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Quantitative study of the fixed threshold model for the regulation of division of labour in insect societies

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SUMMARY

A simple model of regulation of division of labour in insect societies is introduced and studied. Individuals are assumed to respond to task-related stimuli with response thresholds. When the intensity of a particular stimulus exceeds an individual's response threshold, the individual engages in task performance with high probability, and successful task performance reduces the intensity of the stimulus. If individuals belonging to different (physical or behavioural) castes have different response thresholds, and if thresholds are assumed to remain fixed over the timescales of experiments, this model can account for some observations on ant species of *Pheidole* (Wilson 1984).

1. INTRODUCTION

Division of labour is an important and widespread feature of colonial life in many species of social insects (for a review, see Robinson 1992). One of the most striking aspects of division of labour is plasticity, a property achieved through the workers' behavioural flexibility: the ratios of workers performing the different tasks that maintain the colony's viability and reproductive success can vary (i.e. workers switch tasks) in response to internal perturbations or external challenges. An important question is to understand how this flexibility is implemented at the level of individual workers, which certainly do not possess any global representation of the colony's needs. This problem can be divided into two parts: (i) how do workers find or gather the information necessary to decide whether or not they switch tasks or engage in task performance; (ii) how do they actually decide what to do, once they have the information?

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 labour 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 then assume that each insect encounters all stimuli with equal probability within some period of time, and can in principle respond to these stimuli. For simplicity, we neglect the fact that doing a given task may promote contacts with specific stimuli, and prevent other stimuli from being encountered. Let us give a simple example: the task can be larval feeding, and the associated stimulus 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; Pacala et al. 1996), nest 'patrolling' (Lindauer 1952), or more or less random exposure to task-related stimuli).

The focus of the present paper is the second question. A simple model (Calabi 1988; Robinson 1987a, b, 1992), that has been used informally by several authors (that is, without reference to any theoretical basis, quantitative considerations, or accurate results), is the fixed threshold model (FTM): in this model, it is assumed that individuals are charaterized by (genetically determined) fixed response thresholds to the various stimuli. Viewed from this perspective, castes may correspond to possible physical differences, but also to innate differences in response thresholds without any visible physical difference. When individuals performing a given task are withdrawn (they have low response thresholds with respect to stimuli related to this task), the associated demand increases and so 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; the increase of stimulus intensity beyond

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threshold has the effect of stimulating these individuals into performing the task. Note that differences in response thresholds may either reflect actual differences in behavioural responses, or differences in the way task-related stimuli are perceived.

Let us briefly discuss the experimental basis of the model. Several experiments support the idea of thresholds. Robinson (1987a, 1992) showed the existence of hormonally regulated behavioural response thresholds to alarm pheromones in honey bees (*Apis mellifera*). Treatment of young worker honey bees with a juvenile hormone analogue increases their sensitivity to alarm pheromones, which play a role in nest defense. Robinson & Page (1988; Page & Robinson 1991) have shown that honey bee workers belonging to different patrilines 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 ten workers guarding the hive's entrance: workers of patriline B have a higher response threshold to perform this task. Finally, a series of experiments by Detrain & Pasteels (1991, 1992) clearly indicate the existence of differential response thresholds in the ant *Pheidole pallidula* in at least two activities, foraging and nest defence. The intensity of behavioural 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 defence) required of induce the effective recruitment of majors is greater than for minors for both tasks, suggesting that majors have higher response thresholds.

The aim of this paper is to show with quantitative simulations that the FTM can account for some experimental observations, particularly those done by Wilson (1984) on several (dimorphic) species of *Pheidole*. Wilson artificially reduced the minor:major ratio to below 1:1 and observed a change in the rate of activity within 1 h of the ratio change: for small ratios, majors engage in tasks usually performed by minors and efficiently replace the missing minors. To explain this result, Wilson (1985) invoked between-caste aversion, that is, active avoidance of minors by majors in the vicinity of task-related stimuli, but this explanation has never been really confirmed. If the rate of activity of majors is plotted as a function of the fraction of majors in the colony, the obtained curve has characteristic features which can be reproduced by the FTM. This shows explicitly that such a model can constitute the basic mechanism for a theory of the regulation of division of labour in insect societies. However, some aspects of division of labour, including age polyethism, require variable thresholds adjusted by reinforcement (or learning) processes. Such learning processes may result in decreasing response thresholds and increasing efficiency in task performance (Theraulaz *et al.* 1991; see also Deneubourg *et al.* 1987). Finally, whereas the focus of many studies has been the adaptive significance of the various features of division of labour, we believe that it is both worthwhile and important to understand proximate mechanisms underlying evolutionary arguments (Mangel 1995).

2. FIXED THRESHOLD MODEL WITH ONE TASK AND TWO DISTINCT CASTES

Assume that one task only has to be performed. 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 assume for simplicity that demand increases at a fixed rate per unit time. In this section, we consider the case where there are two castes, characterized by their response thresholds to the demand. Because the timescales that we intend to simulate are relatively short (for example, Wilson (1984) reports that *Pheidole pubiventris* majors begin to care for brood, a task they do not usually perform, 1 h after minors have been withdrawn), it can be assumed that thresholds are fixed: castes can therefore either reflect worker polymorphism (physical castes) or age polyethism (age castes), or simply groups of individuals with different behaviours, although the word 'caste' is usually not used to describe this latter case. In what follows, we shall use mostly the vocabulary associated with physical castes, but results can in principle be applied to all three cases.

Let X be the state of the individual ($X = 0$ corresponds to inactivity, $X = 1$ corresponds to performing the task), and θ_i the response threshold of caste i. An inactive individual belonging to caste i ($i = 1, 2$) starts performing the task with a probability P_i per unit time:

$$P_i(X = 0 \rightarrow X = 1) = \frac{s^2}{s^2 + \theta_i^2}, \tag{1}$$

As can be seen, the probability that an individual will perform a task depends on s, 'the magnitude of the task, that affects the probability of being exposed to it', and on θ_i, the probability of responding to task-related stimuli, given exposure (Robinson 1992). Figure 1 shows response curves corresponding to expression (1) for 'minors' and 'majors', where it is assumed that 'majors' have a greater response threshold. The choice of the detailed nonlinear functional form (1) is rather arbitray, because any threshold function is expected to generate qualitatively similar results.

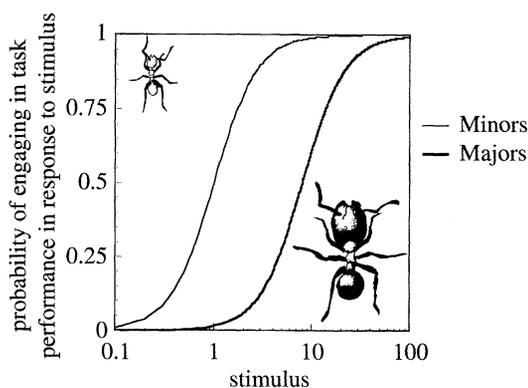An active individual of caste i ($i = 1, 2$) gives up task

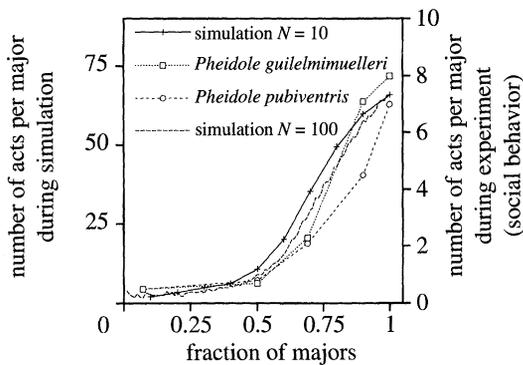Figure 1. Illustration of the notion of response curves with different thresholds for minors and majors.

Figure 2. Comparison between results of simulations ($N = 10$ and 100, $\theta_1 = 8$, $\theta_2 = 1$, $a = 3$, $d = 1$, $p = 0.2$) and experimental results obtained by Wilson (1984), who measured the number of acts of social behaviour per major for two species of *Pheidole*: *P. guilelmimuelleri* and *P. pubiventris* as a function of the fraction of majors in the colony. Simulation results are independent of the chosen initial conditions.
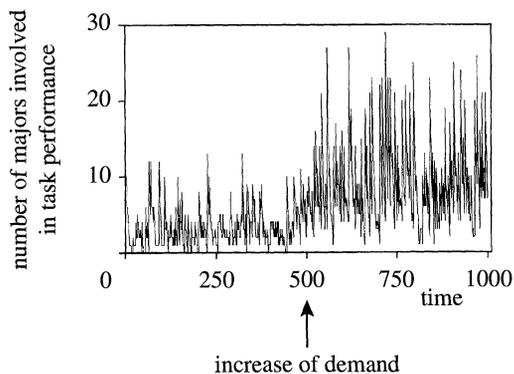

Figure 3. Time evolution (in simulation steps) of the number of majors engaged in task performance when the fraction of majors is equal to 0.2, and when the rate of increase of the demand associated with the task is suddenly multiplied by 2 at $t = 500$ ($N = 100$, $\theta_1 = 8$, $\theta_2 = 1$, $a = 3$, $d = 1$, $p = 0.2$).

performance and becomes inactive with probability p per unit time (that we take identical for both castes):

$$P_i(X = 1 \rightarrow X = 0) = p. \tag{2}$$

p can be found experimentally, as $1/p$ is the average time spent by an individual in task performance before giving up this task. It is assumed that p is fixed, and independent of stimulus. Therefore, individuals involved in task performance spend $1/p$ time units working even if their work is no longer necessary: such a behaviour has been reported in several cases (e.g. building behaviour; see Deneubourg & Franks 1995). Finally, individuals give-up task performance after $1/p$, but may become engaged again immediatly if stimulus is still large.

Variations in stimulus intensity are caused by: (i) task performance, which reduces stimulus intensity; and (ii) the natural increase of demand irrespective of whether or not the task is performed. The resulting equation for the evolution of stimulus intensity s is therefore (in discrete time):

$$s(t+1) = s(t) + \delta - \frac{\alpha}{N}(N_1 + N_2) \tag{3}$$

where N_i is the number of individuals belonging to caste i that perform the task, N is the total number of potentially active individuals in the colony, δ is the increase in stimulus intensity per unit time, and α is a scale factor measuring the efficiency of task performance (we assume here identical efficiencies in task performance for individuals belonging to caste 1 and caste 2; it is further assumed that efficiencies do not vary significantly, a plausible assumption provided the timescales of experiments are sufficiently short, whereas learning may take place over longer timescales). There is an additional assumption in this equation: the amount of work performed by active individuals is scaled by N to reflect the intuitive idea that the demand is an increasing function of N, that we take linear here. To make contact with experiments (Wilson 1984), this scaling term corresponds to the idea that brood should be divided by 2 when colony size is divided by 2: in other words, colony requirements scale (more or less) linearly with colony size; from the presence of the scaling term, we expect results to be largely independent of colony size. In what follows, we shall call members of caste 1 'majors' and members of caste 2 'minors'. This choice is not arbitrary: although the present model is too simplistic, it is not disconnected from biological reality, and majors often (but not always) have a lower probability of becoming active than minors.

Figure 2 shows a comparison between simulation results with $N = 10$ and 100 individuals (average total time spent per major in task performance during the simulation, expressed in (individual × time step) as a function of the fraction of majors in the colony) and the same quantities obtained in experiments reported in Wilson (1984) for *Pheidole guilelmimuelleri* and *Pheidole pubiventris* (where the task is 'social behaviour'): the qualitative overlap between these curves is striking. The number of acts per individual undergoes an rapid change when the fraction of majors exceeds some 'critical' value (around 0.4 in figure 2). Given the number of acts per individual observed in these simulations, one time step should roughly correspond to 10 min (see, for example, Wilson 1984); $p = 0.2$ step^{-1} means that the average time spent in task performance before task switching is of the order of $T = 1/p = 50$ min. All other parameter values have been adjusted so as to prevent the stimulus from diverging or from becoming much smaller than the thresholds. Figure 3 shows that majors can respond to a challenge by becoming more involved in task performance when there is a sudden increase in the rate of increase of the demand associated with the task (δ has been multiplied by 2 at $t = 500$ in figure 3): most minors are already involved in task performance before this change, so that the involvment of majors is required to maintain the demand at a low enough level. Note that this model can also very easily account for the experimental observation that majors switch back to their original tasks once minors are put back into the colony. Finally, figure 4 shows how curves are modified when the ratio $z = \theta_1^2/\theta_2^2$ increases: the transition becomes more abrupt, and the point at which this transition takes place decreases and seems to converge towards a limit
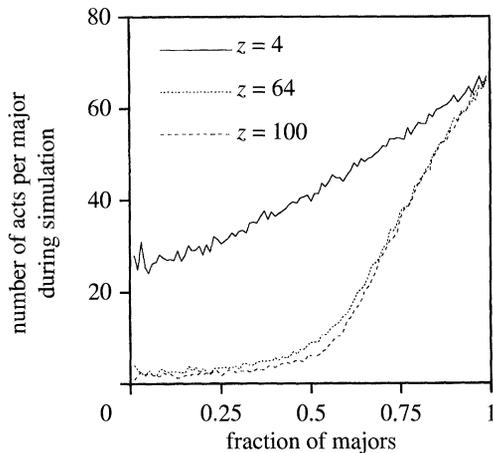
Figure 4. Number of acts per major during simulation as a function of the fraction of majors in the population for different values of $z = \theta_1^2/\theta_2^2$ ($N = 100$, $\theta_1 = 2, 3, 5, 8, 10$, $\theta_2 = 1$, $a = 3$, $d = 1$, $p = 0.2$).

(around 0.5 in figure 4). When z is close to 1, the proportion of majors engaged in task performance starts from a larger value (around 30 acts per major) than when z is large. All these results can be understood qualitatively by a simple analysis of the deterministic equations associated with the stochastic model expressed in equations (1), (2) and (3).

3. FIXED THRESHOLD MODEL WITH TWO TASKS AND TWO DISTINCT CASTES

We now assume that there are two tasks to be performed by individuals belonging to two distinct castes. The previous model can easily be generalized, but two cases now appear: (i) minors are specialized in both tasks (i.e. have lower thresholds than majors for both tasks), but thresholds may be different; and (ii) minors are specialized in one task and majors in the other task (then the distinction between minors and majors becomes somewhat arbitrary in the model).

Generalization of the previous section's variables is straightforward: $X = 0$ corresponds to inactivity, $X = j$ ($j = 1, 2$) to performing task j. N_{ij} is the number of individuals belonging to caste i that perform task j, θ_{ij} is the response threshold of caste i to the stimulus associated with task j, and $s_j(t)$, δ_j and α_j are parameters associated with task j. The generalization of equations (1), (2) and (3) is easy and does not require explicit description. We simply assume that $P_i(X = 1, 2 \to X = 0) = p$ and that task switching requires first a transition to the inactive state.

(a) Minors have lower response thresholds for both tasks

When minors have lower response thresholds to both tasks, curves similar to those found in §2 are obtained. Figure 5 shows the number of acts per major for both tasks, with different thresholds and efficiencies. These results are compared with the experimental curves of Wilson (1984) who measured the same quantities for two tasks (social behaviour and self-grooming) in *Pheidole megacephala*. One curve exhibits a rapid change
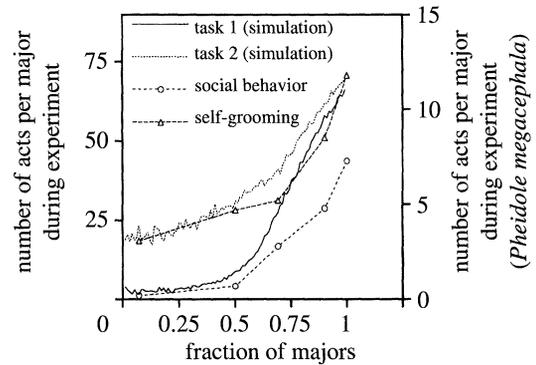

Figure 5. Number of acts per major for two tasks during simulation as a function of the fraction of majors in the population. Minors have lower response thresholds in both cases ($N = 100$, $\theta_{11} = 5$, $\theta_{12} = 10$, $\theta_{21} = 1$, $\theta_{22} = 1$, $a_1 = 1$, $a_2 = 3$, $d_1 = d_2 = 1$, $p_1 = p_2 = 0.2$). Comparison between results of simulation and experimental results obtained by Wilson (1984), who measured the number of acts of social behaviour and self-grooming per major in *Pheidole megacephala* as a function of the fraction of majors in the colony.
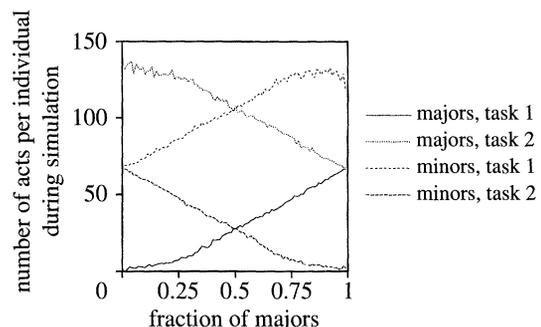

Figure 6. Number of acts per major and per minor for two tasks during simulation as a function of the fraction of majors in the population. Minors have a lower response threshold to stimuli associated with task 1 than majors, and larger threshold than majors in the case of task 2 ($N = 100$, $\theta_{11} = 8$, $\theta_{12} = 1$, $\theta_{21} = 1$, $\theta_{22} = 8$, $a_1 = a_2 = 3$, $d_1 = d_2 = 1$, $p_1 = p_2 = 0.2$).

at a lower value of the fraction of majors, whereas the second one shows a smoother change at a somewhat larger value. This result can be simply understood from results of the previous section showing (figure 4) how the proportion of majors engaged in task performance vary with the threshold ratio z: if task 1 corresponds to a greater value of z than task 2, then the curve associated with task 1 undergoes a more abrupt change at a lower value than task 2.

(b) Each caste is specialized in one task

When a caste is specialized in one of the two tasks, and the other caste in the other task, behavioural flexibility is observed on both sides: 'majors' can replace 'minors', and vice versa, as can be seen on the curves of figure 6. As minors cannot always be induced to perform major-specific tasks (while majors can always be induced to perform tasks usually performed by minors) (see, for example, Wilson 1984), this example may not apply to the case of physical castes, but can certainly apply to less rigid castes, or to intra-

caste behavioural flexibility. One can model such an observation by assuming that minors have very large (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.

4. DISCUSSION AND FUTURE DIRECTIONS

We have shown that the FTM may be able to account, at least partly, for the behavioural flexibility observed in ants, when manipulations such as those reported by Wilson (1984) on several species of *Pheidole* are done. Reproducing these experimental results with the FTM did not require the notion of between-caste aversion (Wilson 1985). The same type of experiments done on other species of ants would help support the threshold model. It would be especially interesting, but certainly more difficult, to study the behaviour of monomorphic species under the same experimental conditions. More direct experiments, evidencing differential response thresholds in different groups of workers as a stimulus varies quantitatively (see, for example, Detrain & Pasteels 1991, 1992) would also be extremely useful.

The FTM applies to cases involving sufficiently short timescales and cannot account for age polyethism, or for simple observations showing that the probability of behavioural reversion from task B to task A (e.g. from foraging to nursing in honey bees (Seeley 1982)) is a decreasing function of the time spent performing task B (e.g. the number of days spent foraging), which suggests that some kind of learning or habituation occurs (physiological ageing may also play a role). Theraulaz *et al.* (1991) developed a model of regulation of division of labour combined with hierarchical differentiation based on variable thresholds (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) to describe the emergence of a flexible social organization. Such a model can serve as a basis to understand stable or strong age polyethism, if it is combined, for example, with the foraging-for-work algorithm (Tofts & Franks 1994).

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