

# The synchronization of recruitment-based activities in ants

Eric Bonabeau <sup>a,\*</sup>, Guy Theraulaz <sup>b</sup>, Jean-Louis Deneubourg <sup>c</sup>

<sup>a</sup> Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA

<sup>b</sup> Laboratoire d'Ethologie et de Psychologie Animale, CNRS-UMR 5550, Université Paul Sabatier, 118 route de Narbonne, 31062 Toulouse, Cédex, France

<sup>c</sup> Unit of Theoretical Behavioural Ecology, Service de Chimie-Physique, CP 231, Université Libre de Bruxelles, Boulevard du triomphe, 1050 Brussels, Belgium

Received 22 August 1997; received in revised form 14 November 1997; accepted 26 November 1997

---

## Abstract

A simple model of recruitment-based foraging in ants illustrates the idea that synchronized patterns of activity can endow a colony with the ability to forage more efficiently when a minimal number of active individuals is required to establish and maintain food source exploitation. This model, which can be extended to other activities that involve recruitment, may help explain why bursts of synchronization have been observed in several species of ants. © 1998 Elsevier Science Ireland Ltd. All rights reserved.

*Keywords:* Ant colony; Synchronization; Division of labor; Foraging; Recruitment

---

## 1. Introduction

### 1.1. Synchronized patterns of activity: how and why?

The occurrence of rhythmical patterns of activity, or bursts of synchronized activity, has been reported in ants several times (Calabi et al., 1983; Goss and Deneubourg, 1988; Franks et al., 1990; Cole, 1991a,b,c, 1994; Cole and Cheshire, 1996). The duration of one pulse, where a large per-

centage of the workers become active more or less simultaneously, may range from a few minutes to several hours. As is usual in the study of behavior, one may ask two complementary questions about this phenomenon (Tinbergen, 1963): (1) how do many individuals synchronize to become active simultaneously? (2) why does this phenomenon occur, what is its adaptive value? The first question is about proximate mechanisms, the second about ultimate causation and the evolutionary origins of the phenomenon.

(1) The potential proximate mechanisms to explain this type of behavior are numerous, be they

---

\* Corresponding author. E-mail: bonabeau@santafe.edu

exogeneous—environmental conditions, temperature, humidity, presence of other colonies, etc. (Bernstein, 1979; Gordon, 1983)—or endogeneous—recruitment, mutual activation (Goss and Deneubourg, 1988; Hemerik et al., 1990; Cole and Cheshire, 1996), level of satiation (Franks et al., 1990; Bonabeau and Cogne, 1996)—.

(2) At the ultimate level, synchronization due to external stimuli may have a trivial explanation connected to the stimuli in question: for example, Baroni Urbani and Kanno (1974) reported the occurrence of alternating foraging rhythms in competing sympatric ant species (*Solenopsis invicta* and *Monomorium minimum*). However, ultimate explanations are still scarce when synchronization is generated endogeneously. If the advantage of synchronization has been shown without ambiguity in many cases, such as the synchronous bioluminescent displays of male fireflies (*Photinus consimilis*) that increase mating success (Branham and Greenfield, 1996), the synchronized moulting of collembola (*Hypogastrura lapponica*, *H. socialis*) that facilitates coordinated migration (Leinaas, 1983), or the synchronization of prey capture in a social spider (*Anelosimus eximius*) which provides individuals with an efficient way of perceiving prey vibrations during the silent part of one oscillation (Krafft and Pasquet, 1991), its adaptive significance remains unclear in the case of ants.

The focus of this paper is the why question. It is aimed to illustrate, with a simplified model of recruitment and foraging, how synchronization can have an adaptive value when a minimal number of workers is required for a task to be performed with efficiency. Although only a few cases of synchronized patterns of activity in ants have been documented (*Leptothorax acervorum*, *L. alardycei*, *Pheidole hortensis*) (Calabi et al., 1983; Goss and Deneubourg, 1988; Franks et al., 1990; Cole, 1991a,b,c, 1994; Cole and Cheshire, 1996), we believe that this phenomenon is rather general, and has not been reported more systematically simply because its observation is not easy (which does not mean that all species exhibit this kind of behavior: for example, Cole (1994) mentions explicitly that *Tapinoma sessile* does not exhibit synchronized colony activity). Some other cases

have been reported but not documented (Cole, 1994; Cole and Cheshire, 1996; Goss and Deneubourg, 1988): *Leptothorax muscorum*, *Pseudomyrmex elongatus*, *P. cubaensis*, *Crematogaster ashmeadi*, *Zacryptocerus varians*, *Tapinoma littorale*, *Myrmecina grammicola*, *Messor capitata*. We also observed bursts of synchronized activity in *Messor barbarus* (Theraulaz, pers. obs.). The model is therefore not only aimed at explaining how synchronization may increase colony efficiency, but also at determining the conditions under which it can be the case, and at making general qualitative predictions about the timescales of the bursts of synchronization one should observe in colonies of variable sizes. New examples of synchronized patterns of activity in ants will allow these predictions to be tested.

## 1.2. Previous work

Several other explanations for observed patterns of synchronization have been suggested. Cole (1991a) proposed that synchronization is not adaptive by itself, but is a consequence of behavioral traits (spontaneous activity and strength of coupling between activity patterns) which are subject to selection at the colonial level: synchronization would therefore have nothing to do with colony efficiency. Franks and Bryant (1987) suggested that bursts of synchronized activity promote information exchanges and group cohesion, an appealing idea that is substantiated in this paper. Along similar lines, Robinson (1992) conjectured that such bursts of synchronized activity could facilitate information sampling, in relation to division of labor: information about what tasks should be performed would be collected and integrated more easily. Franks et al. (1990) proposed that workers are inactive most of the time because they do 'as much work as is necessary to satisfy the immediate requirements of the colony'. Hatcher et al. (1992) provided a very simple and elegant ultimate explanation of synchronization: it allows mutual exclusion, a mechanism that can lead to efficient brood care through a more uniform allocation of care to the larvae. A brood worker is prevented from tending brood items that other workers are already tending. If brood

workers were active independently, some brood items would receive too much care, and others not enough and would risk death (Bourke and Franks, 1995). Deneubourg and Franks (1995) argued that bursts of synchronized building activity in ants, resulting from a snowball effect in task performance in response to specific stimuli, could be an adaptive feature if there are costs (such as demolition costs before building can start) associated with building, and if the colony is more vulnerable when it is building (since synchronized bursts of activity allow the colony to build a lot within a short amount of time). We shall argue that our model provides a more general principle than those explanations, and helps understand them better within a broader framework.

### 1.3. Synchronization and division of labor

Our model of the adaptive value of synchronization is related to division of labor: when several tasks have to be performed (for example, food retrieval, exploration, brood care, etc.), and when some tasks require a critical number of active individuals in order to be performed efficiently, synchronization offers a solution if the colony is not sufficiently large to maintain pools of workers performing the various tasks simultaneously above the required level: tasks can then be performed sequentially by workers that switch tasks in synchrony. This approach requires not only that ants become active in synchrony, but also synchronize to perform the same task (they could become active simultaneously and engage in different tasks, so that minimal number requirements for each task might not be satisfied): such an assumption is reasonable when the task in question is foraging, as recruitment to food sources stimulates individuals to follow foragers (either directly or through pheromone trails), but it is conceivable that other tasks could be associated with a similar self-synchronization. The Hatcher et al., (1992) model required just the same assumption.

If active ants do not synchronize to all perform the same task, but rather synchronize to perform different tasks, it is still possible, in a sufficiently large colony, that critical numbers be exceeded if

ants become active at the same time. Even if the colony is large enough in principle to maintain enough individuals in each task force, colony needs may not require that each task be performed all the time above the critical level: in that case, it is advantageous, in term of total energy spent, to perform a task in synchrony, because synchronization leads to more efficient task performance for the same invested energy than when the task is performed continuously by a small number of workers.

All these ideas are variations on the same theme, namely, that tasks that require a certain number of workers to be performed efficiently (increasing returns) are widespread (for example, recruitment-based activities), and that it is therefore better for a colony, be it small or large, to allocate enough individuals simultaneously to such tasks: synchronization is then a solution.

## 2. A simple model of recruitment

### 2.1. Foraging in ants

Foraging is an important component of colony life in social insects in general and ants in particular. The process whereby an ant is influenced towards a food source by another ant or by a chemical trail is called recruitment. Beckers et al. (1989) distinguish several types of recruitment: tandem recruitment, whereby an individual signals to another one by direct physical interaction that she found a food source; group recruitment, in which chemical signalling by one recruiting individual has the effect of effectively recruiting a few individuals; and mass recruitment, which is performed through independent trail-laying and trail-following behaviors. Other types of foraging strategies, such as individual foraging, group raiding, the use of trunk trails, or group hunting also exist (Beckers et al., 1989), but will not be considered here. The three recruitment strategies mentioned above usually require some constraints to be satisfied in order to be implemented efficiently: for example, owing to the finite lifetime of pheromones (evaporation, diffusion, etc.), stable pheromone trails can be established only if there

is a sufficient number of foragers to maintain them. A clear observation of this phenomenon has been made in the context of collective exploration in *Pheidole pallidula* (Detrain et al., 1991) and *Monomorium pharaonis* (Fourcassié and Deneubourg, 1994). The model of recruitment presented below is a simple expression of this minimal number requirement.

## 2.2. Model with fixed number of active individuals

Let us consider one of the simplest possible models of recruitment in ants, suggested by Verhaeghe and Deneubourg (1983), Verhaeghe (1982) to account for experimental observations in *Termitarium impurum*. Let  $N$  be the total number of potential foragers in the colony (that is, the number of individual ants which may be involved in exploiting a food source; some individuals may never, or very rarely, do so because they are involved in performing other tasks), and  $X$  the number of individuals exploiting the food source (it is assumed that there is only one food source in the colony's foraging environment). In this model, the temporal evolution of  $X$  is given by

$$\frac{dX}{dt} = aX(N - X) - bX \quad (1)$$

where  $a$  is the effective recruitment rate (which includes the effects of the size of the foraging area, the speed of motion of individuals, their physiological states, food source quality), and  $1/b$  is the average time that an individual ant spends exploiting the food source (before switching to another task, or before becoming an uncommitted follower). It is assumed that  $a$  does not depend on  $N$ . From Eq. (1), it can be seen that the source can only be exploited ( $X_\infty > 0$ , where  $X_\infty$  is the solution of  $dX/dt = 0$ ) if the total number of available foragers exceeds some critical value: the condition on  $N$  reads

$$aN - b > 0 \quad (2)$$

There is a bifurcation from random to structured foraging as  $N$  exceeds  $b/a$ . Let us define  $N_c = b/a$ .  $X_\infty = 0$  is the only stable solution for  $N < N_c$  (there is also a non-biological unstable solution with  $X_\infty < 0$ ), and  $X_\infty = 0$  loses stability

at  $N_c$ , where a stable solution with  $X_\infty > 0$  appears. More precisely,  $X_\infty = N - N_c$ , and the stationary fraction of potential foragers that actually exploit the source is given by  $f_\infty \equiv X_\infty/N = 1 - (N_c/N)$ . In this example, the minimal number of active workers required to forage efficiently can be seen as a constraint for efficient information transfer, as hypothesized by Franks and Bryant (1987). The full temporal solution of Eq. (1) is given by:

$$X(t) = \frac{N - N_c}{1 + C e^{-at(N - N_c)}} \quad (3)$$

where  $C = (N - N_c - X(0))/X(0)$  is a constant, and  $X(0)$  is the number of foragers exploiting the food source at  $t = 0$ . It follows from Eq. (3) that the timescale of establishment of a pool of foragers exploiting the food source is given by:

$$\tau_e = \frac{1}{a(N - N_c)} \quad (4)$$

Using the values of the parameters suggested by Verhaeghe and Deneubourg (1983) in their studies of single food source recruitment in *T. impurum*,  $a = 0.0035 \text{ min}^{-1}/\text{indiv}$ ,  $b = 0.07 \text{ min}^{-1}$ , we obtain  $N_c = 20$ , and  $\tau_e \approx 28.5 \text{ min}$  for  $N = 30$ , but  $\tau_e \approx 285 \text{ min}$  for  $N = 21$ , and  $\tau_e \approx 2.85 \text{ min}$  for  $N = 120$ : the more foragers, the shorter the time needed to reach efficient exploitation of the food source. For a small colony, if the number of active foragers is  $< 20$  at any one time, the only possibility for food retrieval is independent exploration and exploitation by foragers; if there is only one valuable source in the neighborhood of the nest, the exploitation of that source can only proceed through workers that independently find the source by chance. Even with individual memory, which allows individual foragers to go back to a food source that they found, the inefficiency of information exchange will prevent other foragers from benefiting from the food source already found by one forager.

## 2.3. Model with variable number of active individuals (periodic forcing)

If division of labor in a small colony relies on the simultaneous performance of various tasks by different groups of workers, foraging will not be

efficient. For example, let us assume that there are  $n = 30$  workers in the colony, that two tasks have to be performed, including foraging, and that 15 individuals are performing the non-foraging task and 15 individuals are foraging. In this case, with all the parameters set to the values defined above, the number of foragers is less than  $N_c$ . The only chance for the colony to retrieve food is by independent random exploitation of the food source. Now, if these workers are polyvalent and potentially available for foraging or any other task, the number of active foragers may vary in time. Bursts of synchronized foraging can allow the colony to exceed the critical number required to exploit the food source efficiently. For example, let us assume that  $N$  varies periodically as

$$N(t) = \frac{n}{2} \left[ 1 + \cos\left(\frac{2\pi t}{T}\right) \right], \quad (5)$$

where  $T$  is the period of one oscillation. It is assumed that  $T > 1/b$  (which may not be the case if, for example, oscillations are quick and ants stay a long time at the food source). We see that if  $n = 30$ ,  $N(t)$  varies between 0 and 30, with a time average  $\langle N \rangle$  of 15 foragers, that is, the same number as in the fixed number case. Therefore, the energy spent by the colony for foraging is the same in the two cases. However, the temporal repartition of workers among tasks is different. Here, we have chosen a periodic variation of  $N$ , but any other type of variation which allows the colony to exceed the critical number for some amount of time (the exact time required is discussed below) would do the job. There exist many mechanisms that can either generate oscillations or patterns of synchronized activity endogenously (Goss and Deneubourg, 1988; Hemerik et al., 1990; Miramontes et al., 1993; Cole and Cheshire, 1996), and the focus of this paper is not how such patterns are generated but their adaptive significance. Both aspects are in fact connected: for example, recruitment itself plays a role in stimulating inactive individuals into activity, so that decoupling recruitment from the variation in  $N$  is certainly an oversimplification. However, the main conclusion that the minimal number of active individuals required to perform a task efficiently can be reached through synchronized

bursts of activity remains true, whatever the mechanisms to generate such a synchronization. The next section will be devoted to a study of a model where the variation in  $N$  is coupled to task performance.

In order to avoid making the null state (that is, when no worker is exploiting the food source) an absorbing state of the dynamics in this deterministic model, equation (1) has to be supplemented with a term accounting for the possibility that the source will be found spontaneously by a worker rather than through recruitment: let  $p$  be the probability per unit time that an uncommitted worker finds the food source by chance. Eq. (1) now reads:

$$\frac{dX}{dt} = (aX + p)[N(t) - X] - bX, \quad (6)$$

with  $N(t)$  given by Eq. (5). In what follows,  $p$  is set to  $0.001 \text{ min}^{-1}$ . Note that when  $N$  is fixed, Eq. (6) does not exhibit the bifurcation to structured foraging exhibited by Eq. (1), but exhibits instead an imperfect bifurcation because of the parameter  $p$ . This means that there is always a positive solution  $X_\infty$ . More precisely, assuming for now that  $N$  is fixed,

$$X_\infty = aN - p - b + \frac{\{(p + b - aN)^2 + 4apN\}^{1/2}}{2a}, \quad (7)$$

and the associated timescale is given by

$$\tau_e = \frac{1}{\{(aN - p - b)^2 + 4apN\}^{1/2}} \quad (8)$$

Fig. 1 shows  $f_\infty = X_\infty/N$  as a function of  $N$  for various values of  $p$ . It can be shown that the pitchfork bifurcation observed for  $p = 0$  transforms into an imperfect bifurcation when  $p > 0$ . Although there is no true bifurcation for  $p > 0$ , it is nevertheless more rewarding for the colony to have a number of foragers that go beyond the inflection point of the curve, at a value  $N_i = (b - p)/a$ . As  $p$  increases, the advantage of large numbers decreases, as the curve becomes more flat and  $N_i$  decreases ( $N_i = 0$  for  $p = b$ ). Fig. 2 shows how  $\tau_e$  varies as a function of  $N$  for various values of  $p$  ( $p = 0-0.01$ , increment  $p = 0.001$ ; the diverging curve corresponds to  $p = 0$ ;  $\tau_e$  is smaller and

smaller as  $p$  increases). We see that, when  $p \neq 0$ ,  $\tau_e$  never diverges and is well defined even for  $N < N_i$ .  $N_i(p)$  is also shown on Fig. 2: we can see that  $\tau_e$  increases with  $N$  for  $N < N_i$ , and decreases for  $N > N_i$ ; although the stationary solution  $X_\infty$  is reached rapidly when  $N < N_i$ ,  $X_\infty$  is very small, and it is more advantageous to have  $N > N_i$ , and, in that region, it takes less time as  $N$  increases.

Let us now assume that  $N$  varies according to Eq. (5), and let  $\omega = 2\pi/T$ . Fig. 3 shows the temporal evolution of  $X$  for  $\omega = 0.00525$  ( $T = 1196$ ). It can be seen that the number of foragers effectively exploiting the food source follows the oscillations of  $N(t)$  with a slight time delay that corresponds to the time taken to establish the recruitment, and reaches a maximum of the order of eight individuals. By contrast, the fixed  $N$  strategy ( $N = \langle N \rangle = 15 < N_c$ ) leads to a constant, extremely low level of exploitation, since, as can be seen on Fig. 4, only 0.27 individuals on average exploit the food source.

Fig. 5 ( $\omega = 0.035$  and  $T = 179$  min) shows that the period of one oscillation should allow the establishment of recruitment to a sufficient level:  $T$  must be significantly greater than  $\tau_e$ . Here,

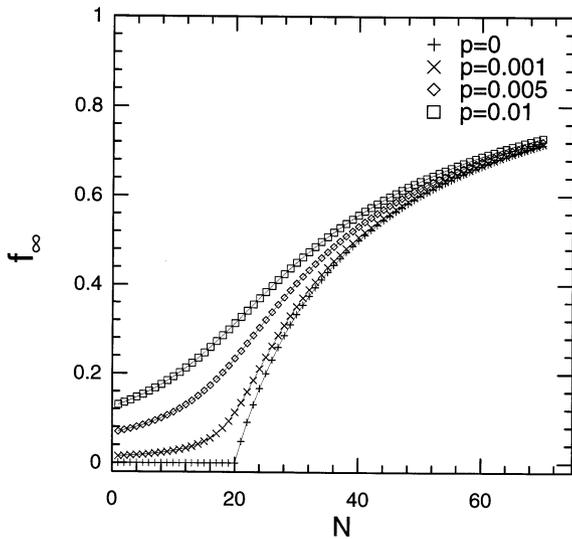


Fig. 1. Fraction  $f_\infty$  of foragers exploiting the food source as a function of the number of active individuals  $N$ , for different values of  $p$  ( $p = 0, 0.001, 0.005, 0.01$ ).

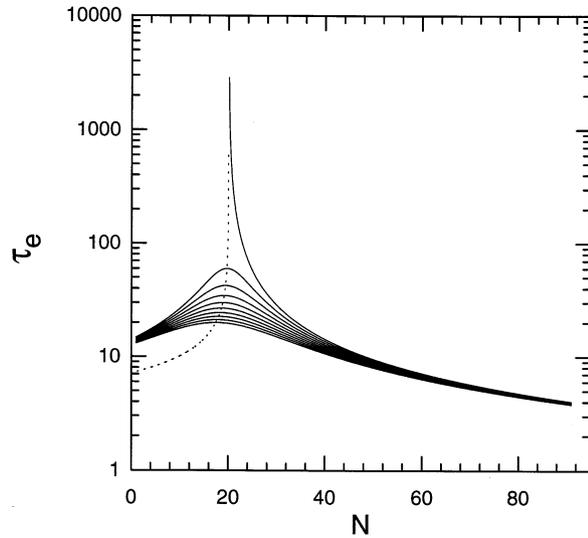


Fig. 2. Timescale  $\tau_e$  required to establish efficient food source exploitation as a function of the number of active individuals  $N$  for different values of  $p$  ( $p = 0-0.05$  from top to bottom,  $\Delta p = 0.005$ ; the diverging curve corresponds to  $p = 0$ ). The dotted line represents  $N_i(p)$ : the intersection of the dotted line and each single curve corresponds to the value of  $N_i$  for this curve.

efficient recruitment can only take place for  $N > N_i \approx 17$ . The number of active foragers exceeds  $N_i$  during  $0.44T = 80$  min per oscillation. Since  $N$  is varying, the minimum  $\tau_e$  is obtained for  $N = 30$ ,  $\tau_e^{\min} \approx 15$  min (given by Eq. (7)), and the maximum  $\tau_e$  is  $\tau_e(N = 17 = N_i) = \tau_e^{\max} \approx 20$  min (because of the presence of  $p$  in Eq. (6), the difference in  $\tau_e$  for different values of  $N$  are less pronounced than when  $p = 0$ ). Although  $0.44T$  is greater than  $\tau_e^{\max}$ , this does not appear to be sufficient to allow for a large value of  $X_\infty$  to be reached: in Fig. 5, the number of foragers exploiting the food source rapidly converges to a small value of  $X_\infty$  ( $X_\infty \approx 0.2$ ).

Fig. 6 shows how  $\max(X_\infty)$ , the maximum number of individuals able to exploit the source simultaneously, varies with the period  $T$  of the oscillations:  $\max(X_\infty)$  starts to increase significantly at  $T = 600$ , so that  $0.44T = 264$  min, which is an order of magnitude greater than  $\tau_e$ . Fig. 7 illustrates that  $\max(X_\infty)$  increases with  $T$  ( $\omega = 0.0007$  ( $T = 8971$  min)), but does so very slowly beyond some value of  $T$ . It is in any case bounded

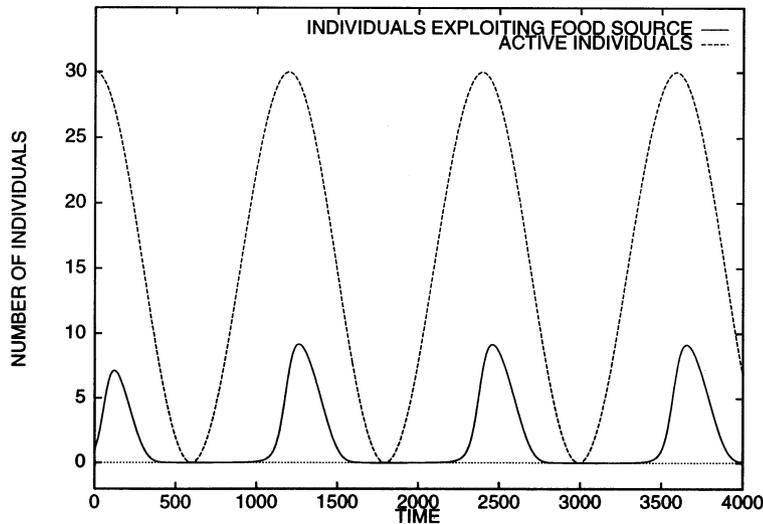


Fig. 3. Number of active foragers ( $N(t)$ ) and number of foragers actually exploiting the source ( $X(t)$ ) for  $a = 0.0035 \text{ min}^{-1}/\text{indiv}$ ,  $b = 0.07 \text{ min}^{-1}$ , and  $\omega = 0.00525$  ( $T = 1196 \text{ min}$ ).

by  $X_{\infty}(n) = (an - p - b + \{(p + b - an)^2 + 4apn\}^{1/2}) / 2a$  ( $\approx 13$ , here).

In conclusion of this section, synchronization, in the form of forced periodic oscillations in  $N$ , can allow a colony to establish an efficient exploitation of a food source if  $N$  exceeds  $N_i$  for a sufficiently long time, that is, if the period of the oscillations is large enough. The minimum period seems to be an order of magnitude larger than  $\tau_c^{\max}$ . In the next section, the synchronization of individuals will not be driven by a periodic forcing, but will rather emerge from recruitment itself: whereas the simple model presented in Section 2 lends itself to analysis, the more complicated model of Section 3 is not analytically tractable. We have therefore used the simpler model to understand formally the constraints imposed on the type of synchronization that can lead to increased colony efficiency.

Note that the values of the parameters used in this section were specific to *T. impurum*, and that results can be quantitatively quite different for other species characterized by different values (recruitment rates, etc): in particular, the timescales reported above can be affected by changes in parameter values. The results remain, however, qualitatively valid.

### 3. Coupling of task performance with synchronization

#### 3.1. One task

Although the simple model of the previous section did convey the essence of the argument, namely that synchronization can be useful when a there is a minimal number requirement for a task to be performed efficiently, one may not be fully convinced as the synchronization-generating mechanism was assumed to be decoupled from task performance (foraging). The same conclusions hold when a coupling is introduced, so that, for example, synchronization results from the need to perform a task. An extension of the previous model consists of assuming the existence of three classes of individuals: (1) inactive workers, (2) 'active' workers that are not exploiting the food source, and (3) active foragers that are exploiting the food source. The numbers of individuals in each class are denoted by  $N_1$ ,  $N_2$  and  $N_3$ , respectively. The total number of potential workers in the colony is denoted by  $N_0$ :  $N_1 + N_2 + N_3 = N_0$ . The idea is that inactive individuals may become active in synchrony in response to colony needs and stimulation from active workers. Once

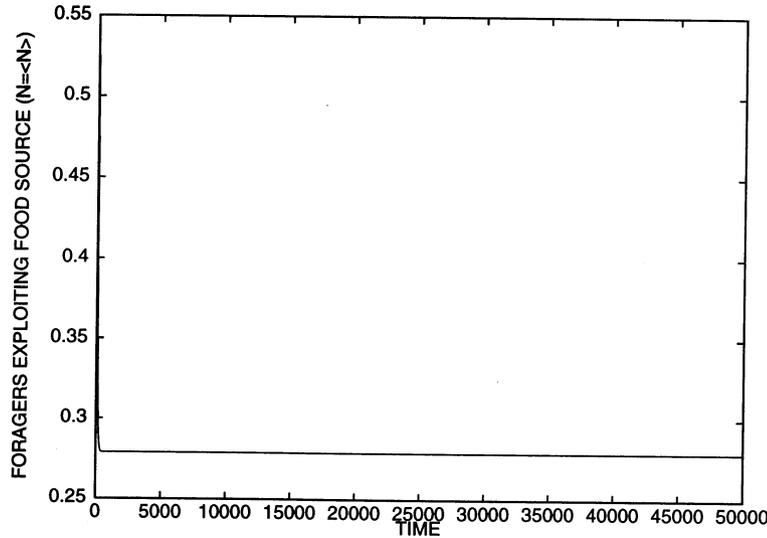


Fig. 4. Number of foragers actually exploiting the source ( $X(t)$ ) with the fixed  $N$  strategy,  $N = \langle N \rangle = 15 < N_c$ .  $a = 0.0035 \text{ min}^{-1}/\text{indiv}$ ,  $b = 0.07 \text{ min}^{-1}$ .

active, they can be recruited to the food source. They exploit the food source for a certain amount of time and switch back to state (2), where they can be recruited again or become inactive. The most appropriate modeling framework to describe these behaviors is a set of globally coupled automata (Bonabeau, 1996). The probability that an inactive individual (denoted by  $i$ ) becomes active depends on a combination of factors: the number of active individuals  $N_2 + N_3$ , the stimulation or recruitment rate  $a_1$ , a factor  $p_1$  corresponding to the probability of becoming spontaneously active, the time spent inactive  $t_i^1$ , a characteristic latency time of inactivity  $T_i$ , stimulus intensity  $D_i$  at time  $t$  ( $D_i$  reflects colony's nutritional status, or more generally colony needs), and a characteristic response threshold to stimulus  $D_c$ . Let  $S_i$  ( $= 1, 2$ , or  $3$ ) be the state of individual  $i$ . The transition probability from  $S_i = 1$  to  $S_i = 2$  is given by:

$$T(S_i = 1 \rightarrow S_i = 2) = a_1(N_2 + N_3 + p_1)(1 - e^{-t_i^1/T_i}) \left( \frac{D_i^2}{D_i^2 + D_c^2} \right). \quad (9)$$

In this equation,  $a_1(N_2 + N_3 + p_1)$  represents the effect of stimulation by active individuals and the

effect of spontaneous activation in the absence of stimulation,  $(1 - e^{-t_i^1/T_i})$  describes the effect of the time already spent in the inactive state (if  $t_i^1$  is small, there is a small chance that individual  $i$  can become active), and  $D_i^2/(D_i^2 + D_c^2)$  represents the response to the task-associated stimulus  $D_i$ . Only when  $D_i \gg D_c$  is  $D_i^2/(D_i^2 + D_c^2)$  close to 1 (Bonabeau et al., 1996). The presence of  $D_i^2/(D_i^2 + D_c^2)$  in Eq. (9) implies that inactive individuals are more easily activated, or, alternatively, that active individuals are more involved in stimulating other ants, when the task-associated stimulus is large. The transition probability from  $S_i = 2$  to  $3$  is simply determined by a recruitment factor  $a_A$  supplemented by a term accounting for colony needs and a term  $p_A$  corresponding to the probability of finding the source spontaneously:

$$T(S_i = 2 \rightarrow S_i = 3) = a_A(N_3 + p_A) \left( \frac{D_i^2}{D_i^2 + D_c^2} \right)^2. \quad (10)$$

If an active individual does not become a forager, it may become inactive with probability

$$T(S_i = 2 \rightarrow S_i = 1) = (1 - e^{-t_i^A/T_A}), \quad (11)$$

where  $t_i^A$  is the time spent in state  $S_i = 2$  since the last transition, and  $T_A$  is a characteristic waiting

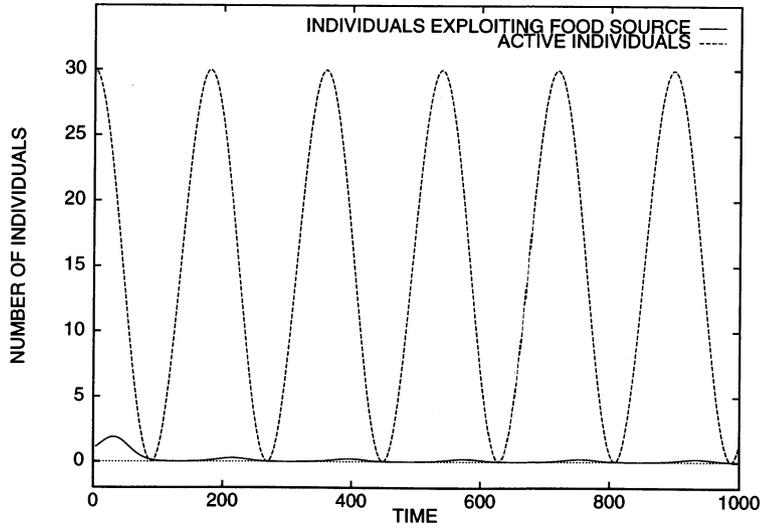


Fig. 5. Same as Fig. 3 with  $\omega = 0.035$  ( $T = 179$  min).

time. A forager exploiting the food source switches to state  $S_i = 2$  with probability

$$T(S_i = 3 \rightarrow S_i = 2) = (1 - e^{-t_F^i/T_F}) \quad (12)$$

where  $t_F^i$  is the time spent in state  $S_i = 3$  since the last transition, and  $T_F$  is a characteristic foraging time (the equivalent of  $1/b$  in the previous section).

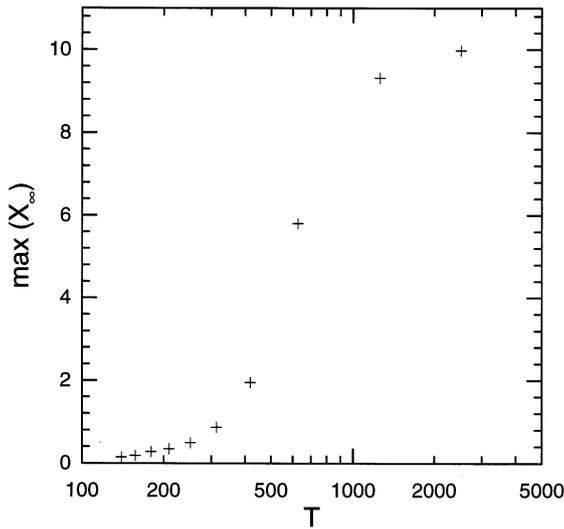


Fig. 6. Peak height  $\max(X_\infty)$  of the  $X$  oscillations as a function of the timescale  $T$ .

Finally, the dynamics of the stimulus  $D_i$  is given (in discrete time) by

$$D_{t+1} - D_t + D_0 - \alpha N_3 \quad (13)$$

where  $D_0$  is the rate of increase of stimulus intensity per unit time and  $\alpha$  is the amount of work (in stimulus currency) performed by a forager per unit time. The mechanism that generates synchronization in this model is close to the one described by Hemerik et al. (1990): hunger (or other colony needs) makes individuals more likely to become active and perform tasks, and task performance reduces hunger. The main difference, of course, is that we include recruitment, which induces a minimal number requirement for efficient task performance.

The following values of the parameters have been used ( $U = 1$  time unit):  $N_0 = 100$ ,  $a_I = 0.0055$   $U^{-1}/\text{indiv}$ ,  $a_A = 0.0035$   $U^{-1}/\text{indiv}$ ,  $p_I = 1$ ,  $p_A = 0.03$ ,  $T_I = 40$   $U$ ,  $T_A = 40$   $U$ ,  $T_F = 14.3$   $U$ ,  $D_c = 80$ ,  $D_0 = 10$ ,  $\alpha = 5$ . Fig. 8 shows a typical simulation run obtained with these parameters. We observe bursts of synchronized activity, which allow the number of active individuals to exceed the threshold for efficient recruitment. Major bursts occur every 55  $U$ , and last for about 20  $U$ . Fig. 9 shows the dynamics of stimulus intensity  $D_t$ , which also exhibits periodic peaks. This phenomenon is

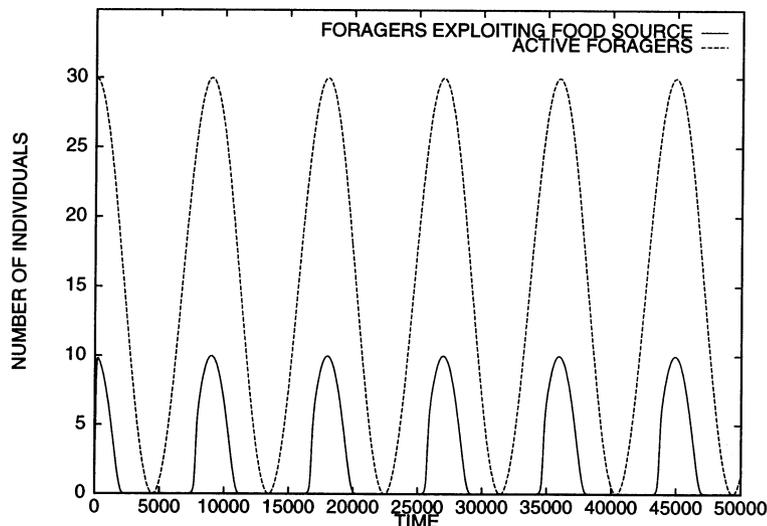


Fig. 7. Same as Fig. 3 with  $\omega = 0.0007$  ( $T = 8971$  min).

similar to the one observed by Deneubourg and Franks (1995) in their model of building in ants: a snowball (recruitment-based) effect occurs when stimulus intensity becomes large, so that a large number of individuals start building together, which reduces stimulus intensity; because there is a momentum in task performance (individuals continue to build for a certain time irrespective of stimulus intensity), stimulus intensity decreases well below the response threshold, and it will take some time for it to exceed the threshold again. It is exactly what happens here: when individuals start to forage,  $D_i$  is quickly brought back to 0, well below the threshold. The average value of  $D_i$  is  $\langle D \rangle = 105$ , the response threshold of individuals being  $D_c = 80$ . The average number of active individuals  $\langle N_2 + N_3 \rangle$  is  $16 \text{ U}^{-1}$ , and the average number of foragers is  $\langle N_3 \rangle = 1.94 \text{ U}^{-1}$ . We know from the previous section that, given the values of the parameters, a colony that would have only 16 individuals permanently active would not be able to exploit the food source efficiently.

To confirm this property within the present model, simulations have been run with a fixed number ( $N = 16$ ) of active individuals. Figs. 10 and 11 show the results of a typical run: there are always foragers active (Fig. 10), but the num-

ber of active foragers at any given time is significantly smaller than the number of active foragers during bursts of synchronized activity in Fig. 8, although the average number of active foragers are comparable in both cases ( $\langle N_3 \rangle = 1.88 \text{ U}^{-1}$  in Fig. 8); this results in a stimulus intensity that increases well above threshold (Fig. 11), with  $\langle D \rangle = 284$ . Synchronization is therefore advantageous in this case, since the same energy spent (expressed in active or foraging individuals per time unit) leads to less food taken back to the nest. Notice that although the peaks observed in Fig. 8 are clearly periodic, other values of the parameters may lead to synchronous activity without a strong periodicity.

### 3.2. Two tasks

Let us now turn to the case of two tasks. Four classes of individuals are assumed: (1) inactive workers, (2) 'active' workers that are not exploiting the food source, (3) active foragers that are exploiting the food source (task 1), and (4) workers that are performing task 2. Contrary to task 1, task 2 is assumed not to rely on direct recruitment, but stimuli associated to task 2 do contribute to the activation of inactive individuals. The transition probabilities are given by:

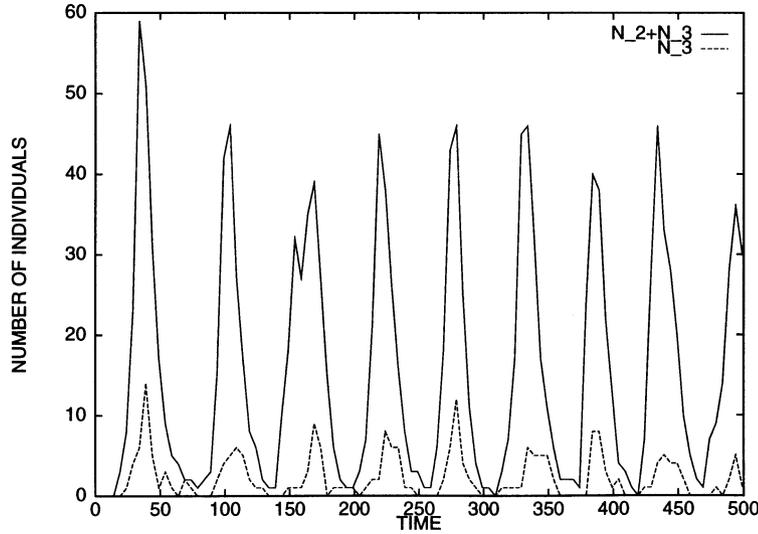


Fig. 8.  $N_3$  and  $N_2 + N_3$  as a function of time for the model described by Eqs. (9)–(13).  $N_0 = 100$ ,  $a_1 = 0.0055 \text{ U}^{-1}/\text{indiv}$ ,  $a_A = 0.0035 \text{ U}^{-1}/\text{indiv}$ ,  $p_1 = 1$ ,  $p_A = 0.03$ ,  $T_1 = 40 \text{ U}$ ,  $T_A = 40$ ,  $T_F = 14.3 \text{ U}$ ,  $D_c = 80$ ,  $D_0 = 10$ ,  $\alpha = 5$ .

$$T(S_i = 1 \rightarrow S_i = 2) = a_1(N_2 + N_3 + N_4 + p_1)(1 - e^{-t_i/T_1}) \left( \frac{D_{1,t}^2}{D_{1,t}^2 + D_{1,c}^2} \frac{D_{2,t}^2}{D_{1,c}^2} \right)^2, \quad (14)$$

where  $N_4$  is the number of workers performing task 2,  $D_{k,t}$  is the stimulus intensity associated to task  $k$ , and  $D_{k,c}$  is the corresponding threshold. The probability that an active individual (state 2) becomes inactive is still given by Eq. (11). The probability that an active individual remains active is therefore given by  $e^{-t_i/T_A}$ . If individual  $i$  remains active, it can become involved in performing task 1, task 2, or no task, with respective conditional probabilities

$$T(S_i = 2 \rightarrow S_i = 3 \mid \text{active}) = a_{A1}(N_3 + p_A) \left( \frac{D_{1,t}^2}{D_{1,t}^2 + D_{1,c}^2} \right)^2, \quad (15)$$

$$T(S_i = 2 \rightarrow S_i = 4 \mid \text{active}) = a_{A2} \left( \frac{D_{2,t}^2}{D_{2,t}^2 + D_{2,c}^2} \right)^2, \quad (16)$$

$$T(S_i = 2 \rightarrow S_i = 2 \mid \text{active}) = 1 - \sum_{k=1,2} T(S_i = 2 \rightarrow S_i = k \mid \text{active}) \quad (17)$$

where  $a_{Ak}$  is a parameter associated with task  $k$ , and  $T(\dots|\text{active})$  denotes conditional probabilities, knowing that individual  $i$  remains active: the full probability is given by  $T(\dots) = T(\dots|\text{active}) e^{-t_i/T_A}$ . An individual performing task  $k$  gives up task performance to be in state 2 again with probability

$$T(S_i = k \rightarrow S_i = 2) = (1 - e^{-t_i/T_k}), \quad (18)$$

where  $t_i^k$  is the time spent by individual  $i$  performing task  $k$  in its current bout, and  $T_k$  is a characteristic time associated with task  $k$ . Finally, the dynamics of  $D_{k,t}$  is given by

$$D_{k,t+1} = D_{k,t} + D_0 - \alpha N_k, \quad (19)$$

where  $N_k$  is the number of individuals performing task  $k$ . It is assumed that  $D_0$  and  $\alpha$  are identical for both tasks. Fig. 12 shows  $N_2$ ,  $N_3$  and  $N_4$  for  $a_{A1} = 0.0035 \text{ U}^{-1}/\text{indiv}$ ,  $a_{A2} = 0.035 \text{ U}^{-1}/\text{indiv}$ ,  $D_{1,c} = D_{2,c} = 80$ ,  $T_1 = T_2 = 40 \text{ U}$ , all other parameters being identical to those of Fig. 8. Individuals become active in synchrony, which induces performance of both tasks simultaneously. Synchronization in performing task 2 is not adaptive per se, but is a consequence of an adaptive feature, namely synchronization in task 1 performance.

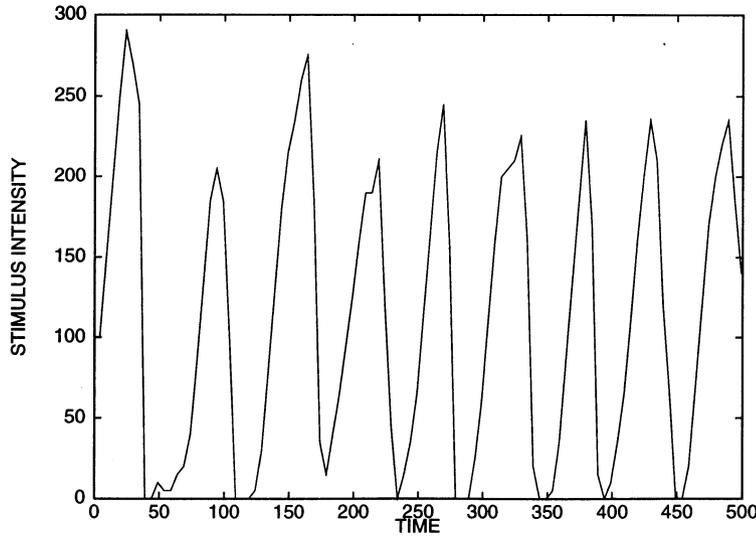


Fig. 9.  $D_t$  as a function of time for the simulation presented in Fig. 8.

Although we will not describe this case in detail, it is also possible to observe an alternance of tasks, if one assumes that performance of task 1 increases the stimulus associated to task 2 and vice versa. Examples of such relationships among tasks are widespread: for instance, nest excavation, by creating a refuse pile just at the entrance of the nest, generates a need for cleaning, and cleaning allows excavation to proceed further. We then have

$$D_{1,t=1} = D_{1,t} + D_0 + \beta N_4 - \alpha N_3, \tag{20}$$

$$D_{2,t=1} = D_{2,t} + D_0 + \beta N_3 - \alpha N_4, \tag{21}$$

where  $\beta$  is a factor that describes how performing a given task affects the other task. In this example, we also modified Eq. (16) to include recruitment:

$$T(S_i = 2 \rightarrow S_i = 4 \mid \text{active}) = a_{A2}(N_4 + p_A) \left( \frac{D_{2,t}^2}{D_{2,t}^2 + D_{2,c}^2} \right)^2, \tag{22}$$

Fig. 13 shows the numbers of individuals involved in each task ( $\beta = 4$ ,  $N_0 = 500$ ,  $a_{A1} = a_{A2} = 0.0065 \text{ U}^{-1}/\text{indiv}$ ,  $T_1 = 200 \text{ U}$ ,  $D_{1,c} = D_{2,c} = 400$ , all other parameters identical to those of Fig. 12): individuals synchronize to perform task 1 and task 2 in alternance.

## 4. Discussion

### 4.1. Limitations

Let us reemphasize at this point that the models presented in the previous sections were extreme oversimplifications of reality, because they neglected parameter fluctuations (for example, a self-regulation of the parameters governing the timescale of oscillations is not unconceivable: foragers not finding any food may spontaneously increase the time they spend foraging, allowing the colony to eventually establish an efficient recruitment), the influence of pheromone trails (Deneubourg et al., 1987; Pasteels et al., 1987), or other factors that play a role in recruitment and foraging, such as memory (Haefner and Crist, 1994), learning, etc. Moreover, this model does not deal explicitly with space: for spatially explicit models, see Haefner and Crist (1994), Crist and Haefner (1994), Edelman-Keshet et al. (1995), Cole and Cheshire (1996). Despite these limitations, we believe that the general principle underlying these models is robust: more efficient modes of task performance can be obtained through synchronization.

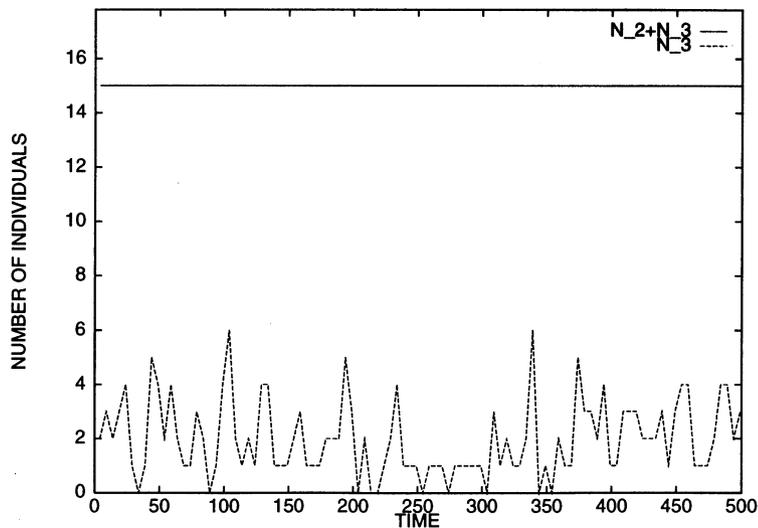


Fig. 10.  $N_3$  and  $N_2 + N_3$  as a function of time for the model described by Eqs. (9)–(13), but assuming that  $N_2 + N_3 = \text{cst} = 16$ . Parameter values identical to those of Fig. 8.

#### 4.2. Timescales and colony size

Let us first examine the case of relatively small colonies, where ‘sequential partitioning’ of labor, that is, when tasks are performed sequentially by the same pool of individuals (Jeanne, 1986), may be the solution that allows all tasks to be performed efficiently. Such a colony functioning, where workers would have to be polyvalent, would be consistent with the found correlation between colony size and worker polymorphism (Keller, 1995), species with small colonies being often characterized by no worker polymorphism. The model predicts that pulsatile activity should be of higher frequency in large colonies than in small colonies, because of the time  $\tau_e$  it takes to establish efficient exploitation. However, when bursts are high frequency, they become indistinguishable from spiky irregular patterns, because successive bouts of activity overlap; moreover, noise, under various forms, interferes more strongly with the bursts, which become blurred. Therefore, one should expect synchronized patterns of activity with clearly separated peaks, with a timescale of the order of a few minutes to an hour, only in relatively small colonies, with at most a few hundreds of workers. Note that syn-

chronization may not be possible if colony size is too small.

On the other hand, in large colonies resorting to mass recruitment, synchronized patterns of activity can lead to more flexibility if the average interpeak time, that is, the time separating two bouts of foraging activity, is sufficiently large, because of a temporal constraint that operates not at the level of trail establishment but at the level of trail decay: indeed, if the number of active foragers undergoes large variations, a strong trail may have time to disappear partly (because of diffusion, evaporation, adsorption) between two peaks of activity, allowing the colony to choose another source if the environment has changed. Within one foraging bout, the colony may not be able to exhibit such a flexibility (Beckers et al., 1990; de Biseau et al., 1991), and appears to be ‘trapped’ on its trails. Such synchronized patterns of activity, that are separated by a relatively long time (*M. grammicola*, *M. capitata* (Goss and Deneubourg, 1988)), can be regulated by hunger and satiation (Wilson and Hölldobler, 1988; Goss and Deneubourg, 1988; Franks et al., 1990; Bonabeau and Cogne, 1996).

In summary, three timescales must be distinguished:

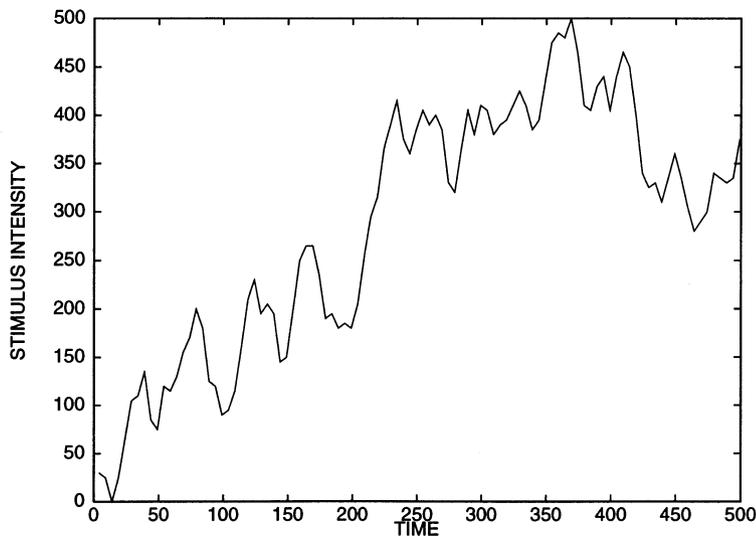


Fig. 11.  $D_t$  as a function of time for the simulation presented in Fig. 10.

1. a long timescale, such as the one just discussed, over which variations of colony needs can regulate foraging activities and pheromone trails can partially decay;
2. an intermediate timescale, over which colony needs do not vary significantly, but which can still be sufficiently large to allow the establishment of efficient recruitment in small colonies, as discussed in this paper;
3. a short timescale, over which colony needs can be assumed to be constant, but which is sufficient to induce efficient recruitment in large colonies.

An example of the intermediate timescale (2) is provided by *Leptothorax* ants. Franks et al. (1990) report that *L. acervorum* foragers actually forage or move in the nest only 47% of the time, and remain inactive or perform self-grooming 31% of the time (other activities, such as worker feeding, account for the remaining 12%). Moreover, image analysis of the nest indicates synchronized patterns of activity: ants remain quiescent for about 15 min, and then become active simultaneously for 5 min. Colonies of this species are relatively small, containing of the order of 100–250 individuals. The colonies observed by Franks et al. (1990) were comprised of 20–70 workers, plus the queen and the larvae. Although the timescale of

activity bouts is small with respect to colony size, 3–5 min might still be sufficient, depending on other parameters, to generate efficient recruitment, especially since this species relies on tandem recruitment: if individual memory of food sites is involved, those ants who know where food sites are located can quickly recruit nestmates to these sites within an activity bout. Cole (1991a,b,c) reports similar observations in *L. allardycei*.

#### 4.3. Conclusion

In conclusion, we have presented a simple model of foraging that shows that synchronized patterns of activity can be advantageous, if workers perform foraging in synchrony. This principle, which can apply to any task for which there are increasing returns for increasing group size, does not contradict other possible ultimate explanations but rather provides a broader view of such explanations: Franks and Bryant (1987) or Robinson (1992) suggested that flows of information and/or information sampling are optimized, which means that there are increasing returns when group size increases; Franks et al., (1990) conjecture that workers work only when necessary is more easily satisfied when tasks are performed efficiently (it might even be impossible for the

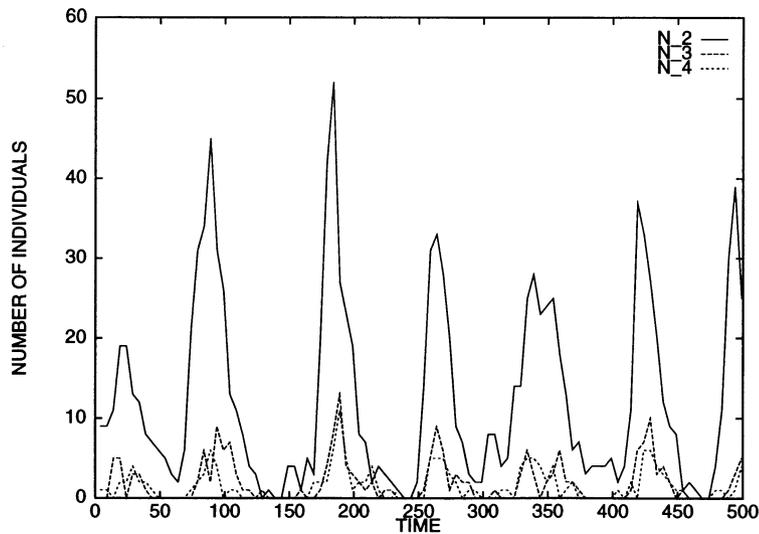


Fig. 12. Dynamics of  $N_2$ ,  $N_3$  and  $N_4$  (two tasks: Eqs. (14)–(19)) for  $a_{A1} = 0.0035 \text{ U}^{-1}/\text{indiv}$ ,  $a_{A2} = 0.035 \text{ U}^{-1}/\text{indiv}$ ,  $D_{1,c} = D_{2,c} = 80$ ,  $T_1 = T_2 = 40 \text{ U}$ , and all other parameters identical to those of Fig. 8.

colony to satisfy its ‘immediate requirements’ without synchronization, as was shown in Section 3); Hatcher et al., (1992) mutual exclusion principle is a particular case of increasing returns (in brood care); Deneubourg and Franks (1995) idea that energy expenditure may be minimized by synchronizing task performance is substantiated

here, as the energy required to maintain stimulus intensity below a given viable level is greater when there is no synchronization (Section 3); furthermore, if, as they suggest, the colony is more vulnerable when building, increasing returns in task performance as the task force size increases further reduces the time during which the colony

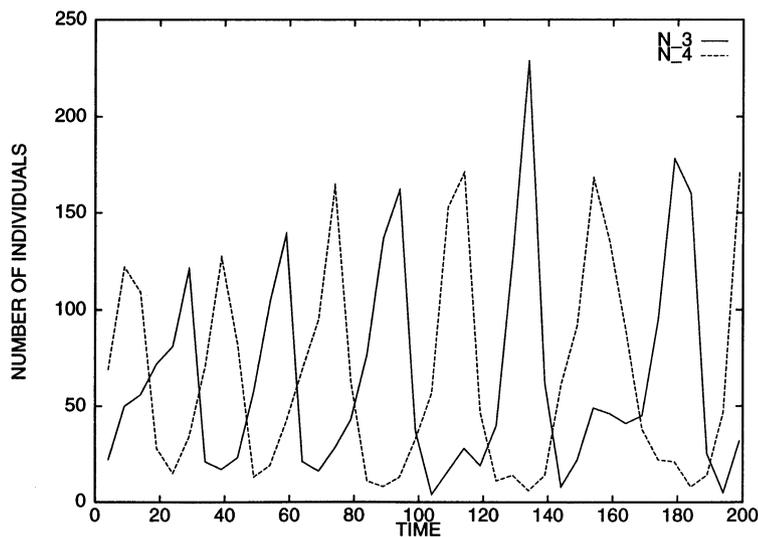


Fig. 13. Dynamics of  $N_3$  and  $N_4$  (two tasks: Eqs. (14), (15), (17), (18) and (20)–(22)) for  $\beta = 4$ ,  $N_0 = 500$ ,  $a_{A1} = a_{A2} = 0.0065 \text{ U}^{-1}/\text{indiv}$ ,  $T_1 = 200 \text{ U}$ ,  $D_{1,c} = D_{2,c} = 400$ , all other parameters identical to those of Eq. (14).

is vulnerable. Even Cole (1991a) suggestion that synchronization is a consequence of colony-level selected traits can be accommodated: in effect, it may be that only one task, say task 1, among all tasks, would benefit from synchronization, whereas other tasks are neutral with respect to synchronization; in that case, synchronization may be selected for at the colonial level because it increases the colony's performance with respect to task 1, but the other tasks would also be synchronized, not because it is more advantageous to perform these tasks in synchrony, but as a side effect of performing task 1 in synchrony. Therefore, synchronization in performing these tasks would not be adaptive per se.

### Acknowledgements

This work was supported in part by a grant from the GIS (Groupe d'Intérêt Scientifique) Sciences de la Cognition. E.B. is supported by the Interval Research postdoctoral fellowship at the Santa Fe Institute.

### References

- Baroni Urbani, C., Kannowski, O.B., 1974. Patterns in red imported fire ant settlement of a Louisiana pasture: some demographic parameters, interspecific competition and food sharing. *Environ. Entomol.* 3, 755–760.
- Beckers, R., Goss, S., Deneubourg, J.-L., Pasteels, J.-M., 1989. Colony size communication and ant foraging strategy. *Psyche* 96, 239–256.
- Beckers, R., Deneubourg, J.-L., Goss, S., Pasteels, J.-M., 1990. Collective decision making through food recruitment. *Insectes Soc.* 37, 258.
- Bernstein, R., 1979. Schedules of foraging activity in species of ants. *J. Anim. Ecol.* 48, 921–930.
- de Biseau, J.-C., Deneubourg, J.-L., Pasteels, J.-M., 1991. Collective flexibility during mass recruitment in the ant *Myrmica sabuleti* (Hymenoptera: Formicidae). *Psyche* 98, 323–336.
- Bonabeau, E., 1996. Marginally stable swarms are efficient and flexible. *J. Phys. I (France)* 6, 309–324.
- Bonabeau, E., Cogne, F., 1996. Oscillation-enhanced adaptability in the vicinity of a bifurcation: the example of foraging in ants. In: Maes, P., Mataric, M., Meyer, J.-A., Pollack, J., Wilson, S. (Eds.), *From Animals to Animats 4: Proc. 4th Int. Conf. on Simulation of Adaptive Behavior*. MIT Press, Cambridge, MA, pp. 537–544.
- Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., 1996. Quantitative study of the fixed threshold model for the regulation of division of labour in insect societies. *Proc. Roy. Soc. Lond. B* 263, 1565–1569.
- Bourke, A.F.G., Franks, N.R., 1995. *Social Evolution in Ants*. Princeton University Press, Princeton, NJ.
- Branham, M.A., Greenfield, M.D., 1996. Flashing males win mate success. *Nature* 381, 745–746.
- Calabi, P., Traniello, J.F.A., Werner, M.H., 1983. Age polyethism: its occurrence in the ant *Pheidole hortensis*, and some general considerations. *Psyche* 90, 395–412.
- Cole, B.J., 1991a. Short-term activity cycles in ants: generation of periodicity by worker interaction. *Am. Nat.* 137, 244.
- Cole, B.J., 1991b. Short-term activity cycles in ants: A phase-response curve and phase resetting in worker activity. *J. Ins. Behav.* 4, 129.
- Cole, B.J., 1991c. Is animal behaviour chaotic? Evidence from the activity of ants. *Proc. R. Soc. Lond. B* 244, 253.
- Cole, B.J., 1994. Chaos and behavior: the perspective of nonlinear dynamics. In: Real, L.A. (Ed.), *Behavioral Mechanisms in Evolutionary Ecology*. The University of Chicago Press, Chicago, pp. 423–443.
- Cole, B.J., Cheshire, D., 1996. Mobile cellular automata models of ant behavior: movement activity of *Leptothorax allardycei*. *Am. Nat.* 148, 1–15.
- Crist, T.O., Haefner, J.W., 1994. Spatial models of movement and foraging in harvester ants (*Pogonomyrmex*) (II): the roles of environment and seed dispersion. *J. Theor. Biol.* 166, 315–323.
- Deneubourg, J.-L., Aron, S., Goss, S., Pasteels, J.-M., Duerinck, G., 1987. Random behaviour, amplification processes and number of participants: how they contribute to the foraging properties of ants. *Physica D* 22, 176–186.
- Deneubourg, J.-L., Franks, N.R., 1995. Collective control without explicit coding: the case of communal nest excavation. *J. Insect Behav.* 8, 417–432.
- Detrain, C., Deneubourg, J.-L., Goss, S., Quinet, Y., 1991. Dynamics of collective exploration in the ant *Pheidole pallidula*. *Psyche* 98, 21–31.
- Edelstein-Keshet, L., Watmough, J., Ermentrout, G.B., 1995. Trail following in ants: individual properties determine population behaviour. *Behav. Ecol. Sociobiol.* 36, 119–133.
- Fourcassié, V., Deneubourg, J.-L., 1994. The dynamics of collective exploration and trail-formation in *Monomorium pharaonis*: experiments and model. *Physiol. Entomol.* 19, 291–300.
- Franks, N.R., Bryant, S., 1987. Rhythmical patterns of activity within the nests of ants. In: Eder, J., Rembold, H. (Eds.), *Chemistry and Biology of Social Insects*. Verlag, München.
- Franks, N.R., Bryant, S., Griffiths, R., Hemerik, L., 1990. Synchronization of the behaviour within nests of the ant *Leptothorax acervorum* (Fabricius)—I. Discovering the phenomenon and its relation to the level of starvation. *Bull. Math. Biol.* 52, 597–612.

- Gordon, D.M., 1983. The relation of recruitment rate to activity rhythms in the harvester ant *Pogonomyrmex barbatus* (F. Smith) (Hymenoptera: Formicidae). *J. Kans. Entomol. Soc.* 56, 277–285.
- Goss, S., Deneubourg, J.-L., 1988. Autocatalysis as a source of synchronized rhythmical activity in social insects. *Insectes Soc.* 35, 310–315.
- Haefner, J.W., Crist, T.O., 1994. Spatial models of movement and foraging in harvester ants (*Pogonomyrmex*) (I): the roles of memory and communication. *J. Theor. Biol.* 166, 299–313.
- Hatcher, M.J., Tofts, C., Franks, N.R., 1992. Mutual exclusion as a mechanism for information exchange within ant nests. *Naturwissenschaften* 79, 32–34.
- Hemerik, L., Britton, N.F., Franks, N.R., 1990. Synchronization of the behaviour within nests of the ant *Leptothorax acervorum* (Fabricius)— II. Modelling the phenomenon and predictions from the model. *Bull. Math. Biol.* 52, 613–628.
- Jeanne, R.L., 1986. The evolution of the organization of work in social insects. *Monitore Zool. Ital.* 20, 119–133.
- Keller, L., 1995. Parasites, worker polymorphism, and queen number in social insects. *Am. Nat.* 145, 842–847.
- Krafft, B., Pasquet, A., 1991. Synchronized and rhythmical activity during the prey capture in the social spider *Anelosimus eximus* (Araneae Theridiidae). *Insectes Soc.* 38, 83–90.
- Leinaas, H.P., 1983. Synchronized moulting controlled by communication in group-living collembola. *Science* 219, 193–195.
- Miramontes, O., Solé, R.V., Goodwin, B.C., 1993. Collective behaviour of random-activated mobile cellular automata. *Physica D* 63, 145.
- Pasteels, J.M., Deneubourg, J.-L., Goss, S., 1987. Self-organization mechanisms in ant societies (I): Trail recruitment to newly discovered food sources. *Exp. Suppl.* 54, 155–175.
- Robinson, G.E., 1992. Regulation of division of labor in insect societies. *Ann. Rev. Entomol.* 37, 637–665.
- Tinbergen, N., 1963. *The Herring Gull's World. A Study of the Social Behaviour of Birds.* Collins, London.
- Verhaeghe, J.-C., 1982. Food recruitment in *Tetramorium impurum* (Hymenoptera: Formicidae). *Insectes Soc.* 29, 67–85.
- Verhaeghe, J.-C., Deneubourg, J.-L., 1983. Experimental study and modelling of food recruitment in the ant *Tetramorium impurum* (Hym. Form). *Insectes Soc.* 30, 347–360.
- Wilson, E.O., Hölldobler, B., 1988. 'Dense heterarchies and mass communication as the basis of organization in ant colonies. *Trends Ecol. Evol.* 3, 65–68.