they are not very responsive to these tasks (Calderone and Page, 1988; Frumhoff and Baker, 1988). According to Calderone and Page (1988, 1991, 1996) genes may have effects on (1) the rate of behavioral ontogeny, and (2) the probability of task performance independent of the rate of behavioral ontogeny.

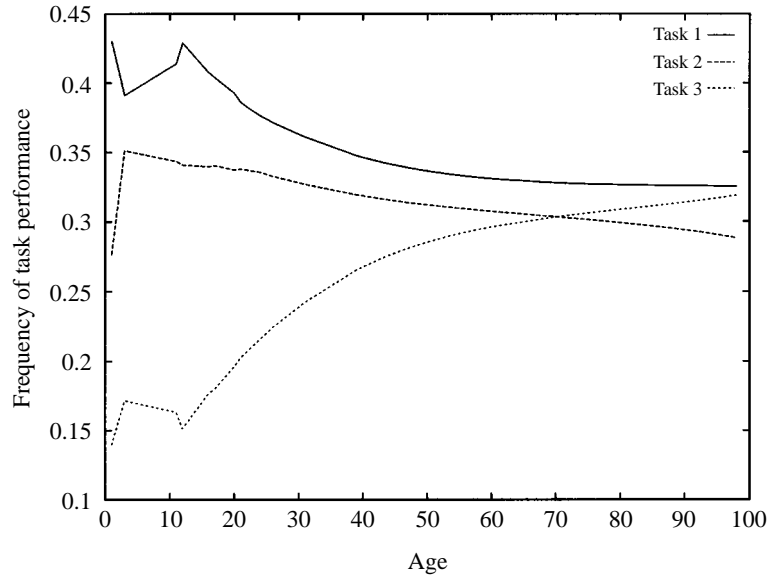


Figure 26. Snapshot of the x_{ij} -age relationship at $t = 5000$ for individuals of Group 1: $\theta_{11} = 1$, $\theta_{12} = 5$ and $\theta_{13} = 10$.

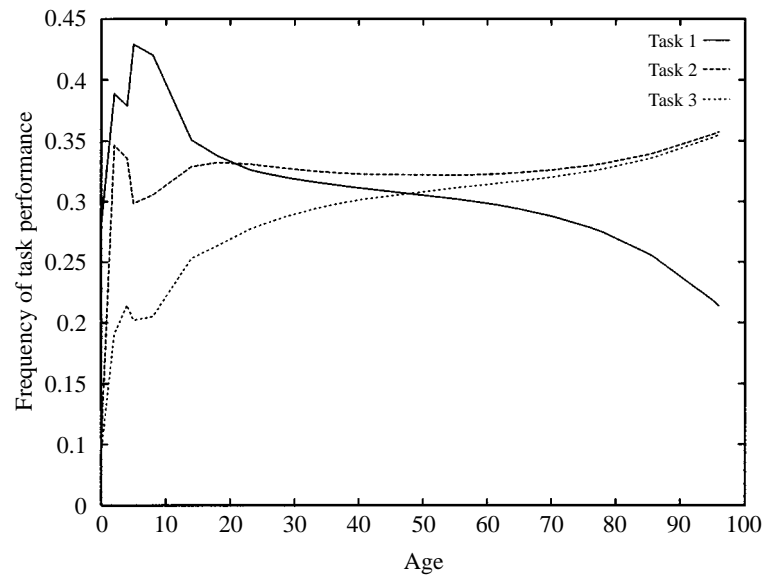


Figure 27. Same as Fig. 19 for Group 2: $\theta_{21} = 5$, $\theta_{22} = 1$, $\theta_{23} = 5$.

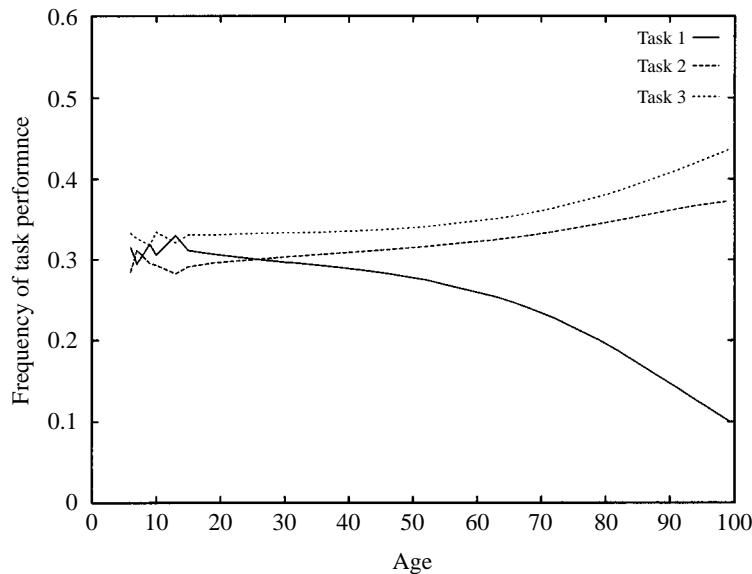


Figure 28. Same as Fig. 19 for Group 3: $\theta_{31} = 10$, $\theta_{32} = 5$, $\theta_{33} = 1$.

Our model suggests that the rate of behavioral ontogeny itself may be influenced by how sensitive individuals are to the various task-sensitive stimuli, provided there is a ‘driving force’ that promotes temporal polyethism, such as the emergent centrifugal flow observed under certain conditions in the FFW model. Figures 26–28 show the age– x_{ij} relationship for a snapshot of the colony for three groups of workers characterized by different response thresholds to the various tasks (Group 1 : $\theta_{11} = 1$, $\theta_{12} = 5$ and $\theta_{13} = 10$; Group 2 : $\theta_{21} = 5$, $\theta_{22} = 1$ and $\theta_{23} = 5$; Group 3 : $\theta_{31} = 10$, $\theta_{32} = 5$ and $\theta_{33} = 1$). Although all three groups exhibit the same global trend in temporal polyethism (Task 1 first, then Task 2, and eventually Task 3), they differ quantitatively in the way this temporal polyethism occurs. Group j is biased toward Task j , but age modulates this bias. *These results indicate that the rate of behavioral ontogeny can be influenced by response thresholds.* Figure 29 shows a snapshot of the age–task distribution in a simulated colony where all members (including newly emerged individuals) have randomly generated thresholds (uniform distribution in $[0, 10]$). The general structure of temporal polyethism is conserved, but is highly fluctuating. By contrast, the lifetime evolution of a single worker’s behavioral profile is smoother, but only loosely follows the expected pattern of temporal polyethism, as it is influenced by its own pattern of response thresholds. For the individual whose profile is shown on Fig. 30, we have $\theta_{11} = 3$, $\theta_{12} = 9$ and $\theta_{13} = 1$. Individuals with different patterns of temporal polyethism can be found, for example, in honeybees, where different patriline have different genotypes and therefore probably different responses with respect to the various tasks.

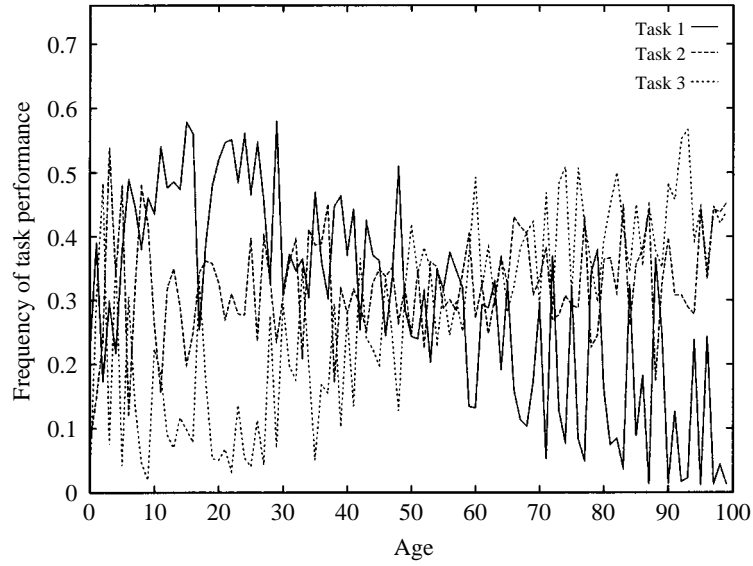


Figure 29. Snapshot at $t = 5000$ of the age–task distribution in a simulated colony where all members, including newly emerged individuals, are characterized by randomly generated thresholds (uniform distribution in $[0, 10]$).

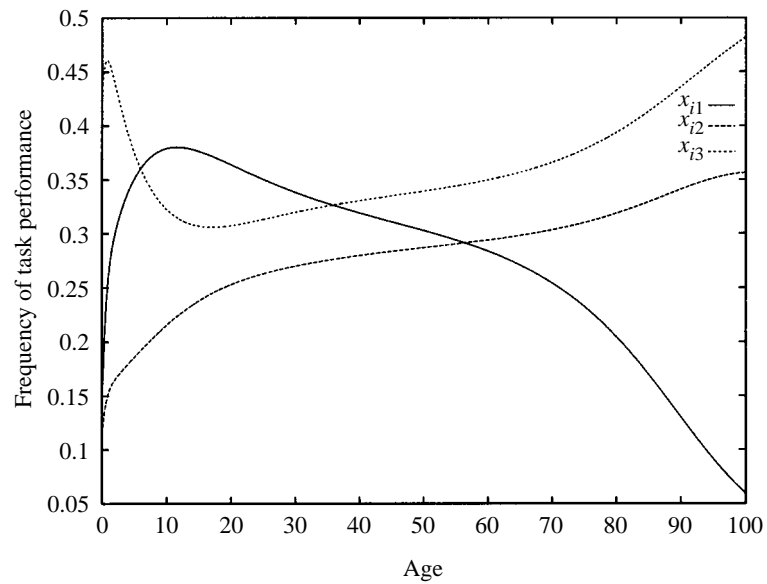


Figure 30. x_{ij} –age relationship of a single worker characterized by $\theta_{11} = 3$, $\theta_{12} = 9$ and $\theta_{13} = 1$.

4.5. Genotypic diversity (2): modulation of individual response vs collective modulation. An interesting theoretical question related to genotypic diversity is whether the collective response of a colony is as efficient when the modulation of the response results from a distribution of thresholds as to when it results from individual modulation. Let us illustrate this rather abstract question in the context of the choice of food sources in ants. Let us assume that N foragers are exploiting m food sources. The quality or richness of source i is given by r_i . Trails to the various food sources are reinforced by pheromone deposited by foragers. At the exit of the nest, an ant has to choose among all possible trails. We assume that the choice of a trail to Source i is probabilistic: the probability of selecting Trail i is given by (Deneubourg *et al.*, 1989; Deneubourg and Goss, 1989)

$$P_i = \frac{(k + C_i)^2}{\sum_{j=1}^m (k + C_j)^2}, \quad (29)$$

where C_i is the pheromone concentration on Trail i and k is a threshold-like parameter. We assume for simplicity that pheromone concentration does not decay over the time scale of the experiment. A forager coming back from Source i adds a quantity $Q(i)$ of pheromone to Trail i . This deposition behavior can be modulated as a function of r_i . Such a modulation can be implemented in either one of two ways (other alternatives will not be considered here).

MODEL 3. The amount of pheromone deposited per individual is a direct function of r_i . For example, it can be given by

$$Q(i) = \frac{r_i^2}{r_i^2 + \rho^2}, \quad (30)$$

where ρ is, once again, a deposition threshold. Here, all individuals have the same threshold, but are able to modulate their own trail as a function of source quality (resource quality may vary between food sources; also, the quality of a source can vary as a function of how many foragers are already present at the source, but, for the sake of simplicity, we do not consider this possibility). This is an example of individual modulation.

MODEL 4. A forager, j , deposits 1 unit of pheromone if $r_i > \theta_j$, where θ_j is an all-or-nothing deposition threshold. Individuals are characterized by different values of θ_j . In order for this collective modulation to be compared to individual modulation, the distribution $P(\theta)$ of θ in the colony must be such that the fraction of individuals that deposit pheromone for a source of richness r_i be given by $r_i^2/(r_i^2 + \rho^2)$. Therefore,

$$P(\theta) = \frac{\partial}{\partial \theta} \left(\frac{\theta^2}{\theta^2 + \rho^2} \right) = \frac{\theta \rho^2}{(\theta^2 + \rho^2)^2}. \quad (31)$$

This is obviously an example of collective modulation, for no individual is capable of fine tuning the amount of pheromone it deposits as a function of source quality.

Two situations can be tested in order to compare individual and collective modulation of trail laying (we consider for simplicity the case of two food sources: $m = 2$):

QUESTION 1. Two sources of identical quality are offered to the colony simultaneously at the same distance from the nest. It is known that, in species that resort exclusively to trail laying and trail following [as modeled, for example, by equations (29) and (30) or (31)], one of the sources is eventually far more exploited than the other source (Beckers *et al.*, 1990). How rapidly is the winning source selected over the other?

QUESTION 2. A single poor-quality source (Source 1) is presented to the colony, and, after a certain amount of time, a second, better-quality source (Source 2) is presented to the colony at the same distance from the nest. When the second source is presented, the colony is actively exploiting the first source, and a well-marked pheromone trail leads to Source 1. What is the probability that the colony be able to switch to the better source?

It is clear that differences between the two modes of trail laying will disappear as N becomes large: in effect, the theoretical distribution given by equation (31) is better and better approximated as N grows. Figure 31 shows the theoretical distribution and its simulated approximation for different values of N . We see that significant deviations from the theoretical distribution occur for N up to 2000. Results presented below correspond to $N = 200$, where deviations are visible, but the distribution is nevertheless reasonably well approximated.

The answer to the first question is that both Models 3 and 4 yield undistinguishable behaviors. Let t_1 and t_2 be the time it takes in Model 3 and Model 4, respectively, to reach a state where one source attracts 80% of the foragers. Variables t_1 and t_2 are random, the values of which depend on particular realizations of the food-source selection stochastic process. The question one is interested in is whether t_1 is greater than t_2 or vice versa. Applying a two-tailed Mann–Whitney U-test to a set of 100 values of t_1 and 100 values of t_2 obtained from 200 simulations with identical food sources presented simultaneously to the colony (and parameters $r_1 = r_2 = 15$, $k = 10$, $\rho = 10$, $N = 200$, $C_1(t = 0) = C_2(t = 0) = 0.2$), we find that $P > 0.5$, which means that Models 3 and 4 yield similar convergence times. In other words, individual or collective modulation has no significant influence on how fast the colony selects a food source.

In the context of the second question, Models 3 and 4 have different behaviors. Notice that Question 1 deals, in some sense, with efficiency, while Question 2 has to do with flexibility. Figure 32 shows the proportion of simulations where the second, richer food source is eventually selected although it has been presented after the first, poorer source (with $r_1 = 5$, $r_2 = 15$, $k = 10$, $\rho = 10$, $N = 200$, $C_1(t = 0) = 10-60$, $C_2(t = 0) = 0.2$). Model 3 curve lies below Model 4

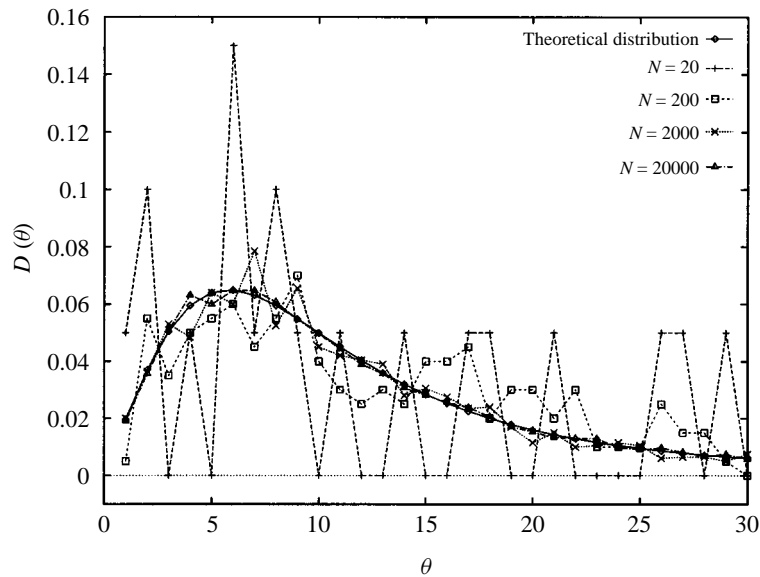


Figure 31. Theoretical distribution $P(\theta)$ given by equation (31) compared with simulated distributions for $N = 20, 200, 2000, 20\,000$.

curve, indicating that collective modulation endows the colony with more flexibility than individual modulation. These results would deserve further developments, as they point to a possible adaptive significance of genetic diversity, which leads to collective modulation. In the context of food-source selection, many factors that have not been taken into account, such as, for example, pheromone decay or the time taken to go to, and come back from, the food source, should be added to the model. Finally, alternatives to the simple models of individual and collective modulations described here can be devised, such as hybrid models with a mixture of individual and collective modulation.

5. RELATED WORK AND DISCUSSION

5.1. Related work on modelling the regulation of division of labor. Several models have been previously introduced to describe task allocation and its regulation in social insects. We believe that our approach is more tractable, more understandable and finally closer to the data than the other models presented in this section, although these models have, to a variable extent, inspired the present one.

5.1.1. The FFW model. We must emphasize that our model has some important similarities with the FFW model, introduced by Tofts and Franks (1992), where individuals actively seek work, and continue in their current role if they find work within that role. If they do not find work within their current role, or fail to find work

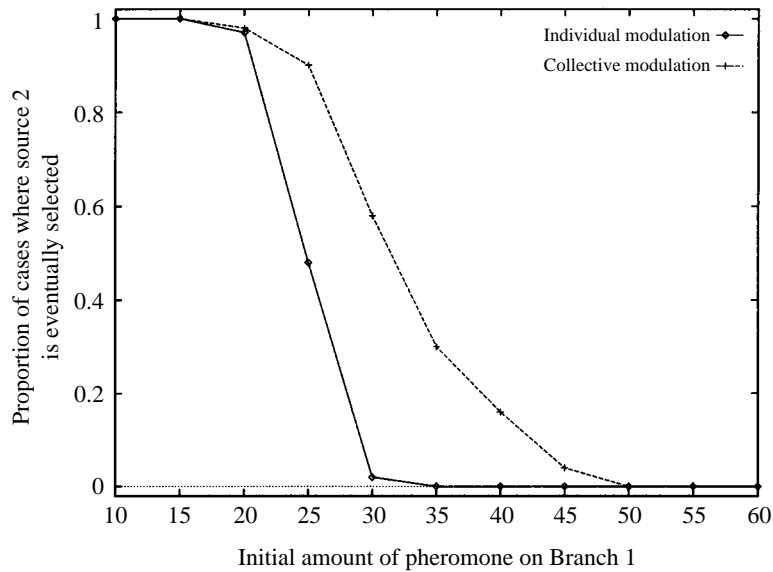


Figure 32. Proportion of simulations in which the second, richer source is selected although it has been presented to the colony after the poor source, as a function of the initial pheromone concentration $C_1(t=0)$ on Trail 1. $r_1 = 5$, $r_2 = 15$, $k = 10$, $\rho = 10$, $N = 200$, $C_2 = 0.2$. For $C_1 > 10$, the richer source is always selected, and for $C_1(t=0) > 60$, the richer source is never selected.

too frequently, they randomly move to adjacent zones until they find work. The FFW model assumes that tasks are spatially ordered: the simplest possible ordering is a one-dimensional line, where spatial locations are represented as a function of their distance from the centre of the nest. This ordering induces neighborhood relationships among tasks associated with spatial locations. For example, brood care, that necessarily takes place in the center of the nest, is far away from foraging, that takes place outside the nest, but foraging is close to nest defense. Our basic fixed-threshold model (Bonabeau *et al.*, 1996) belongs to the same family as the FFW model, as individuals may engage in task performance when they encounter appropriate stimuli. In that respect, individuals in our model are indeed ‘seeking’ work, but the addition of response thresholds and of differential responses by different groups of workers are important extensions. Adding explicit relationships between tasks [by defining, for example, how the probabilities of encountering the various task-associated stimuli depends on the current task, equation (24)] is a step toward the FFW model. Finally, in the FFW, a globally centrifugal motion of individuals as they age (from the middle of the nest to outside the nest) can be caused by an inflow of newly born individuals, who first actively seek work in the nest, pushing older individuals to seek work outside the center of the nest. By this mechanism, the FFW model can, in principle, produce temporal polyethism. This model is remarkable in that it does not require any kind of biological clock that would physiologically transform individuals at the ‘right’ time, to generate tempo-

ral polyethism. Sendova-Franks and Franks (1993) argue that the FFW model is fully consistent with their observations of *Leptothorax* ants, which are characterized by weak temporal polyethism. Their argument is further supported by more recent experiments (Sendova-Franks and Franks, 1995a), in which they showed the existence of individual-specific SFZ, (see Section 4.1), which appear to be independent of the individual's age: workers tend to perform tasks within their SFZ, irrespective of their age. In view of recent experimental evidence [e.g., Calderone and Page (1996); Robinson *et al.* (1994)], however, it is almost certain that other mechanisms (such as ageing, under one form or another, including learning) play a role in temporal polyethism in some species of social insects, including honeybees. The FFW model could be supplemented with a learning mechanism to account for stronger patterns of age polyethism.

Our mechanism is similar to that of the FFW algorithm (Tofts and Franks, 1992; Franks and Tofts, 1994), except that we use a direct dependence of spatial specialization on age (by spatial specialization, we mean that workers are more likely to be found in some region of space). Our model allows for behavioral reversion when required, but is less flexible than FFW. On the other hand, temporal polyethism is more stable than in the pure FFW case. When we tried to set up the parameters of our model so that it reproduces exactly the FFW model (although with a slightly different formulation), we were unable to generate temporal polyethism solely with spatial relationships between task-associated stimuli, which indicates that the 'pure' FFW model generates a somewhat unstable form of temporal polyethism. We could, however, generate a less 'emergent' pattern of temporal polyethism in our model by coupling spatial relationships between tasks with the assumption that the younger workers tend to remain a certain time in the nest, where they perform local tasks. This constraint, if it is sufficiently strong, i.e., if the time that newly emerged workers spend in the center of the nest is sufficiently long, can effectively force older workers to find tasks associated with stimuli which are not found at the center of the nest. Finally, while we owe a conceptual debt to the FFW model, we believe that our model is formulated in such a way that it will be more understandable than the theory of the FFW model (Tofts, 1993), which was based on a probabilistic extension of Milner's (1990) process algebra. In such a formalism, initially introduced in the context of theoretical computer science to study general concurrent systems comprised of interacting individuals, ants correspond to probabilistic processes composed in parallel. The language of Tofts' (1993) paper, being most unfamiliar to ethologists, obscured rather than clarified the scope of the FFW model.

5.1.2. *Modelling division of labor in social insects.* Given a recent set of commentaries (Traniello and Rosengaus, 1997; Robson and Beshers, 1997) 'against' modeling in general, modeling division of labor in particular, and even more specifically the FFW model [see also the reply by Franks *et al.* (1997)], we feel that it is useful to justify our own modeling approach, all the more as it is related to FFW. First, as clearly explained by Franks *et al.* (1997), a modeling approach implies that

only a (usually small) fraction of reality be studied and formalized; furthermore, any scientific enterprise—stamp collecting not being considered scientific here—is aimed at finding at least some degree of regularity in the world, and scientific explanation is explanation (by virtue of necessarily simplifying models) of such regularity. Physicists, obsessed as they are about universality, are responsible for a global tendency to seek common underlying theories for virtually all phenomena [see Bak (1997) for an extreme, provocative, but inspiring version of this tendency], which may not always be justified. Any good theory should be characterized by what it cannot explain and what it can explain, and both sides are equally important. For instance, in the context of division of labor, finding a potential general mechanism, such as FFW, is an honorable quest provided one understands that what Traniello and Rosengaus (1997) call species-specific traits are not part of this theoretical framework, the aim of which is precisely to point to common features rather than to differences. Such differences are not explained by FFW, but suggests that there may be common underlying mechanisms responsible for division of labor, including observed patterns of temporal polyethism. This approach is particularly important if one is seeking ancestral mechanisms that allowed for the emergence of eusociality (for example, mechanisms upon which an efficient division of labor can be based): evolution may have refined and perhaps sometimes substantially modified such ancestral mechanisms, but finding common features is essential as they point to possible common ancestral features that were important for the appearance of eusociality. The threshold model is also a general model of task allocation, which can be useful not only to explain observed behavior, but also, perhaps, to point to potential common ancestral mechanisms. Finally, the assumptions of the basic model presented in this paper are based on experimental evidence (Detrain and Pasteels, 1991, 1992), and can account for other experimental results [Wilson (1984) for example]. This gives more weight to the extensions of the model, and at the same time the model allows us to test what is and what is not possible within its framework. For example, we have indicated several times that only a weak form of temporal polyethism can be obtained in this model, with highly specific values of the parameters, which suggests that other ingredients are required to account for some observed patterns of temporal polyethism.

5.1.3. *Boolean network model.* Page and Mitchell (1990) and Page and Robinson (1991) have developed a model of task allocation in honeybees based on the threshold principle, where individuals are represented as boolean automata embedded within a network. They did not try, however, to relate quantitatively their results to any specific experimental observation. In their model, each worker bee is a binary switching element (that can either be 1 or 0: performing or not performing a given task), connected to K other elements. An element switches on and off depending on how many 0s and 1s it perceives from the K elements it is connected to. The idea is that individuals receive information from other individuals (in particular, they can perceive the current task of the K individuals they encounter per unit time)

in the colony and decide to become engaged or to give up task performance depending on this information. There is also an external input to each element, which represents task-associated stimuli. This external 'field' is decreased by one unit by unit time for each individual performing the task, and is regularly incremented to represent the dynamics of colony needs irrespective of task performance. When the combined input to a given inactive element (state 0) exceeds a threshold, this individual becomes engaged in task performance (state 1), and vice versa. The magnitude of the external field has a positive effect on task performance, while the number of workers already performing the task acts as a negative feedback. This model is obviously very similar in spirit to the model described in the present paper. Page and Mitchell (1990) found that a boolean network following these rules converges to a steady state, where the proportion of active elements depends on the value of the threshold. They also studied the effect of the variance of the threshold distribution on the properties of the network, and found that responses to disturbances drive the stimulus back to its predisturbance level for highly peaked distributions, while the regulation of stimulus level was not as good in wider distributions, although the number of active elements did change in response to the perturbation. These findings show that a network of simple interconnected elements can exhibit remarkable homeostatic properties, but they are not clearly related to quantitative experimental results. Note that our model shows that the same type of properties can be obtained without any explicit interaction among individuals (although such interactions certainly do play a role in evaluating colony needs), as the magnitude of the stimulus alone is sufficient to determine approximately the number of individuals involved in task performance. Therefore, in principle it is not necessary for individuals to know how many other colony members are active. A combination of task-associated stimuli and interactions with other workers is, however, likely to be the relevant information acquisition mechanism.

5.1.4. *Connectionist model of task allocation.* In an attempt to account for the field observations of Gordon (1986, 1987, 1989) on the dynamics of task allocation in harvester ants, Gordon *et al.* (1992) have developed a model based on a connectionist (neural net) model, which can be seen as a more complex (and a more experiment-driven) version of Page and Mitchell's (1990) boolean network, where units correspond to ants, possible states of a given unit to tasks that can be performed by the ant, and patterns of connections to observed patterns of interaction among individuals. They modeled eight categories of ants. Ant k is represented by a set of three binary values ($a_k = \pm 1, b_k = \pm 1, c_k = \pm 1$), so that all eight categories can be represented: inactive patrollers $(-1, 1, 1)$, active patrollers $(1, 1, 1)$, inactive foragers $(-1, 1, -1)$, active foragers $(1, 1, -1)$, inactive nest maintenance workers $(-1, -1, 1)$, active nest maintenance workers $(1, -1, 1)$, inactive midden workers $(-1, -1, -1)$, and active midden workers $(1, -1, -1)$. Matrices of interactions α_{jk}, β_{jk} and γ_{jk} , and between Ant j and Ant k are defined for $a_k, b_k,$ and c_k respectively. One specific feature of this model is that the set of interactions of a given unit

with other units changes when the unit changes state. The dynamics of the fully connected system proceeds by elementary moves (changing a_k , b_k , or c_k) at each discrete time step, depending on the signs of $\sum_k \alpha_{jk} a_k$, $\sum_k \beta_{jk} b_k$, and $\sum_k \gamma_{jk} c_k$:

$$a_k(t+1) = 2 \left[\left(\Theta \sum_k \alpha_{jk} a_k(t) \right) - \frac{1}{2} \right], \quad (32.1)$$

$$b_k(t+1) = 2 \left[\left(\Theta \sum_k \beta_{jk} b_k(t) \right) - \frac{1}{2} \right], \quad (32.2)$$

$$c_k(t+1) = 2 \left[\left(\Theta \sum_k \gamma_{jk} c_k(t) \right) - \frac{1}{2} \right], \quad (32.3)$$

where $\Theta(x) = 1$ if $x > 0$, and $\Theta(x) = 0$ otherwise. Notice that these conditions are deterministic threshold conditions: when some weighted input exceeds, or goes below, some threshold (here, 0), an individual switches tasks or becomes (in)active. Their model is therefore fundamentally a threshold model, where stimulus intensity is a weighted sum of inputs from other individuals. They showed that, depending on the pattern of interactions among individuals, the system can have one or several attractors, and that perturbations of one activity propagates to others. One important assumption of their model is that the evaluation of colony needs by an individual is performed only through interactions with other members of the colony, i.e., only numbers of workers engaged in the different tasks are used by an individual to decide what task to perform next (depending also on its current state). The magnitude of task-associated stimuli are not taken into account, which makes the functioning of the system rely solely on an internal dynamics. Gordon *et al.* (1992) were able to reproduce some experimental results qualitatively, but other results are unlikely to be explained, as the model cannot be robust with respect to certain perturbations (for example, because it is insensitive to colony needs).

5.1.5. *A general model of task allocation.* Pacala *et al.* (1996) have recently developed a rather general, simple model of task allocation. Let Q be the number of different tasks to be performed, N the total number of individuals, x_i the number of workers engaged in task i , σ_i the probability that individuals performing Task i are successful (an individual that views the environment as profitable (respectively, unprofitable) is in the successful (respectively, unsuccessful) state), ρ_{ij} the mean local density of Task j individuals about a Task i individual, ρ_{Ii} the mean local density of Task i individuals about a inactive individual, q the probability per unit time that an unsuccessful individual becomes inactive. Interactions among individuals are modeled as simple collisions. The rate at which an individual engaged in Task i encounters individuals engaged in Task j is proportional to ρ_{ij} . An inactive individual is recruited to perform Task i if it interacts with a successful

Task i individual: the rate of activation into Task i is therefore proportional to ρ_{Ii} . The dynamics of x_i is given by

$$\partial_t x_i = -x_i(1 - \sigma_i)q + \sum_{j=1}^Q [x_i \sigma_i \rho_{ij}(1 - \sigma_j) - x_j \sigma_j \rho_{ji}(1 - \sigma_i)] + x_i \sigma_i \rho_{Ii}. \quad (33)$$

Equation (33) is similar in spirit to equation (12), where stimulus intensity s_i has been replaced by σ_i , and where the response function depends linearly on σ_i and also on a recruitment process [in equation (33), two mistakes present in Pacala *et al.*'s (1996) equation (1) have been corrected]. The dynamics of σ_i must be specified in order for the model to be complete. Pacala *et al.* (1996) assume that a successful individual switches to the unsuccessful state with a probability τ^{-1} per unit time, and that processing a unit of resource within a time unit increases σ_i . Let φ_i be the resource density (per unit area) and k a parameter affecting the rate of increase of σ_i . The dynamics of σ_i is given by

$$\partial_t \sigma_i = -\frac{\sigma_i}{\tau} + k\varphi_i(1 - \sigma_i). \quad (34)$$

If crowding avoidance is taken into account, equation (34) has to be supplemented with a new term:

$$\partial_t \sigma_i = -\frac{\sigma_i}{\tau} + k\varphi_i(1 - \sigma_i) - \xi \frac{x_i}{\alpha_i} \sigma_i, \quad (35)$$

where ξ is a constant of proportionality and α_i is the area over which Task i is being performed. Clearly, φ_i can change over time, because resources get depleted. The dynamics of φ_i is then given by

$$\partial_t \varphi_i = \Gamma_i - \mu\varphi_i - k\varphi_i x_i, \quad (36)$$

where Γ_i is the rate of creation of the resource (for example seeds that fall to the ground), and μ is the 'natural' rate of disappearance of the resource (wind, other colonies, and so forth). Pacala *et al.* (1996) considered three cases for σ_i and φ_i : (1) there is no crowding avoidance and φ_i does not vary with time (resources are abundant), (2) there is no crowding avoidance but φ_i varies because resources get depleted, and (3) there is crowding avoidance and φ_i varies because resources get depleted. In all three cases, Pacala *et al.* (1996) assumed that the dynamics of σ_i and φ_i are fast with respect to variations in x_i . Curiously, they did not consider the case where there are increasing returns for increasing x_i , which can be the case when, for example, allocating a lot of workers to a given task is safer. More importantly, they did not consider how variations in colony needs resulting from task performance, which obviously have an influence on σ_i , could influence patterns of task allocation. Their model is therefore aimed at describing short-term task allocation, or, alternatively, can be seen as a general model of recruitment.

In equation (33), Pacala *et al.* (1996) assumed that ρ_{ij} is given by $x_j I(N)/N$, where $I(N)$ is the ‘*per capita* rate of social interaction as a function of group size’. They studied the influence of $I(N)$ on patterns of task allocation. They showed that some parameter values allow individual- or colony-level evolutionarily stable strategies to be implemented by means of simple individual behavior. Although they presented simulations of their model with $I(N)$ proportional to N , they showed that $I(N)$ should be tuned to maximize fitness. Larger groups may be more efficient than smaller ones at tracking a changing environment when rates of interactions per individual increase with group size, but there may be an overload of social information in very large groups, that can become trapped in suboptimal states. Pacala *et al.* (1996) predict that, in order to balance optimally, the flows of information from environmental stimuli and social exchanges (antennation, mandibular contacts, trophallaxis, etc.) across a range of group sizes, ants should regulate their *per capita* rates of social interaction.

5.2. Predictions of the model and connection to experimental work. The fixed threshold model is arguably the simplest model that connects flexibility at the worker level with the resiliency observed at the colony level, in a way that is consistent with experimental data. In that respect, this model makes an important prediction: that fixed response thresholds are sufficient to reproduce and possibly explain numerous aspects of task allocation in social insects. An important task is now to study response curves and show the existence of response thresholds in experiments. Several experiments, some results of which are briefly described in Section 2, have shown the existence of response thresholds, but they do not allow us to connect individual and colonial levels. It would be extremely valuable to find empirical evidence for differential response thresholds in minors and majors in the polymorphic species studied by Wilson (1984). Our model generates results that are consistent with these experiments, which indicates that differential response curves at the individual level might be the underlying mechanism of colony-level flexibility. Preliminary experiments on *Lasius niger* (Deneubourg *et al.*, in prep.) indicate that different response thresholds to different seed sizes might be responsible for the fact that small seeds are processed first, followed by medium-sized and large seeds, thereby suggesting that Model 1 may be valid. Finally, we also believe that our model will be useful to students of social insects when interpreting results of experiments on division of labor. Before looking for complex mechanisms, it may make more sense to ask whether an empirical result could be explained by the fixed-threshold model.

5.3. Limitations of the fixed threshold and future modeling directions. The fixed threshold model can account, at least partly, for the behavioral flexibility observed in ants, when manipulations such as those reported by Wilson (1984) on several species of *Pheidole* are carried out (Bonabeau *et al.*, 1996). Because this model is also biologically plausible, our aim in this paper was to explore what could be expected from the model. Clearly, it can explain some aspects of division

of labor, including colony-level flexibility in polymorphic species, within-‘caste’ flexibility and task switching, spatial fidelity, weak temporal polyethism, or task succession, but it is not always consistent with experimental observations, especially when ‘long’ time scales are involved. Until recently the ‘classical’ view of division of labor (Oster and Wilson, 1978) was that it was a relatively static phenomenon, with caste ratios, or more generally ‘class ratios’ (Calabi, 1988), determined by ergonomic and energetic considerations. Although within- and between-caste task switching and flexibility are observed (Wilson, 1984; Lenoir, 1987; Calabi, 1988; Gordon, 1989), such considerations do appear to be important, and observed (age, physical or behavioral) class ratios have certainly been selected for in the course of evolution on the basis of these factors. For example, Wilson (1983b) observed flexibility in *Atta cephalotes* ants when one class of workers is removed; replacement workers perform similarly to ‘specialized’ workers in terms of frequency and effectiveness of task performance, but are 30% less efficient with respect to oxygen consumption (Calabi, 1988). It is therefore tempting to think, following Calabi (1988), that ‘optimal’ caste ratios predicted on the basis of energetic factors (Oster and Wilson, 1978) are relevant over evolutionary time scales, and that observed caste ratios have been shaped more or less accordingly, but on short time scales, changing ecological conditions make flexibility an absolute necessity—flexibility has also been selected for. ‘Where colony survival is at issue, considerations of behavioral and/or metabolic efficiency should be secondary. By this reasoning, the caste distribution function only approximately reflects long-term selective pressures, because flexibility among classes allows short-term compensation for any ‘slop’ or inappropriateness in caste ratios’ (Calabi, 1988). The same argument applies in support of West-Eberhard’s (1981) hypothesis of centrifugal task allocation (see Section 4.1): selection acting at the level of the individual exerts a long-term pressure leading to a more or less marked centrifugal pattern of temporal task allocation, and short-term flexibility, driven by immediate colony requirements, tends to blur this pattern. The threshold model is able to reconcile both views, i.e., both time scales. For example, in polymorphic species, response thresholds may be determined by physical caste, with caste ratios being determined (at least partly) by energetic factors. In ‘normal’ conditions, i.e., when all individuals belonging to all physical castes are present and when there is no particular stress on the colony (such conditions may in fact be quite abnormal!), task allocation should follow exactly caste distribution. When, however, a large portion of a given caste is missing, individuals belonging to other castes may replace missing workers, through the mechanism developed in this paper. The understanding of ‘age-based’ task allocation and within-age-class flexibility might, however, require a little more than the simple fixed threshold model, although flexibility alone can in principle be understood with this model on short time scales, using the same argument as for physical castes.

Although it has been argued several times by Franks and colleagues (Franks and Tofts, 1994; Franks *et al.*, 1997) that one should not confuse causality with correlation, and specifically correlation between age and task with an age-based division of labor,

recent experiments (Robinson *et al.*, 1994; Calderone and Page, 1996) suggest that response thresholds, if they play a role in task allocation, are unlikely to be fixed. Variability in response thresholds may result from two, somewhat complementary, mechanisms; ageing and learning.

- (1) In the context of response thresholds, ageing would involve the modification of thresholds with time, so that, for example, a young individual would have a naturally high response threshold with respect to nest defense, but that threshold would progressively become lower as the individual ages, until the probability of response to a defense-related stimulus becomes significant.
- (2) Learning would involve, for example, reduction of a response threshold when the associated task is being performed (task 'fixation'), and increase of the response threshold when the task is not being performed ('unlearning') (Deneubourg *et al.*, 1987; Plowright and Plowright, 1988; Theraulaz *et al.*, 1991).

Both mechanisms seem to be involved; in particular, the role of learning has been evidenced. Withers *et al.* (1993) have shown that important changes in some regions of the brain are associated with ageing: foragers (> 20 days old) are characterized by a smaller volume of Kenyon cells (neurons of the mushroom bodies) and a significantly larger neuropil volume (where synaptic connections are located) than 1-day-old bees, suggesting a high synapse-to-neuron ratio in older bees. Nurse bees, intermediate in age, have intermediate volumes of Kenyon cells and neuropil. These observations could result from absolute ageing, but further experiments, carried out on artificial colonies comprising a single age cohort of 1-day-old bees, where worker bees start foraging as early as 4 days old, showed that precocious foragers had similar mushroom bodies as normal foragers, and that nurses were again intermediate. This suggests that behavior influences brain organization, which in turn certainly influences under what conditions tasks are performed. Therefore, ageing alone cannot explain Withers *et al.*'s (1993) observations. Calderone and Page (1996) showed that deprived bees (raised in isolation in wire cages with a queen) exhibit precocious foraging, suggesting that the lack of certain stimuli may influence the rate of behavioral ontogeny [a possibility that Calderone and Page (1996) did not rule out; see also Huang and Robinson (1992)]. More generally, relative age (i.e., age relative to the rest of the colony) is often a more relevant parameter than absolute age (Lenoir, 1979; Jaisson *et al.*, 1988; Calabi, 1988; Van der Blom, 1993; Sendova-Franks and Franks, 1994), which means that stimuli provided by the environment and other colony members are likely to play an important role in shaping behavioral ontogeny. These studies suggest that individual experience shapes behavioral ontogeny, and that response thresholds may be dynamic, rather than static. But whether behavior is a cause or an effect of ageing remains an unsolved question.

As emphasized by Sendova-Franks and Franks (1993, 1994), the FFW model or threshold models can readily be supplemented with learning or reinforcement,

leading to stronger specialization and, under the appropriate conditions, stronger patterns of temporal polyethism: ‘ants become increasingly entrained on certain tasks they practice, and seek out such tasks in preference to others’ (Sendova-Franks and Franks, 1993), leading to the phenomenon of strong ‘task fixation’ (Wilson, 1976). Theraulaz *et al.* (1991) developed a model of regulation of division of labor combined with hierarchical differentiation based on variable thresholds. In their model, a threshold is lowered when the corresponding task is performed, and increased when the corresponding task is not performed [see also Deneubourg *et al.* (1987) and Plowright and Plowright (1988)]. But, although their model is able to generate sociogenesis, it is still necessary to compare its behavior with experiments and to determine what it can explain and what it cannot explain.

There are other limitations inherent to the model presented in this paper: it does not really take into account complex networks of interactions among individuals, it assumes a single way of getting information about a given task or about different tasks, and does not deal accurately with spatial heterogeneities. It is in a sense a mean-field model. But all these limitations can be overcome in future works, while retaining the essence of the concept of response threshold.

Finally, our study has been aimed at clarifying the mechanisms underlying the regulation of division of labor in social insects. We did not discuss the adaptive significance of such patterns. We believe, however, that understanding the mechanisms that allow social insects to perform complex tasks collectively, is a necessary step towards understanding the evolution of social behavior (Mangel, 1995; Bonabeau *et al.*, 1997).

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