



## Emergent Polyethism as a Consequence of Increased Colony Size in Insect Societies

JACQUES GAUTRAIS<sup>†</sup>, GUY THERAULAZ<sup>†\*</sup>, JEAN-LOUIS DENEUBOURG<sup>‡</sup>  
AND CARL ANDERSON<sup>§</sup>

<sup>†</sup>*Laboratoire d'Ethologie et Cognition Animale, CNRS-ERS 2382, Université Paul Sabatier, 118 route de Narbonne, 31062 Toulouse Cédex, France* <sup>‡</sup>*Center for Nonlinear Phenomena and Complex Systems, Université Libre de Bruxelles, C.P. 231, Campus Plaine, B-1050 Brussels, Belgium* and <sup>§</sup>*LS Biologie I, Universität Regensburg, Universitätsstrasse 31, D-93040 Regensburg, Germany*

(Received on 11 July 2001, Accepted in revised form on 27 November 2001)

A threshold reinforcement model in insect societies is explored over a range of colony sizes and levels of task demand to examine their effects upon worker polyethism. We find that increasing colony size while keeping the demand proportional to the colony size causes an increase in the differentiation among individuals in their activity levels, thus explaining the occurrence of elitism (individuals that do a disproportionately large proportion of work) in insect societies. Similar results were obtained when the overall work demand is increased while keeping the colony size constant. Our model can reproduce a whole suite of distributions of the activity levels among colony members that have been found in empirical studies. When there are two tasks, we demonstrate that increasing demand and colony size generates highly specialized individuals, but without invoking any strict assumptions about spatial organization of work or any inherent abilities of individuals to tackle different tasks. Importantly, such specialization only occurs above a critical colony size such that smaller colonies contain a set of undifferentiated equally inactive individuals while larger colonies contain both active specialists and inactive generalists, as has been found in empirical studies and is predicted from other theoretical considerations.

© 2002 Elsevier Science Ltd. All rights reserved.

### 1. Introduction

In social systems, such as insect societies, increased colony size is associated with profound and wide-ranging changes in “internal” organization and operation (Bourke, 1999; Anderson & McShea, 2001). For instance, larger colony size is correlated with increased homeostasis, cooperative activity, spatial organization of work, and caste polymorphism to name but a few “social correlates” (Wilson, 1971; Bourke,

1999; Anderson & McShea, 2001). Perhaps one of the most important correlations is that of increased behavioural specialization: large colony size favours the specialization of workers upon certain tasks, thereby increasing colony productivity (Oster & Wilson, 1978; Jeanne, 1991; Jeanne & Nordheim, 1996; Karsai & Wenzel, 1998).

The benefits of worker specialization in the context of manufacturing were noted more than two hundred years ago (Smith, 1776) and are as true for an insect society as for any company or factory. When individuals improve their

\*Author to whom correspondence should be addressed.  
E-mail: [theraula@cict.fr](mailto:theraula@cict.fr)

performance through repetition of a task (“performance efficiency” Seeley, 1982; Jeanne, 1986a), specialization conveys benefits at the colony level. Also, as work may be concentrated spatially in large colonies, specialization upon a certain task may reduce travel time between tasks (Seeley, 1982). Inherent differences in abilities to perform certain tasks arising from polymorphism will also favour specialization (Anderson & McShea, 2001). Given therefore, these ultimate explanations for the importance of such specialization, it is surprising how little is known of the proximate mechanisms by which such worker specialization is generated. In this study, we use a simple model to show that a single behavioural mechanism known to occur in insect societies—stimulus–response thresholds—gives rise to autonomic behavioural specialization when just a single parameter, colony size, is increased. Not only do our results demonstrate worker specialization but they also generate the elitism (individuals that perform a disproportionately large percentage of the work) and increased group-level performance observed in empirical studies (Chen, 1937a, b; Meudec, 1973; Abraham, 1980, Lenoir & Ataya, 1983; see also Robson & Traniello, 1999 for a review).

The concept of a response threshold is simple and has been discussed previously (Bonabeau *et al.*, 1996, 1998, 1999; Theraulaz *et al.*, 1998; Beshers *et al.*, 1999; Bonabeau & Theraulaz, 1999): an individual has some internal threshold to the level of demand for a certain task. If the worker encounters this task yet the task stimulus is lower than the individual’s threshold, then there is only a small, even zero, probability of her tackling the task. If, however, the task stimulus exceeds her threshold then she responds to the task with some higher probability (which may be fixed or a function of threshold and task stimulus levels) and may begin work. Response thresholds are likely (and are assumed) to be task specific and that an individual may have different thresholds for different tasks. As a worker (or a set of workers) tackles a task in the nest or on a foraging trail, the task stimulus may decline (depending upon the increase or regeneration rate of task demand) so that the stimulus may fall below an individual’s threshold and she stops work. This generates a very simple, yet

powerful, feedback system that can assign the appropriate numbers of workers to different tasks. There is ample evidence of such threshold responses in insect societies (for overviews see Robinson, 1992; Bonabeau & Theraulaz, 1999; Beshers & Fewell, 2001).

The above scenario comes under the class of “fixed response thresholds” (Bonabeau *et al.*, 1996, 1998) as a worker’s threshold does not change over time. An extension of this concept is that of reinforced thresholds that change over time (Theraulaz *et al.*, 1998), in particular the more often that a worker tackles a certain task. That is, workers reduce their threshold for task  $X$  each time they tackle task  $X$ . This will have the effect of making an individual more likely to tackle the same task again when it encounters the stimulus. This idea, first introduced by Plowright & Plowright (1988; see also Deneubourg *et al.*, 1987), introduces a positive feedback component—termed “learning”—that reinforces an individual’s probability to work on a certain task. In addition, there may be a “forgetting” component, in that thresholds for other tasks may increase over time the longer a worker *does not* tackle the task. Empirical evidence exists in favour of the existence of threshold reinforcement in insect societies (Deneubourg *et al.*, 1987; Theraulaz *et al.*, 1991; O’Donnell, 1998; Weidenmüller, 2001).

It is this concept of response threshold reinforcement (Theraulaz *et al.*, 1998) that is the basis of our study and which automatically generates specialization among workers, but as we show for the first time only when colony size is sufficiently large, thus matching theoretical predictions (Bourke, 1999; Anderson & McShea, 2001) and empirical findings (e.g. Jeanne, 1986b, 1991; Schatz, 1997; Karsai & Wenzel, 1998, 2000) in insect societies.

## 2. The Model

Our model makes use of Monte Carlo simulation run in discrete time. We consider two scenarios: first, a set of individuals encountering a single task (i.e. the number of tasks,  $m$ , is 1). Second, we consider two unrelated tasks ( $m=2$ ). The notation and concepts largely follow Theraulaz *et al.* (1998).

## 2.1. TASKS

During a time step, each individual may be engaged in only one task, or is free, i.e. not tackling a task. Every active individual works at the same rate:  $\alpha$  units of work per time step. Each task  $T_j$  is defined by the level of its associated stimulus,  $S_j$ , which spontaneously increases by  $\sigma_j$  per time step. However, at the same time, it is decreased by the number of individuals ( $E_j$ ) working upon it (multiplied by their work effort,  $\alpha$ ). Thus, the dynamics are described by  $dS_j = \sigma_j - E_j \cdot \alpha \quad \forall j = 1, 2, \dots, m$ . Under extreme conditions, such as high  $\alpha$ , low  $\sigma_j$ , or small  $p$  (in short, if  $dS_j > S_j$  during a time step), it is possible that  $S_j$  may become negative, in which case it is set to zero ( $S_j = \max(0, S_j)$ ). However, under the parameter settings explored in this model, this does not occur.

## 2.2. INDIVIDUALS

Each individual  $i$  has a threshold  $\theta_{i,j}$  for task  $T_j$ . When free, an individual may commence working upon a task depending upon its threshold value(s) and the stimulus(-li) levels. We assume here that each task is encountered with equal probability, i.e. that there is no spatial heterogeneity in the distribution of tasks and their associated stimuli. When encountering task  $T_j$ , individual  $i$  engages in  $T_j$  with probability:

$$P(i \text{ engages in } T_j | T_j \text{ encountered}) = \frac{S_j^2}{S_j^2 + \theta_{i,j}^2}. \quad (1)$$

Hence, given  $M$  tasks encountered with equal probabilities,

$$P(i \text{ engages in } T_j) = \frac{1}{m} \frac{S_j^2}{S_j^2 + \theta_{i,j}^2}. \quad (2)$$

Each time step that an active individual is engaged, it decreases the stimulus by  $\alpha$  and may quit the task spontaneously with probability  $p$  per time step. Thus, on average, an individual that commences tackling a task works on it continuously for  $1/p$  time steps. When quitting a task, an individual has a latency period of one time step before it may start work again. Each individual's thresholds are

initialized to zero, thus, initially, making them identical generalists keen to work.

## 2.3. THRESHOLD REINFORCEMENT AND FORGETTING

Positive reinforcement—that the more an individual works on a task, the lower is its threshold for that task—is implemented in the following way: each time step an individual works on  $T_m$ , her threshold is decreased by  $\xi$  (“learning” parameter). Each time step an individual is not working on a task (whether working on a different task or free), her threshold is increased by  $\phi$  (“forgetting” parameter). That is, for individual  $i$  engaged in task  $j$ :  $d\theta_{i,j} = -\xi$  and  $d\theta_{i,j \neq j'} = \phi$ .  $\theta_{i,j} = \min(\max(0, \theta_{i,j}), \theta_j \max) \forall i, j$ .

## 2.4. STIMULUS REGENERATION

For ease of comparison of different colony sizes, stimulus regeneration,  $\sigma_j$ , is defined as a function of colony capabilities. For  $N$  individuals and  $m$  tasks, the maximal amount of work,  $W_{max}$ , the colony can perform in one time step is

$$W_{max} = \frac{N}{m} \frac{1}{1+p} \alpha. \quad (3)$$

As we wish to keep the per capita stimulus regeneration rate constant, we also define a parameter,  $0 < D \leq 1$ , as the proportion of total potential effort the colony has to perform in order to complete the task; for instance, when  $D = 1$ , the colony must work at full capacity.

Consequently, we term  $D$  the “demand” the colony faces. For  $D < 1$ , the dynamics of worker allocations will always lead to enough and just enough (in mean) task force to tackle the task. Hence,  $D$  may be viewed as also the proportion of the colony devoted to work at the stationary state. This facilitates comparison of colonies of different sizes but who are working at the same relative rate, e.g. 50% ( $D = 0.5$ ). The absolute work rate thus is proportional to colony size. Hence, from eqn (3),

$$\sigma_j = D \frac{N}{m} \frac{1}{1+p} \alpha. \quad (4)$$

The stimulus regeneration values,  $\sigma_j$ , are casually independent of each other. That is, a

change in the value of one task stimulus does not directly affect the value of another task stimulus. This could occur for example if task partitioning were involved (reviewed in Ratnieks & Anderson, 1999), such that the output of one task, e.g. forage collection, was the stimulus for a subsequent task, e.g. transportation of collected material. The only relationship between the task stimuli relates to the relative proportion of individuals tackling each task. The stimuli are initialized to 0. Hence, there is a small delay before the stimuli are large enough to stimulate workers to tackle tasks.

### 3. Statistical Measures

#### 3.1. ACTIVITY LEVEL

To investigate elitism among individuals we require a statistical measure to distinguish between those that work relatively little (inactives) and those that work relatively hard (actives, reviewed in Robson & Traniello, 1999). We use activity level, i.e. the proportion of the simulation spent working for individual  $i$ :

$$W_i = \sum_{j=1}^m W_{i,j}/t, \quad (5)$$

where  $W_{i,j}$  is the number of time steps individual  $i$  worked on task  $j$  over some time period  $t$ . In all cases,  $t$  is taken as the first 20 000 time steps of the simulation. Although this includes the period of initial differentiation of individuals from starting conditions ( $i, j = 0$  at time 0  $\forall i, j$ ), after just 100 steps or so the individuals had already become well differentiated, with their thresholds a good predictor of their final roles.

#### 3.2. WORKER SPECIALIZATION

When there are two (or more) tasks, we also require a metric to quantify worker specialization, meaning the partitioning of an individual's work effort among the different tasks. However, the proportions of activity (or related metrics, such as entropy used by O'Donnell & Jeanne, 1990) spent on each task will not distinguish between an individual that spends half her time on task 1 and then switches to task 2 for the remainder of the simulation vs. an individual

that repeatedly alternates between two tasks. Intuitively, the first individual seems more of a specialist than the latter.

During a simulation, a typical worker tackles a task, quits (for one or more time steps), starts working on a task, quits and so on. With numbers representing the identity of different tasks tackled, we obtain a sequence such as 211211112. Let  $C_i$  be, for individual  $i$ , the number of transitions to a different task (four in this case) divided by the number of transitions from one period of work to another (eight in this case), so here  $C_i = 0.5$ . For two tasks, let  $F_i = 1 - 2C_i$ . Thus, when a worker is highly specialized and so continues to work on the same task repeatedly, a sequence such as 11111111 is obtained, giving  $C_i = 0$  and  $F_i = 1$ . (At the other extreme, when a worker alternates repeatedly between tasks, e.g. 12121212,  $C_i = 1$  and  $F_i = -1$ . However, with the parameter values in our simulations, and also because tasks 1 and 2 are independent, negative values of  $F_i$  are not obtained.) When a worker switches among tasks randomly,  $C_i = \frac{1}{2}$  and  $F_i = 0$ . Thus, we use  $F_i$  as our metric of specialization which effectively varies from 0 (random and therefore generalist workers) to 1 (full specialists).

### 4. Results

Figure 1 shows the differentiation among individuals in terms of their activity level ( $W_i$ , as defined in Section 3) for three levels of demand (with  $m = 1$ ). When demand is low [ $D = 0.2$ , Fig. 1(a)], all workers have a low activity level, as would be expected, and there is little or no differentiation among individuals. That is, the results appear as a single continuous ridge. However, at the largest colony sizes, we observe a small amount of elitism in that a few individuals (10%) are working considerably harder than the others (activity levels=0.8–0.9). This effect is much more pronounced when demand is higher. Figure 1(b) shows the same scenario when  $D = 0.5$ . Here, we can see greater differentiation among individuals. At low colony sizes (<30), all individuals have activity levels between 0.3 and 0.5. At larger colony sizes, however, there is distinct differentiation, i.e. two separate ridges, in that one set of individuals

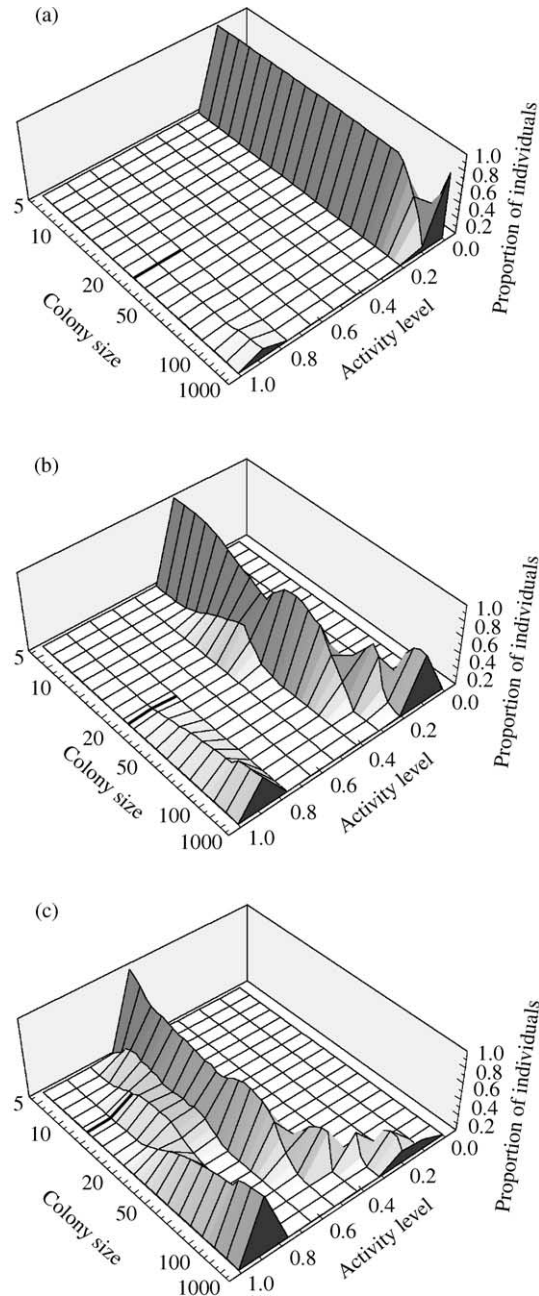


FIG. 1. The differentiation in activity level (proportion of time steps active during a simulation) among individuals with increasing colony size for three levels of demand: (a)  $D = 0.2$ , (b)  $D = 0.5$  and (c)  $D = 0.8$ . In all cases,  $\alpha = 0.1$ ,  $p = 0.2$ ,  $m = 1$ ,  $\xi = 4$ , and  $\varphi = 10$  (see Section 2 for explanation). Black lines indicate the colony size at which at least one elite is observed. Note the non-regular scale on the colony size axis ( $N \in \{5, 6, \dots, 20, 25, \dots, 100, 200, \dots, 500, 1000\}$ ). Data are the average of 100 simulations.

works hard (leftmost ridge) while the remainder work at a decreasingly lower rate (curved rightmost ridge). At the largest colony sizes, we see an unmistakable differentiation with one set of largely inactive individuals with another set of hard-working elites. At the highest demand

considered [ $D = 0.8$ , Fig. 1(c)] this differentiation is both more pronounced and occurs at much lower colony sizes. Finally, the critical colony size in which at least one elite is observed are indicated in Fig. 1 as the thick black lines in the 0.8–1.0 columns; for the three increasing levels

of demand (with these parameter values), the colony sizes are 30, 25, and 13.

It is of course the positive feedback effects of the threshold reinforcement that drive this differentiation. However, these can only come into play, for some individuals (those that eventually become elites), with sufficiently high  $\sigma$  [which from eqn (4) is proportional to colony size and demand]. In large colonies and/or high demand, the relatively large rate of increase in stimulus produces a high probability of commencing work for some individuals at the start of the simulation. These individuals that start working, learn (i.e. reduce their thresholds, and hence are more likely to continue working in future time steps) and importantly, drive down the mean level of the stimulus (reducing the probability of other workers from starting) and damp the fluctuations of the stimulus, with the same effect. In small colonies, the low rate of increase of  $S$  provides little impetus to work, and so individuals mostly “forget” (thresholds increased) rather than learn, preventing specialization.

The distribution of activity levels among the workers in a colony ( $N=500$ ), in relation to the learning and forgetting parameters ( $\xi$  and  $\varphi$ , respectively) are explored in Fig. 2. Subfigures 2 I–IV are the set of activity levels,  $W_i$  ( $y$ -axis), in the 500 individuals ranked from highest to lowest (hence the  $x$ -axis is simply worker number). Thus, in Fig. 2 I, there is little difference in activity levels among individuals, whereas in Fig. 2 IV there is a set of around 100 individuals who work hard while the remaining 400 colony members are largely inactive. The  $\xi$  and  $\varphi$  values giving rise to these four illustrative activity level distributions (I–IV) are indicated on the lower part of Fig. 2. Contours on this lower subfigure join  $\{\xi, \varphi\}$  combinations that generate the same percentage of the colony (preferentially including the hardest-working individuals) who, together, conducted 50% of all the work. In other words, it quantifies how many individuals, (as a proportion of the colony) were responsible for half of all work output and thus the degree of elitism in the colony.

Under this measure, the degree of elitism is clearly highly dependent upon the learning and forgetting parameters (Fig. 2). When  $\varphi > \xi$ ,

essentially the region to the left of the 45% contour, we find very little differentiation among individuals (i.e. flat activity level distributions as in subfigure I). When  $\xi > \varphi$ , a reduction in  $\varphi$  causes an increase in elitism [i.e. lower percentage values and a shift towards ever more skewed distributions: Gaussian (subfigure II), exponential (III), and bimodal (IV)]. This is true of  $\xi$  too, until a steep “cliff face” is encountered in the bottom left-hand corner of the figure. A striking feature is the steep set of parallel contours, independent of  $\xi$ , when  $\varphi \approx 2.5$ . This indicates that very low forgetting rates (producing thresholds that tend to zero) fail to provide sufficient feedback to generate differentiation among individuals.

When there are two tasks, it becomes meaningful to talk about worker specialization, meaning that a worker preferentially tackles one task over the other(s). We would also argue that when there is a single task, elitism is a form of specialization too with individuals preferentially tackling the task rather than performing the other “activity”, resting. Figure 3 shows the distribution of specialization (as defined in Section 3) among individuals vs. colony size, for three levels of demand when there are two tasks. Similar results are obtained to those for activity levels (Fig. 1). At a low level of demand [ $D = 0.2$ , Fig. 3(a)] for virtually the whole range of colony size, individuals remain generalists, tackling the two tasks randomly. As demand increases [ $D = 0.5$ , Figure 3(b)] specialist individuals begin to appear at colony sizes greater than 30. With increasing colony size the proportion of highly specialized individuals increases at the expense of a declining ridge of generalists. As in Fig. 1, this effect is most pronounced with the highest level of demand [ $D = 0.8$ , Fig. 3(c)] in which there is a large increase in the proportion of specialists (curved leftmost ridge) with a decrease of generalists. Interestingly, the degree of specialization (meaning the position of the ridge) is at a lower specialization index at this level of demand than for  $D = 0.5$  [Fig. 3(c) vs. 3(b)]. This is likely because task stimuli remain relatively higher with higher demand such that a specialist for one task must sometimes work on the other, albeit temporarily, thus decreasing their overall specialization indices.

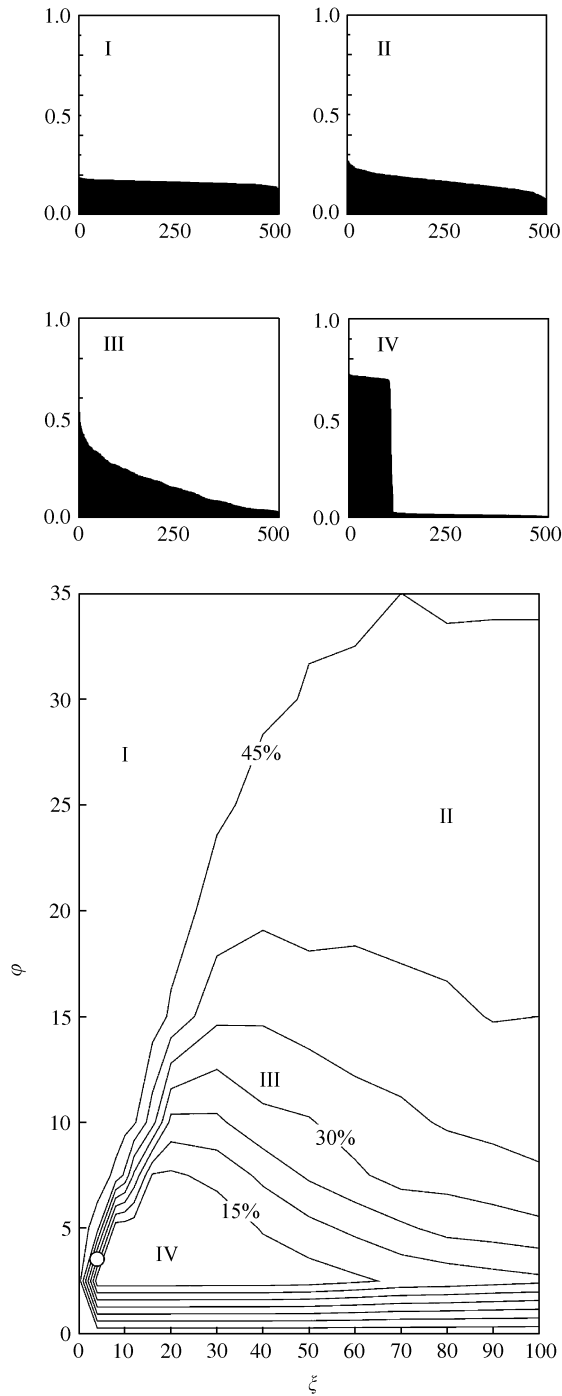


FIG. 2. The effect of the learning ( $\xi$ ) and forgetting ( $\varphi$ ) parameters upon the distribution of activity levels among individuals within a colony ( $m = 1$ ,  $D = 0.2$ ,  $N = 500$ ; other parameters as for Fig. 1). The upper subfigures, I–IV, are representative distributions of the activity levels,  $W_i$ , of the 500 colony members, ranked from highest to lowest. The  $\{\xi, \varphi\}$  combinations that gave rise to these four illustrative distributions are indicated on the lower subfigure (I:  $\{\xi = 10, \varphi = 27\}$ ; II:  $\{80, 24\}$ ; III:  $\{40, 12\}$ ; IV:  $\{20, 4\}$ ). Contours on this lower subfigure link  $\{\xi, \varphi\}$  combinations that generate the same proportion of the colony (preferentially including the hardest-working individuals) who, together, conducted 50% of all the work. Thus, if there is little difference in activity levels among individuals (e.g. subfigure I), this proportion is close to 0.5 whereas greater elitism (e.g. subfigure IV), meaning fewer doing a greater proportion of the work, will generate a smaller proportion. The white dot in the left-hand corner indicates the parameter settings ( $\xi = 4$ ,  $\varphi = 3.5$ ) used.

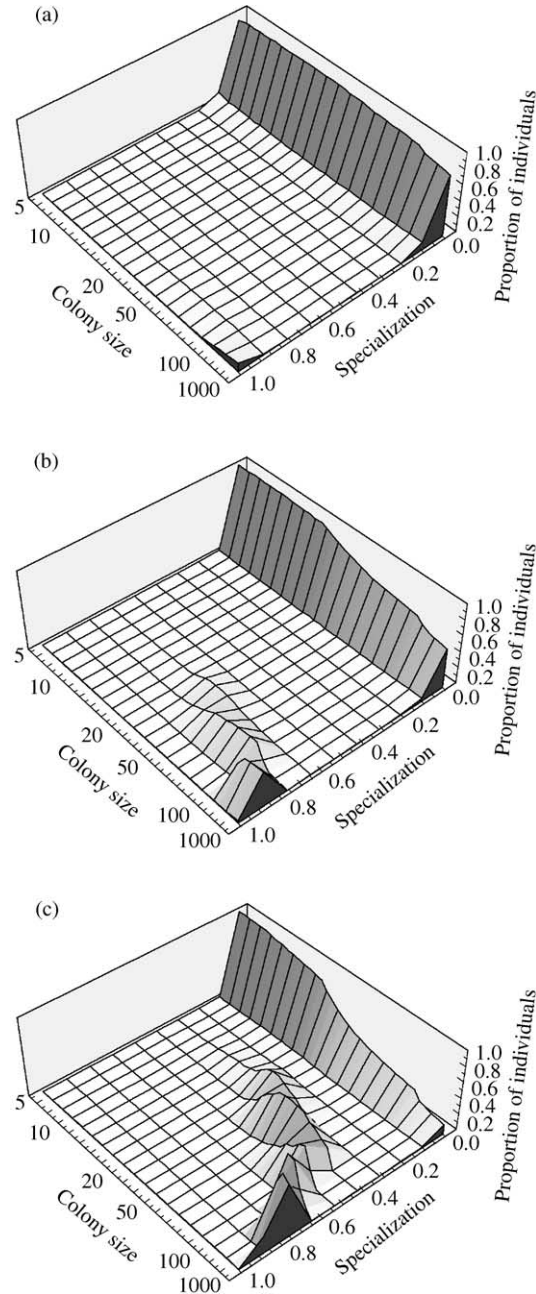


FIG. 3. Individual specialization indices (see Section 3) with increasing colony size for three levels of demand: (a)  $D = 0.2$ , (b)  $D = 0.5$  and (c)  $D = 0.8$ . Parameters are as for Fig. 1 except that  $M = 2$  and  $\varphi = 3.5$ . Both larger colony size,  $N$ , and higher work demand,  $D$ , generate a greater proportion of specialists in a colony.

The mechanisms driving specialization are similar to that described above for one task only ( $m=1$ ). Larger demand is a larger  $\sigma$ , thus generating a greater impetus to start work. Now, however, we have two stimuli and it is the magnitude and time-scale of the fluctuations of their difference ( $S_1 - S_2$ ) that is crucial. Figure 4 shows the time course of  $S_1 - S_2$  for

three colony sizes. It is clear that in small colonies [Fig. 4(a)] large absolute differences are sustained for longer periods than in large colonies. Thus, periods of high  $S_1 - S_2$  will break down any specialization that individuals may have for task 2 because they are more likely to tackle task 1 (and so learn) while forgetting task 2 (and vice versa for high  $S_2 - S_1$ ). In large



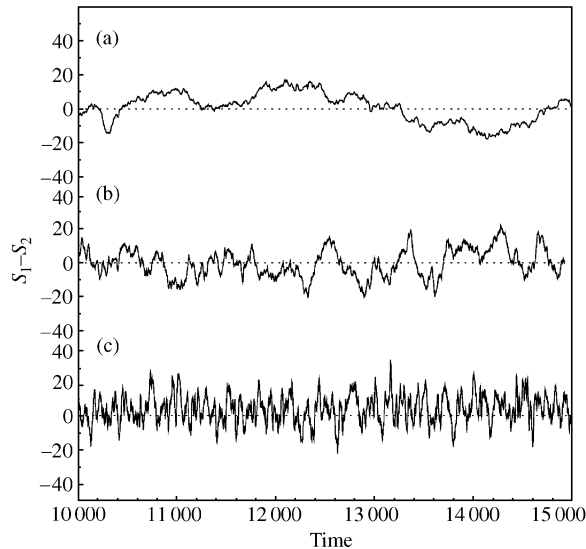


FIG. 4. The difference in stimulus levels ( $S_1 - S_2$ ) over time for three colony sizes: (a)  $N = 10$ , (b)  $N = 100$  and (c)  $N = 1000$ . Parameters are as for Fig. 3.

colonies [Fig. 4(c)] these fluctuations are far less sustained allowing individuals sufficient time working on the same task for the positive feedback of learning to take effect.

We should point out that, quantitatively, there is some sensitivity to initial conditions, e.g. the degree of specialization or the critical colony size at which specialization occurs. However, qualitatively, which is the thrust of our results, the relationships described above always hold true, e.g. that specialization is positively correlated with colony size. Such sensitivity will be explored in another study.

## 5. Discussion

Our model generates several important findings. First, we demonstrate how individuals may become differentiated in terms of their activity levels (Fig. 1), for which there is a wealth of empirical evidence (Chen, 1937a, b; Meudec, 1973; Abraham, 1980; Lenoir & Ataya, 1983; see also Robson & Traniello, 1999 for a review), but for which little is known of the generative proximate mechanisms. Our model clearly demonstrates that a single mechanism, threshold reinforcement, known to exist in insect societies (Deneubourg *et al.*, 1987; Theraulaz *et al.*, 1991; O'Donnell, 1998; Weidenmüller, 2001) can generate such differentiation as a function of colony size.

As can be seen in Fig. 2, the model gives rise to a whole suite of possible distributions of activity levels among colony members. Such a variety of profiles are indeed observed in empirical studies (e.g. Lenoir & Ataya, 1983; Retana & Cerda, 1991; Schatz, 1997; Jeanne, 1991; O'Donnell, 1998) but how they might be generated has not previously been explained. Our results could account why, for example, Retana & Cerda (1991, Fig. 4) found qualitatively different profiles (which closely match our subfigures 2 II and III) in different colonies of the same species but which, importantly, were of different sizes. Although there is good agreement with the empirical finding, we should acknowledge that we cannot rule out the fact that other mechanisms could be involved in different species.

Figure 3 clearly shows the increase in specialization of individuals with both increasing colony size and increasing demand. Because initial conditions set the individuals as generalists, the specialization observed here is solely an emergent phenomenon that cannot be explained by any individual genetic pre-disposition. Several empirical studies report a cohort of seemingly similar individuals specializing upon different tasks (e.g. seed specialization in Rissing, 1981; foraging vs. nursing in Agbogba, 1994). Such partitioning when there may be no inherent differences in abilities of individuals to tackle different tasks (e.g. in a monomorphic

species) can be explained under a threshold reinforcement paradigm without any need to invoke spatial segregation of tasks (Hart & Ratnieks, 2001a,b) or performance efficiency improvement (Seeley, 1982; Wehner *et al.*, 1983; Jeanne, 1986a). However, dedicated experiments will have to be conducted to fully test these ideas, and our results strongly suggest that this may be a productive avenue for future empirical research.

Importantly, differentiation in activity levels and specialization only occurs when colony size exceeds some critical value. In other words, we have a bifurcation phenomenon, and we find that the critical colony size is lower with increasing demand. This means that small colonies are expected to contain a set of undifferentiated equally active individuals while large colonies are predicted to contain both active specialists and inactive generalists. This is exactly what is found empirically (Traniello, 1978; Jeanne, 1991; Karsai & Wenzel, 1998, 2000) and theoretically (Bourke, 1999; Anderson & McShea, 2001) in terms of enhanced colony organization and operation. It should be stressed that our results have very wide-ranging implications because they are suggestive of adaptive emergent organizational changes at several levels: (1) within a colony as it grows from incipient to maturity (Beekman *et al.*, 2001), (2) among colonies within a species (with natural variation or ecological factors causing differences in colony size, see for instance, Beckers *et al.*, 1989), and (3) among species (Bourke, 1999; Anderson & McShea, 2001).

That a single mechanism can generate various patterns of division of labour among colony members when just a single (but important) variable, colony size, changes, indicates the capacity of self-organized processes (as we have demonstrated here) to economize on encoding rules (e.g. Camazine *et al.*, 2001). That is, different behavioural rules do not need to be encoded at the individual level for different colony stages, e.g. incipient vs. mature; a single mechanism is sufficient.

C. A. gratefully acknowledges support from a Philip Steinmetz Fellowship at the Santa Fe Institute in 1998 and a grant from the European Science Foundation's Theoretical Biology of Adaptation Program. This work was supported in part by a

grant from the GIS (Groupement d'Intérêt Scientifique) Sciences de la Cognition to G. T.

## REFERENCES

- ABRAHAM, M. (1980). Comportement individuel lors de déménagements successifs chez *Myrmica rubra* L. In: *Ecologie des insectes sociaux* (L'Union Internationale pour l'Etude des Insectes Sociaux, Section Française, Compte Rendu Colloque Annuel, Lausanne, 1979) (Cherix, D., ed.), pp. 17–19. Nyon: Cherix et Filanosa S.A.
- AGBOGBA, C. (1994). Absence of temporal polyethism in the ponerine ant *Pachycondyla caffraria* (Smith) (Hymenoptera: Formicidae): early specialization of the foragers. *Behav. Processes* **32**, 47–52.
- ANDERSON, C. & MCSHEA, D. W. (2001). Individual versus social complexity, with particular reference to ant colonies. *Biol. Rev. (Cambridge)* **76**, 211–237.
- BECKERS, R., GOSS, S., DENEUBOURG, J. L. & PASTEELS, J. M. (1989). Colony size, communication and ant foraging strategy. *Psyche* **96**, 239–256.
- BEEKMAN, M., SUMPSTER, D. & RATNIEKS, F. L. W. (2001). Phase transition between disordered and ordered foraging in Pharaoh's ants. *Proc. Natl Acad. Sci. U.S.A.*, **98**, 9703–9706.
- BESHES, S. N. & FEWELL, J. H. (2001). Models of division of labor in insect societies. *Ann. Rev. Entomol.* **46**, 413–430.
- BESHES, S. N., ROBINSON, G. E. & MITTENTHAL, J. E. (1999). Response thresholds and division of labour in insect colonies. In: *Information Processing in Social Insects* (Detrain, C., Deneubourg, J.-L. & Pasteels, J. M., eds), pp. 115–139. Basel: Birkhäuser.
- BONABEAU, E. & THERAULAZ, G. (1999). Role and variability of response thresholds in the regulation of division of labour in insect societies. In: *Information Processing in Social Insects* (Detrain, C., Deneubourg, J.-L. & Pasteels, J. M., eds), pp. 141–163. Basel: Birkhäuser.
- BONABEAU, E., THERAULAZ, G. & DENEUBOURG, J.-L. (1996). Quantitative study of the fixed threshold model for the regulation of division of labour in insect. *Proc. R. Soc. London B* **263**, 1565–1569.
- BONABEAU, E., THERAULAZ, G. & DENEUBOURG, J.-L. (1998). Fixed response thresholds and the regulation of division of labour in insect societies. *Bull. Math. Biol.* **60**, 753–807.
- BONABEAU, E., DORIGO, M. & THERAULAZ, G. (1999). *Swarm Intelligence: From Natural to Artificial Systems*. Santa Fe Institute Studies in the Sciences of Complexity. New York: Oxford University Press.
- BOURKE, A. F. G. (1999). Colony size, social complexity and reproductive conflict in social insects. *J. Evol. Biol.* **12**, 245–257.
- CAMAZINE, S., DENEUBOURG, J.-L., FRANKS, N. R., SNEYD, J., THERAULAZ, G. & BONABEAU, E. (2001). *Self-organization in Biological Systems*. Princeton: Princeton University Press.
- CHEN, S. C. (1937a). Social modification of the activity of ants in nest-building. *Physiol. Zool.* **10**, 420–436.
- CHEN, S. C. (1937b). The leaders and followers among the ants in nest-building. *Physiol. Zool.* **10**, 437–455.
- DENEUBOURG, J.-L., GOSS, S., PASTEELS, J. M., FRESNEAU, D. & LACHAUD J.-P. (1987). Self-organization

- mechanisms in ant societies (II): learning in foraging and division of labor. In: *From Individual to Collective Behavior in Social Insects* (Pasteels, J. M. & Deneubourg, J.-L., eds), pp. 177–196. Basel: Birkhäuser.
- HART, A. G. & RATNIEKS, F. L. W. (2001a). Task partitioning, division of labour and nest compartmentalisation collective isolate hazardous waste in the leaf-cutting ant *Atta cephalotes*. *Behav. Ecol. Sociobiol.* **49**, 387–392.
- HART, A. G. & RATNIEKS, F. L. W. (2001b). Leaf caching in the leafcutting ant *Atta colombica*: organisational shift, task partitioning and making the best of a bad job. *Anim. Behav.* **62**, 227–234.
- JEANNE, R. L. (1986a). The evolution of the organization of work in social insects. *Monit. Zool. Ital.* **20**, 119–133.
- JEANNE, R. L. (1986a). The organization of work in *Polybia occidentalis*: costs and benefits of specialization in a social wasp. *Behav. Ecol. Sociobiol.* **19**, 333–341.
- JEANNE, R. L. (1991). The swarm-founding Polistinae. In: *The Social Biology of Wasps* (Ross, K. G. & Matthews, R. W. eds), pp. 191–231. Ithaca, NY: Cornell University Press.
- JEANNE, R. L. & NORDHEIM, E. V. (1996). Productivity in a social wasp: per capita output increases with swarm size. *Behav. Ecol.* **7**, 43–48.
- KARSAI, I. & WENZEL, J. W. (1998). Productivity, individual-level and colony-level flexibility, and organization of work as consequence of colony size. *Proc. Natl Acad. Sci. U.S.A.* **95**, 8665–8669.
- KARSAI, I. & WENZEL, J. W. (2000). Organization and regulation of nest construction behavior in *Metapolybia* wasps. *J. Insect Behav.* **13**, 111–140.
- LENOIR, A. & ATAYA, H. (1993). Polyéthisme et répartition des niveaux d'activité chez la fourmi *Lasius niger* L. *Z. Tierpsychol.* **63**, 213–232.
- MEUDEEC, M. (1973). Note sur les variations individuelles du comportement de transport du couvain chez les ouvrières de *Tapinoma erraticum* Latr. *C. R. Acad. Sci. Paris D* **277**, 357–360.
- O'DONNELL, S. (1998). Effects of experimental forager removals on division of labour in the primitively eusocial wasp *Polistes instabilis* (Hymenoptera: Vespidae). *Behaviour* **135**, 174–193.
- O'DONNELL, S. & Jeanne, R. (1990). Forager specialization and the control of nest repair in *Polybia occidentalis* Olivier (Hymenoptera: Vespidae). *Behav. Ecol. Sociobiol.* **27**, 359–364.
- OSTER, G. F. & WILSON, E. O. (1978). *Caste and Ecology in the Social Insects*. Princeton: Princeton University Press.
- PLOWRIGHT, R. C. & PLOWRIGHT, C. M. S. (1988). Elitism in social insects: a positive feedback model. In: *Interindividual Behavioral Variability in Social Insects* (Jeanne, R. L., ed.), pp. 419–431. Boulder, CO: Westview Press.
- RATNIEKS, F. L. W. & ANDERSON, C. (1999). Task partitioning in insect societies. *Insectes Soc.*, **46**, 95–108.
- RETANA, J. & CERDA, X. (1991). Behavioural variability and development of *Cataglyphis cursor* ant workers (Hymenoptera, Formicidae). *Ethology* **89**, 275–286.
- RISSING, S. W. (1981). Foraging specializations of individual seed-harvester ants. *Behav. Ecol. Sociobiol.* **9**, 149–152.
- ROBINSON, G. E. (1992). Regulation of division of labor in social insects. *Ann. Rev. Entomol.* **37**, 637–665.
- ROBSON, S. K. & TRANIELLO, J. F. A. (1999). Key individuals and the organization of labor in ants. In: *Information Processing in Social Insects* (Detrain, C., Deneubourg, J.-L. & Pasteels, J. M., eds), pp. 239–259. Basel: Birkhäuser Verlag.
- SCHATZ, B. (1997). Modalités de la recherche et de la récolte alimentaire chez la fourmi *Ectatomma ruidum* Roger: flexibilité individuelle et collective. Unpublished Ph. D. Thesis, Université Paul Sabatier, Toulouse, France.
- SEELEY, T. D. (1982). Adaptive significance of the age polyethism schedule in honeybee colonies. *Behav. Ecol. Sociobiol.* **11**, 287–293.
- SMITH, A. (1776). *The Wealth of Nations, Books I–III*. Reprinted 1986 (A. Skinner, ed.). Harmondsworth, U.K. Penguin.
- THERAULAZ, G., GERVET, J. & SEMENOFF, S. (1991). Social regulation of foraging activities in *Polistes dominulus* Christ: a systemic approach to behavioural organization. *Behaviour* **116**, 292–320.
- THERAULAZ, G., BONABEAU, E. & DENEUBOURG, J.-L. (1998). Response threshold reinforcements and division of labour in insect societies. *Proc. R. Soc. London B* **265**, 327–332.
- TRANIELLO, J. F. A. (1978). Caste in a primitive ant: absence of age polyethism in *Amblyopone*. *Science* **202**, 770–772.
- WEIDENMÜLLER, A. (2001). From individual behavior to collective structure: pollen collection and nest climate control in social bees. Unpublished Ph.D. Thesis, Julius-Maximilians-Universität, Würzburg, Germany.
- WEHNER, R., HARKNESS, R. D. & SCHMID-HEMPEL, P. (1983). Foraging strategies in individually searching ants *Cataglyphis bicolor* (Hymenoptera: Formicidae). In: *Information Processing in animals* (Lindauer, M., ed.), pp. 1–79. New York: Fischer.
- Wilson, E. O. (1971). *The Insect Societies*. Cambridge: Harvard University Press.