FLEXIBILITY AT THE EDGE OF CHAOS: A CLEAR EXAMPLE FROM FORAGING IN ANTS

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ABSTRACT

Starting from a clear, experimentally verified, example of a flexible biological system — an ant colony —, it is hypothesized that adaptability is enhanced at the "edge of chaos", that is, in the vicinity of a point of instability. An ant colony exhibiting an appropriate combination of group and mass recruitment can adaptively switch to a newly introduced food source if it is richer: this is precisely the case of some species, such as *Tetramorium caespitum*, whose behavioral parameters are argued to be those characterizing the edge of chaos. Several simple models of foraging show the robustness of the argument.

1. INTRODUCTION

The notion of the edge of chaos (EOC) has attracted considerable interest among biologists in the last few years. The exact meaning of EOC depends on the context within which it is used, but roughly speaking, it describes the vicinity of some instability point separating a region of more ordered (or less random) behaviour, from a region of less ordered (or more random, or more chaotic) behaviour. Such an instability point, if it is critical in the same sense as second-order equilibrium phase transitions in physics are critical, has some interesting characteristic features: events of all sizes are taking place (powerlaw distribution of sizes), the susceptibility diverges, that is, the response function becomes infinitely sensitive to external perturbations, the correlation functions decay slowly (algebraically) in space and time, fractal structures are generated, and finally it can be related to symmetry-breaking (SB), a notion to which I shall come back in detail.

Why should biologists feel concerned with such a concept, that remains theoretical and apparently confined to the realm of physics? There are two separate biological contexts where the EOC has been discussed and may be insightful:

(i) Evolution can be considered as a process just at the edge of chaos (Kauffman & Johnsen, 1991; Kauffman, 1993). This results from the fact that evolutionary processes amount, to a first simple approximation, to adaptive walks in rugged interconnected fitness landscapes where the fitness of a given species depends on other species. Therefore, the

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disappearance of a species can trigger the disappearance of many other directly or indirectly connected species : such events, that one might call 'punctuated equilibria' (Gould, 1977), may be of all sizes, and constitute the highly sensitive response of the evolutionary system to a perturbation. Several simple models of evolution have been developed by physicists, that rely on the notion of barrier against mutation and display powerlaw size distributions of events — that is, large events are not exponentially unlikely (Bak & Sneppen, 1993; Flyvbjerg *et al.*, 1993; Chau *et al.*, 1995; Ray & Jan, 1994). The same idea may be applied to any coevolutionary process, irrespective of its time scale, such as ecosystems, whose interacting species may follow a dynamics reminiscent of that of evolution (Solé *et al.*, 1992; Kaneko & Ikegami, 1992; Solé & Manrubia, 1995a, 1995b). But I shall not be concerned with this aspect of the EOC in the present paper.

(ii) Another important application of the EOC is to adaptive behaviour: it has been suggested by several authors, biologists or physicists, that a behaviour at the EOC might be optimal from the viewpoint of adaptation. (This viewpoint can also be related to evolutionary processes: for example, Kauffman (1993) argued that 'parallel-processing systems' lying at the EOC are those best able not only to adapt, but also to evolve). Here again, there are two possible ways of exploring this statement, which are not at all incompatible, but rather complementary:

(a) Information transfer, storage and processing are optimized precisely at the EOC. There is a simple argument to get an intuition about why this can be true. Let us think in terms of spatially extended, many-body dynamical systems and Lyapounov exponents (or LE, the local divergence rates of nearby trajectories) (Vastano & Swinney, 1988). Negative LE (order) correspond to a storage property: information is kept under the form of attractors, and any perturbation eventually dies out; on the other hand negative LE prevent information from being transmitted, precisely because perturbations die out. Positive LE (chaos or randomness) prevent information from being stored reliably, but perturbations can be transferred since they may be transmitted to the whole system and/or over long time scales. Phrased differently, this means that different parts of a system cannot communicate in the ordered phase because they function as isolated subsystems, and information spread between them is incoherent in the disordered phase. In conclusion, the exact point where information can in principle be stored and transmitted coherently is just when LE are 0, that is, at the EOC. This is only an intuitive argument, and at least two criticisms can be formulated: (1) it may still be possible to store information under the form of strange attractors (although this storage is not necessarily robust), and (2) it is not enough to store and transmit information, it must also be transformed or processed in some way, but this just means that being at the EOC is a necessary but not sufficient condition. However, the point is interesting and has been developed theoretically by Crutchfield and Young (1992), and by Langton (1990, 1991). In particular, the latter showed that mutual information (a basic requirement for cooperative computation to take place is the presence of a large amount of mutual information between elements of a system) is maximized in elementary cellular automata at the frontier between ordered/periodic and random/chaotic behaviour. Other authors (Packard, 1988; Kaneko, 1994; Solé & Miramontes, 1995) have proposed toy models of biological systems, and evidenced optimal information processing at the EOC, although there have been conflicting results (Mitchell *et al.*, 1993). Of particular interest is the model of ant behaviour based on mobile automata introduced by Solé, Miramontes and Goodwin (1994; Solé & Miramontes, 1995; Goodwin, 1995), who suggested that the optimization of mutual information at a particular critical value of ant density might be

useful to ants in the context of alarm spread (Adler & Gordon, 1991; Frehland *et al.*, 1987). They invoked experimental observations showing that some ants regulate either directly their density (Franks *et al.*, 1990), or contact rates (Gordon *et al.*, 1991), to explain how the exact critical density may be maintained. But, although this approach is promising, it remains highly speculative, theoretical and rather ill-defined, and still has a long way to go before being really applicable to biological systems, perhaps because it relies on the notion of computation, a double-edged sword. There may be a biologically more relevant and less formal approach to start with.

(b) The path that I shall now follow may seem less ambitious, but is certainly more directly in contact with biological reality. It is related to the SB property of some instability points. Breaking a symmetry means selecting one among several a priori equivalent (or symmetric) possible states. Hence breaking a symmetry amounts to making a choice or taking a decision, and the reverse is to a large extent true. Besides, fluctuations, while they certainly reduce the stability and reliability of this choice, allow the system to explore new possibilities (Haken, 1984): an optimal trade-off between exploration and exploitation can be realized in the vicinity of a SB bifurcation point. This paradigm is already known to biologists, and has turned out to be insightful for the understanding of many features of morphogenesis (see for example Murray, 1988). But, as emphasized by Goodwin (1995), morphogenetic processes involve an irreversible cascade of SB events until the adult form is reached, there is no way back, while adaptive behaviour requires broken symmetries to be restored as often as necessary. In effect, a viable biological system must be adaptable in order to keep up with changes in its environment: if an irreversible decision has been taken (irreversible SB), any subsequent modification of the environment will not be adequately treated. In an adaptable system, "*new patterns of order can emerge as the symmetries break again, should these be appropriate*" (Goodwin, 1995). Obviously, if a system is to be able to deal with environmental changes, that is, to break symmetries in the right way when required, it must either maintain itself in the vicinity of a SB instability point (the EOC), or come back at more or less regular intervals to the EOC. It is interesting to note that the two viewpoints, (iia) and (iib) are not unrelated: in effect, the ability of a swarm or any collective biological system to flexibly and relevantly shift its activity in response to a perturbation is optimized at the EOC because of dynamical properties that allow for efficient information gathering and "processing" at the collective level. In particular, collective decisions can be taken because domains of synchronized activity increase due to cooperative effects (this corresponds to the divergence of the characteristic size of synchronized clusters as the system reaches its critical point), while a small spatially and temporally localized perturbation is expected to diffuse in space with a diverging diffusion coefficient (rapid spread of information) (Hohenberg & Halperin, 1977; Lekkerkerker & Boon, 1976). Finally, (iib) is in some sense more general than (iia), since it applies to any system possessing points of instability, and includes, but is not restricted to critical points. My aim in this paper is to illustrate this rather theoretical discussion by giving a simple, yet insightful and fully biological example of a system — an ant colony — whose behaviour is adaptable *because* it lies close to a SB bifurcation. There has been an increasing awareness of the self-organizing properties of social insects, and particularly of ants in the last few years (Deneubourg & Goss, 1989; Bonabeau & Theraulaz, 1994; Theraulaz *et al.*, 1994), and some collective behaviours, such as cooperative foraging, can be modeled along these lines.

The rest of the paper is organized around the example of flexible foraging in ants.

Section 2 serves as a brief introduction to foraging in ants, presents the experimental data of de Biseau *et al.* (1991) and Beckers *et al.* (1989), and describes several models based on those developed by Deneubourg *et al.* (1986), Pasteels *et al.* (1987a, 1987b) and Beckers et al. (1990) to account for the experimental observations. Section 2 is also dedicated to a mathematical (bifurcation) analysis of these models, and it will be shown that some species of ants, that combine group and mass recruitment in their foraging strategies, are exactly at the EOC, and are adaptable because of this property. In section 3, several mechanisms will be described, that allow a system to maintain itself at, or to come back regularly to, the EOC.

2. FORAGING IN ANTS

2.1 Introduction

A lot of species of ants have a trail-laying trail-following behaviour when foraging: individuals deposit a chemical substance called pheromone as they return from the food source (sometimes also as they go to the source, or even as they explore the environment), and foragers follow pheromone gradients. The process whereby an ant is influenced towards a food source by another ant or by a chemical trail is called recruitment. In a few words, there are three basic types of recruitments in ants: tandem recruitment, whereby an individual signals to another one by direct physical interaction that it 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 behaviours. While the first two strategies involve a leader that guides another individual or a group of individuals to the food source, mass recruitment is 'anonymous'. See for example the review by Deneubourg & Goss (1989) to know how mass recruitment can lead to the selection of the nearest source. Edelstein-Keshet (Edelstein-Keshet, 1994) recently argued that evolution may have driven societies of trail-followers to the vicinity of behavioral bifurcations, where they can make transitions in a highly sensitive way — in analogy with the diverging susceptibility of critical points. This is a conjecture I would like to develop with a simple example.

I shall not be interested here in how collective behaviour emerges from individuals' actions, but rather focus on macroscopic behaviour directly, from a 'phenomenological' standpoint (in the spirit of Deneubourg *et al.*, 1986, or Edelstein-Keshet, 1994). Millonas (Millonas, 1992; Rauch *et al.*, 1995) developed in the same context an interesting physics-inspired formalism to deal with collective decision making from individual activities: his microscopic model, where the behaviour of individual ants is described by local transition probabilities, allows for a more rigorous treatment of *internal* fluctuations, but the model I shall resort to can be considered as a mean-field version, whose accuracy is sufficient for my purpose. Moreover, it is known that internal fluctuations do not qualitatively modify bifurcation diagrams in most cases, while multiplicative noise, that is, fluctuations of behavioral parameters, can on the contrary modify the picture dramatically (Horsthemke & Lefever, 1984); it would be interesting to study the effects of such fluctuations on the resulting foraging behaviour (for example, it is clear to experimenters that the recruitment rate undergoes fluctuations, since it is more difficult to stimulate foraging when the colony is 'satisfied').

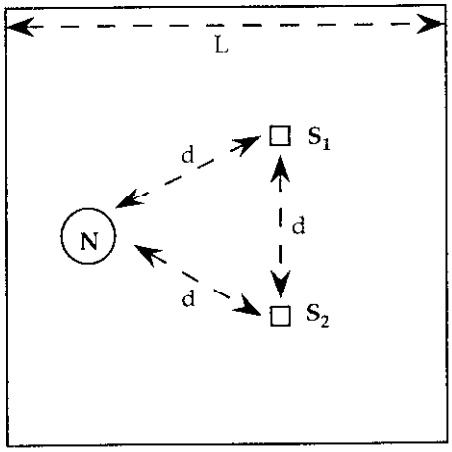


Fig. 1. Experimental setup, comprising a nest (N) and two food sources (S_1 and S_2) located at the same distance from the nest, and forming an equilateral triangle of size d with the nest. The foraging area is a $L \times L$ square. Both L and d are adjusted to the speed of ants, and therefore depend on the species. For example, for all species but Lu, L = 80 cm, while for Lu, L = 30 cm; typically, d is of the order of $L/2$.

2.2 Experimental Results

It may be useful to briefly describe the experiments (Beckers *et al.* (1989a) and de Biseau *et al.* (1991)) that will be discussed and modeled. Colonies are provided with two food sources at a reasonable distance from their nests, after a period of starvation (see Fig. 1). Let S_1 (respectively S_2) be the first (respectively second) source presented to the colony, t_1 (respectively t_2) the time of its introduction, Q_1 (respectively Q_2) its quality, for example its sucrose concentration, and $h = Q_2 - Q_1$ the quality difference between the sources. It will always be assumed that $t_1 = 0$. Three different experiments E1, E2, and E3 have been carried out, characterized by:

(E1) $h = 0$ and $t_1 = t_2 = 0$,
(E2) $h > 0$ and $t_1 = t_2 = 0$,
(E3) $h > 0$ and $t_1 < t_2$.

In (E3), $t_1 < t_2$ means that the second source is presented to the colony after a 'stationary' state has been reached with the first source only. Three basic types of behaviours B1, B2, and B3 have been observed, depending on the species:

(B1) Colonies exhibiting behaviour B1:
  (B1i) strongly break the symmetry between the identical sources in E1,
  (B1ii) clearly choose S_2 in E2, and
  (B1iii) select S_1 before S_2 is introduced in E3, but cannot switch to the better quality source S_2 when it is presented.

(B2) Colonies exhibiting behaviour B2:
  (B2i) strongly break the symmetry between the identical sources in E1,
  (B2ii) clearly choose S_2 in E2, and

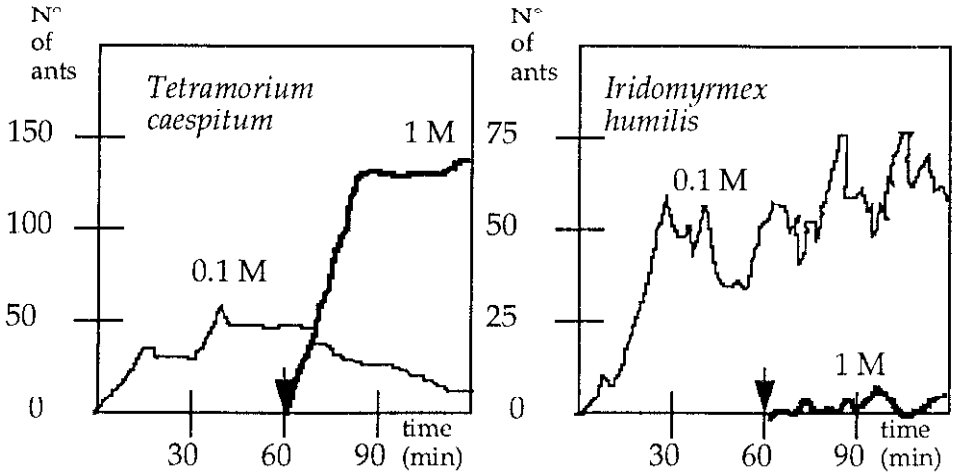


Fig. 2. (modified from(Beckers *et al.*, 1990): Evolution of the number of individuals exploiting two sources put successively in the environment. The first source is a 0.1 *M* sugar source, while the second one is richer, since it is 1*M*. **a)** *Tetramorium caespitum* (mass and group) (the arrow indicates that a new 1 *M* source has been placed in the environment), **b**) *Iridomirmex humilis* (= *Linepithema humile*) (mass).

(B2iii) select S_1 before S_2 is introduced in E3, but switch to the better quality source S_2 when it is presented, which is then much more exploited than the lower quality source. (B3) Finally, colonies exhibiting behaviour B3 exploit both sources symmetrically in all experiments.

Some of the results reported by Beckers *et al.* (1989a) are presented in Fig. 2. There is actually an intermediate type of behaviour, B2', where the colony can switch to the richer source introduced after a delay only when the difference h between the sources is sufficiently large.

Tetramorium caespitum (Tc) can resort to mass recruitment and to group recruitment, while *Iridomyrmex humilis* (Ih) uses mass recruitment only. Tc can always switch to the richer source as it is introduced, until there are many more individuals exploiting the richer source than the poorer one (B2). Another species, *Myrmica sabuleti* (Ms) can do so only when the difference between the sources is sufficiently large (B2'). On the contrary, Ih is unable to adapt to the new environment and remains trapped in the first trail (the same is also true for *Lasius niger*, a species resorting to mass recruitment) (B1). This is so because mass recruitment is 'too' efficient (Beckers *et al.*, 1989a). Other experiments on *Leptothorax unifasciatus* (Lu), using tandem recruitment only, are also reported: Lu is capable to exploit the richer source, but individuals are evenly distributed among both sources (B3). An appropriate combination of group and mass recruitment seems to allow a maximum adaptive efficiency, since group recruitment enables reasonably sized exploration groups to exist and mass recruitment enables the amplification of the better trail. Therefore, ants resorting to such a combination of recruiting strategies can compare and then choose: ants using mass recruitment cannot compare (the alternative source remains

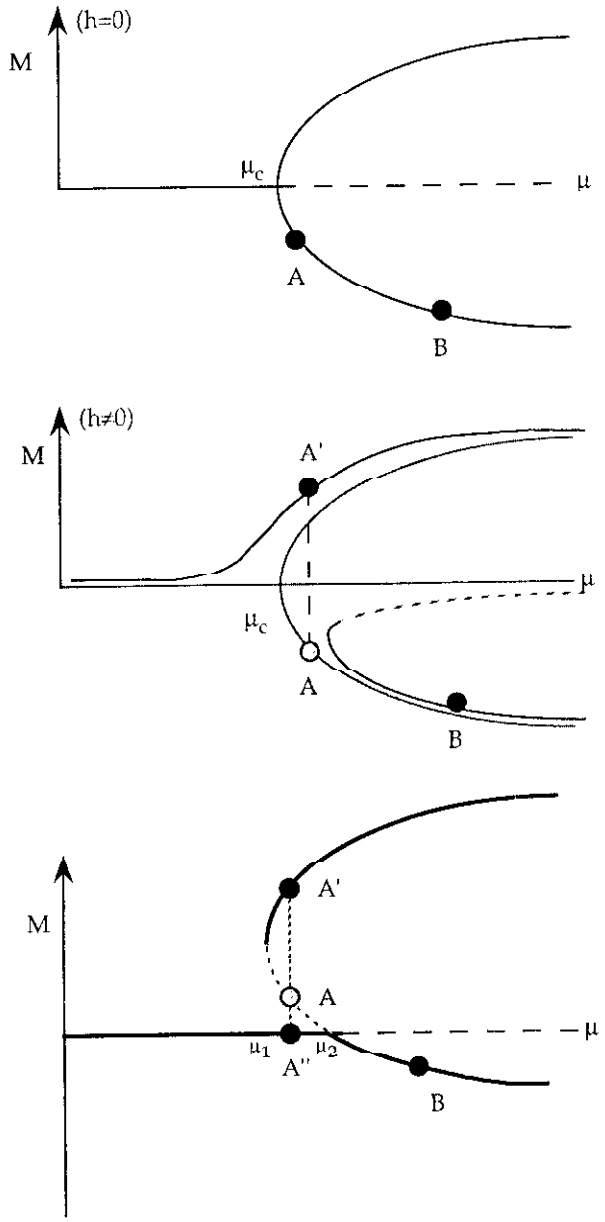


Fig. 3. **a)** Sketch of a bifurcation diagram in the absence of external field (critical or pitchfork bifurcation); *A* and *B* are characterized by $\mu_c \leq \mu(A) << \mu(B)$, and are both on the same branch of stable solutions for the order parameter *M*. **b)** Sketch of a bifurcation diagram in the presence of an external field (imperfect bifurcation); *B* remains on its branch, while *A* is attracted towards the more favorable state. **c)** Sketch of a bifurcation diagram in the presence of a perturbation which destroys the $M \rightarrow -M$ symmetry (double sided transcritical bifurcation); *B* remains on its branch, while *A* is attracted towards the more favorable state.

unknown), while colonies resorting to tandem recruitment can compare but cannot choose (a trail to a new, richer source is not sufficiently amplified to win). de Biseau *et al.* (1991) also invoked recruitment rate modulation as a function of source's quality (a phenomenon observed in several species, see Hantgartner, 1969; Cammaerts, 1977; Cammaerts & Cammaerts, 1980; Veraeghe, 1982) as a very reasonable explanation of some experimental results, particularly those concerning the B2' behaviour of Ms.

There are clues allowing us to suggest that colonies exhibiting flexible behaviour (B2) in the two sources experiment are certainly close to a point of instability, as can be seen from the simple argument depicted in Fig. 3. In effect, they are able to break the symmetry between two equivalent sources, indicating that they are beyond some bifurcation point, and at the same time they can reorganize when a richer source is introduced, whatever small the difference may be (up to a scale which experiments have not been able to determine), indicating that they must be very close to that point. Note that since they are close to the bifurcation point, a small variation in the number of foragers (due for instance to a fluctuating recruitment rate) can cross the critical value.

To see this more clearly, let us assume that the system's behaviour can be characterized at the macroscopic level by a quantity M, whose dynamical evolution undergoes a (codimension 1) critical bifurcation as a behavioral control parameter μ reaches a critical value μ_c. One very simple equation (see e.g., Manneville, 1986) displaying a critical bifurcation at $\mu = \mu_c$ is: $\partial_t M = (\mu-\mu_c)M-M^3$. When $\mu < \mu_c$, the only stationary solution to this equation is $M = 0$, which becomes unstable at $\mu = \mu_c$, so that there are two solutions $M = \pm(\mu-\mu_c)^{1/2}$ for $\mu > \mu_c$. This situation is depicted in Fig. 3a, where dashed lines represent unstable solutions. Consider two different systems (e.g., two species A and B) with two different values of μ, both greater than μ_c (usually, $\mu > \mu_c$ is the ordered phase and the stable solution for $\mu < \mu_c$ is the disordered state): system A is close to μ_c, while B is deeper in the ordered phase. For $\mu > \mu_c$, there are two branches of equivalent stable solutions, corresponding to the broken symmetry (for instance, here, the symmetry between the sources); we assume that A and B are on the same branch. The addition of an 'environmental' (external) field h (such as a difference between the sources) can be modeled by

$$\partial_t M = (\mu-\mu_c)M - M^3 + h, \qquad (1)$$

the corresponding bifurcation diagram for fixed h being that of Fig. 3b. (Alternatively, the new bifurcation could as well be two-sided transcritical because of the loss of the $M \to -M$ symmetry, but the argument would still be valid: see Fig. 3c). We see in particular that system A cannot be in the same state as in Fig. 3a and is attracted towards A', while B is still on the same branch of solutions, which is less favourable given the field h. In other words, A has been able to shift its activity towards a state better adapted to the environment. If the field reverses direction, A will still be able to switch. Note also that A cannot switch to the better state if the field is too small: the advantage of being close to the point of instability slightly in the ordered phase is now clear, since the ordered phase allows structured patterns of activity to be sustained, and prevents the system from switching too often if the gain is not sufficient, while the system can still switch if the gain is large enough.

2.3 Model (A)

In what follows, the total number of available foragers N will play the role of the control parameter μ of Fig. 3. This may not be the most relevant choice, and more refined or complicated models with many more behavioral parameters accounting for the detailed activities of the foragers can be developed. Yet, the same argument, I believe, remains valid, namely colonies whose behavioral parameters lie close to bifurcation values are more adaptable, or more precisely, flexible. At fixed N, the mean-field equations of motion, that is, neglecting fluctuations, are given by (see Deneubourg *et al.*, 1987a; Pasteels *et al.*, 1987a, 1987b):

$$\begin{aligned} \frac{dX_i}{dt} &= a_i \frac{X_i}{N} \frac{X_i}{g_i + X_i} \left(N - E - \sum_{i=1}^{n} X_i \right) + cE - bX_i \\ \frac{dE}{dt} &= \left(\sum_{i=1}^{n} a_i \left(1 - \frac{X_i}{g_i + X_i} \right) \frac{X_i}{N} \right) \left(N - E - \sum_{i=1}^{n} X_i \right) - ncE - pE \end{aligned} \tag{2}$$

where n is the number of sources, E the number of exploring (or lost) ants, X_i the number of ants exploiting source i (i = 1,2 in the present case), and $N - E - \sum_{i=1}^{n} X_i$ the number of foragers in the nest, $1/p$ the time taken by explorers before returning to the nest if they do not find any source, c the probability that any source is found by chance by an explorer, and $1/b$ the average residence time of a forager at the source. If α is the recruitment rate, δ is the fraction of ants encountered by 1 individual within one coarse grained unit of time, $\delta \frac{X}{N}$ is the probability for a non-foraging ant to meet a foraging ant, and $\alpha\delta \frac{X}{N}$ is the fraction of non-foraging ants effectively recruited: $a \equiv \alpha\delta$ therefore plays the role of an effective recruitment rate including factors such as the foraging area or the physiological state of the colony. In a number of species, the accuracy with which recruitment is performed depends not only on the recruitment rate (the influence of those ants who found a food source over the remaining ants), but also on the ability of a given ant to follow a trail, which in turn depends on the strength of the trail, i.e. on the number of individuals X foraging at the food source: the fraction $f = \frac{X}{g+X}$ of recruited foragers reaching the food source corresponds to the reliability of trail following; we see that this reliability increases as X grows above the threshold g (f is small, of the order of $1/g$ when $X << g$, and f is close to 1 when $X >> g$). This is a reasonable assumption provided the timescale of pheromone's variations is of the same order as variations of the number of foragers: this is not always the case, and section 2.4 will extend the present model to the case where pheromone decay is slow with respect to the variations of the number of foragers. A higher (respectively lower) value of a_i (respectively g_i) corresponds to a higher-quality source. I shall make the simplifying assumption that only a_i is affected by the source's quality, but simulations show that this does not qualitatively modify the results. The difference between the sources is expressed in the following form: $a_i^- = (1-\Delta)a_i^+$, where a_i^- (resp. a_i^+) is the effective recruitment rate to the poorer (resp. richer) source ($h \equiv \Delta$).

A short stability analysis shows that the null state ($X_1 = X_2 = E = 0$) is a stable

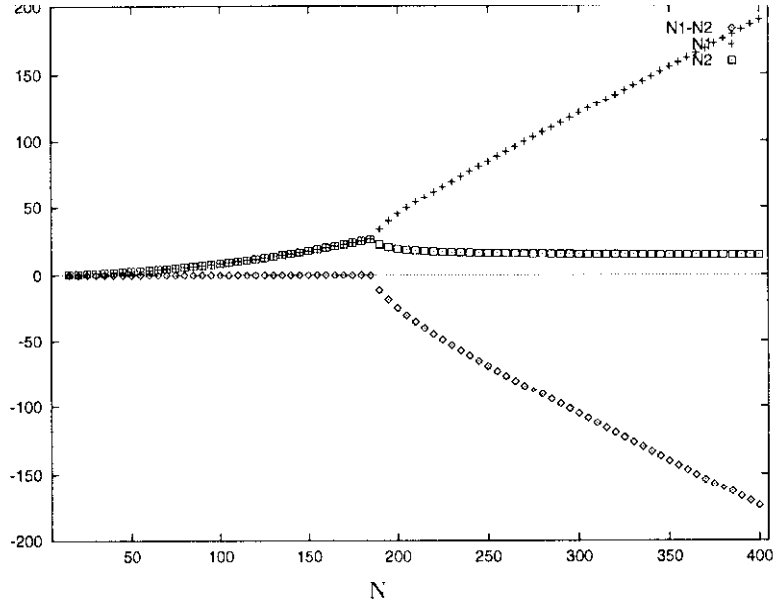


Fig. 4. Simulation of experiment E1 (see text): N_1, N_2, and $M = N_2 - N_1$ as a function of N, with $a_1 = 0.03$, $a_2 = 0.03$, ($\Delta = 0$). $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

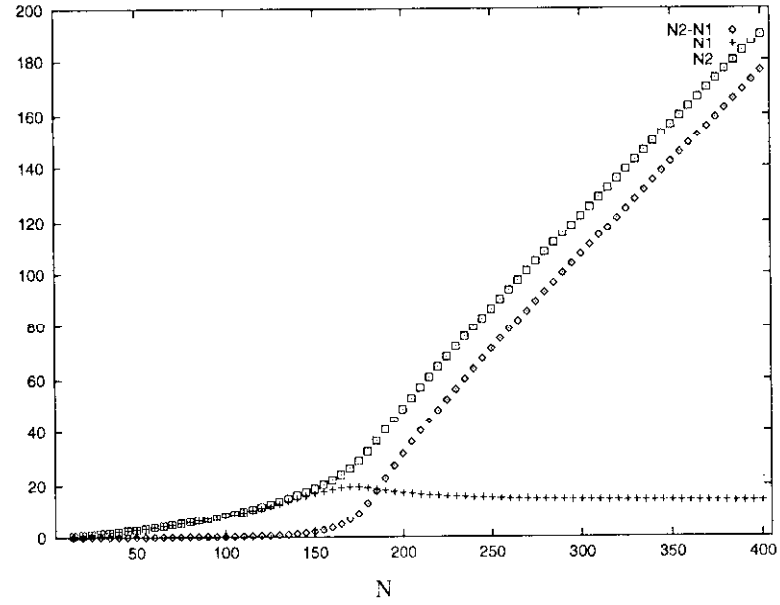


Fig. 5. Simulation of experiment E2: N_1, N_2, and $M = N_2 - N_1$ as a function of N, with $a_1 = 0.0297$, $a_2 = 0.03$, ($\Delta = 0.01$), $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

stationary solution if $c < \frac{1}{2}\frac{bp}{a-b}$, that is, if the probability of finding the source by chance is smaller than some threshold. I shall assume that this is not the case, so that the null state is unstable. Such an assumption can readily be made true experimentally if the foraging area is forced to be small enough. In the figures, the asymptotic value of X_1 (respectively X_2) is denoted by N_1 (respectively N_2). The quantity $N_2 - N_1$ plays the role of the 'order parameter' M of Fig. 3. This simple model leads to an amplification of fluctuations and to the selection of one of the food sources, provided $N \geq N_c$. We have chosen parameters (identical to those proposed in Pasteels *et al.* (1987a, 1987b)) such that $c > \frac{1}{2}\frac{bp}{a-b}$, so that the null state is unstable: for $N < N_c$, foraging exists, but the two food sources are exploited symmetrically. Since fluctuations are not taken into account in this deterministic model, they must appear in the form of 'disorder' in the initial conditions.

In all the simulations, the initial conditions contained slightly more individuals foraging at source 1 than at source 2; each point of the curves or surfaces has been obtained from averaging over Monte Carlo simulations corresponding to equations (2). Let us first study the simulation of experiment E1 (that is, $\Delta = 0$ and $t_1 = t_2 = 0$). The results (N_1, N_2, and $M \equiv N_2 - N_1$ as a function of N) are presented in Fig. 4. The symmetry between the sources is broken if $N > N_c = 185$, where the system undergoes a critical bifurcation. Below that value, foraging is unstructured (i.e. symmetric), the order parameter is equal to 0. The results corresponding to E2 can be found in Fig. 5 (similar to Fig. 4, but with $h = \Delta > 0$). The richer source is clearly more exploited for $N \geq 100$. Foraging is approximately symmetric for low values of N. The order parameter starts to deviate from 0 around $N = 100$, but the richer source is strongly selected only for $N > 150$. There has been a transformation of the critical bifurcation into an imperfect one, exactly as in Fig. 3b. As a further test of the relevance of the imperfect bifurcation, simulations have been performed with many more individuals at source 1, and led to a selection of source 1; note that because the pheromonal field varies on the same timescale as the number of foragers, performing such simulations is equivalent to simulating E3. The results corresponding to E3 are represented in Figs. 6 and 7, with $\Delta = 0.01$ and $\Delta = 0.03$, respectively. As can be seen, if the 'external field', embodied in Δ, is small, the region where the colony can switch to the newly introduced, richer source, is correspondingly small. For example, for $\Delta = 0.01$, s_2 is selected for $160 < N < 210$ (the second bifurcation is strongly discontinuous), while for $\Delta = 0.03$, s_2 is selected for $115 < N < 295$. Despite its simplicity, this model can therefore account for all the experimentally observed behaviours: B1 corresponds to a large number of active foragers (say, $N > 350$), B3 to a small number (say, $N < 100$), and *the adaptable behaviour B2 to a narrow range of values ($185 < N < 195$) very close to the point of instability of the $\Delta = 0$ system*, as expected. Even B2' can be explained by the extension of the adaptive region when Δ gets large: for example, a colony with $250 < N < 295$ cannot switch to the richer source if Δ is too small, but can do so if Δ gets larger.

2.4 Model (B)

The fact that pheromonal trails have a lifetime (possibly much) greater than the variation timescale of foragers on the trails can be accounted for very easily, by modifying equations (2) as follows:

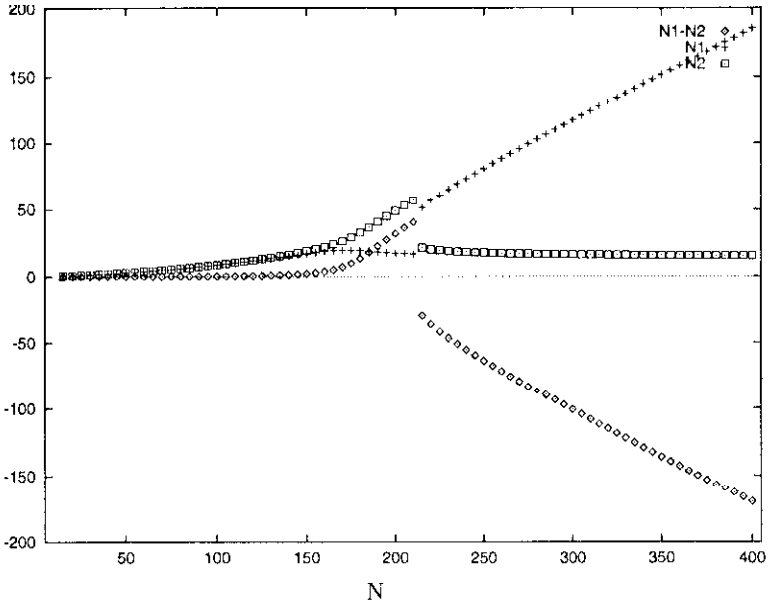


Fig. 6. Simulation of experiment E3: N_1, N_2, and $M = N_2 - N_1$ as a function of N, with $a_1 = 0.0297$, $a_2 = 0.03$, ($\Lambda = 0.01$), $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

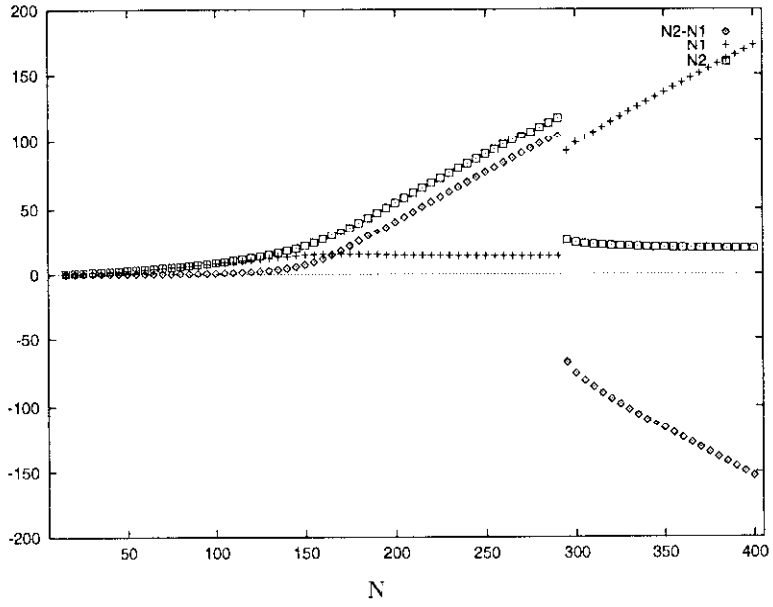


Fig. 7. Simulation of experiment E3: N_1, N_2, and $M = N_2 - N_1$ as a function of N, with $a_1 = 0.0291$, $a_2 = 0.03$, ($\Delta = 0.03$), $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

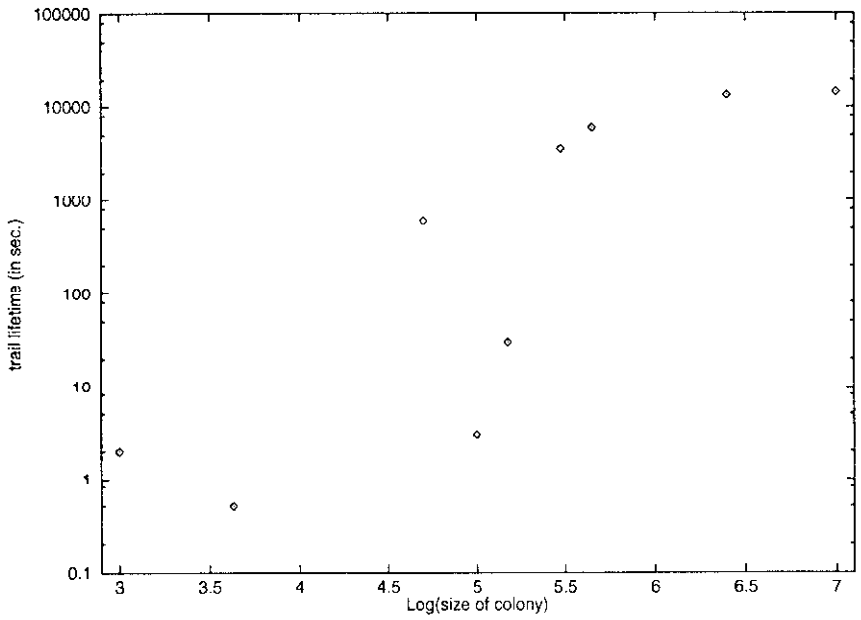


Fig. 8. Log-log plot of trail lifetime vs. size of colony.

$$\frac{dX_i}{dt} = a_i \frac{X_i}{N} \frac{Y_i}{g_i + Y_i}\left(N - E - \sum_{i=1}^{n} X_i\right) + cE - bX_i$$

$$\frac{dE}{dt} = \left(\sum_{i=1}^{n} a_i \left(1 - \frac{Y_i}{g_i + Y_i}\right)\frac{X_i}{N}\right)\left(N - E - \sum_{i=1}^{n} X_i\right) - ncE - pE \qquad (3)$$

$$\frac{dY_i}{dt} = X_i - \chi Y_i$$

where Y_i is the amount of pheromone (on the scale of X) on trails to source i, and $\chi < 1$ is the decay rate due to diffusion and evaporation (the relaxation timescale of the pheromone is then given by $\tau = \frac{1}{\log(1-\chi)}$). The longer lifetime of pheromone gives rise to more strongly marked trails, and therefore to less flexible behaviour over a wider range of behavioral parameters. It is interesting to note also the non-arbitrary relationship that exists between the measured lifetime of trails and the size of the colony (Fig. 8 — the data comes from Edelstein-Keshet *et al.*, 1995 and Beckers *et al.*, 1989b): species with larger colonies have in general long trail lifetimes. This diagram (which contains only a few points for lack of complete data) shows that the effect of pheromone decay can *possibly* be absorbed into the number of active foragers. Note the difference between pheromone and trail lifetimes: one hopes that both are not completely decorrelated, but the interpretation

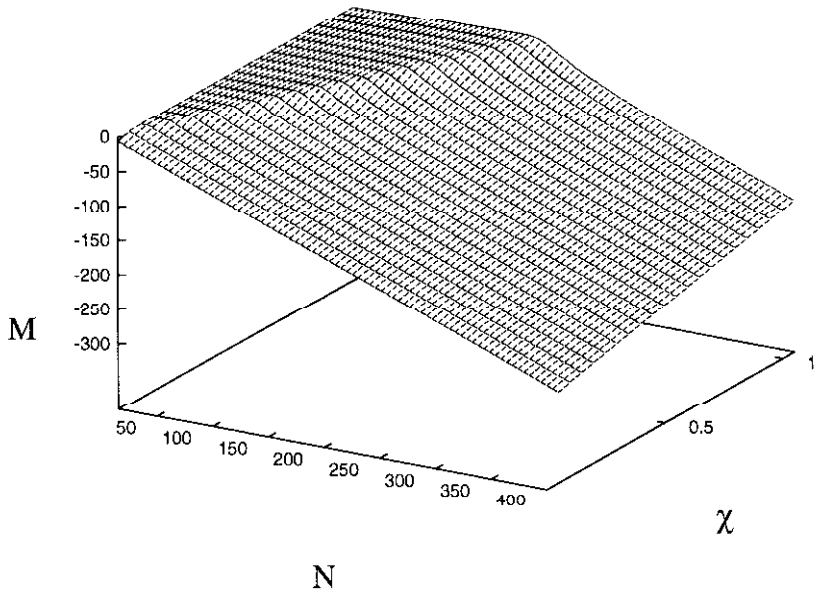


Fig. 9. Simulation of experiment E1: x-axis: N varies from 10 to 400; y-axis: χ varies from 0 to 1; z-axis: $M = N_2 - N_1$; $a_1 = 0.03$, $a_2 = 0.03$, ($\Delta = 0$), $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

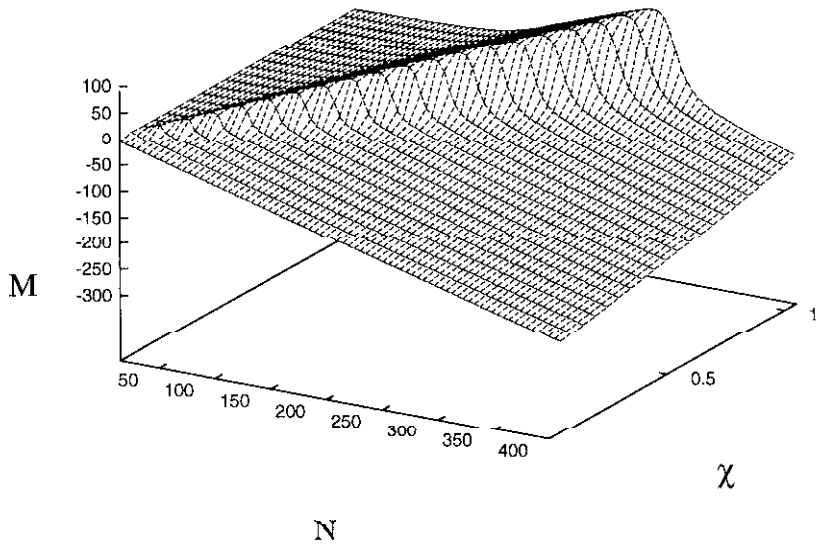


Fig. 10. Simulation of experiment E3: x-axis: N varies from 10 to 400; y-axis: χ varies from 0 to 1; z-axis: $M = N_2 - N_1$; $a_1 = 0.0297$, $a_2 = 0.03$, ($\Delta = 0.01$), $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

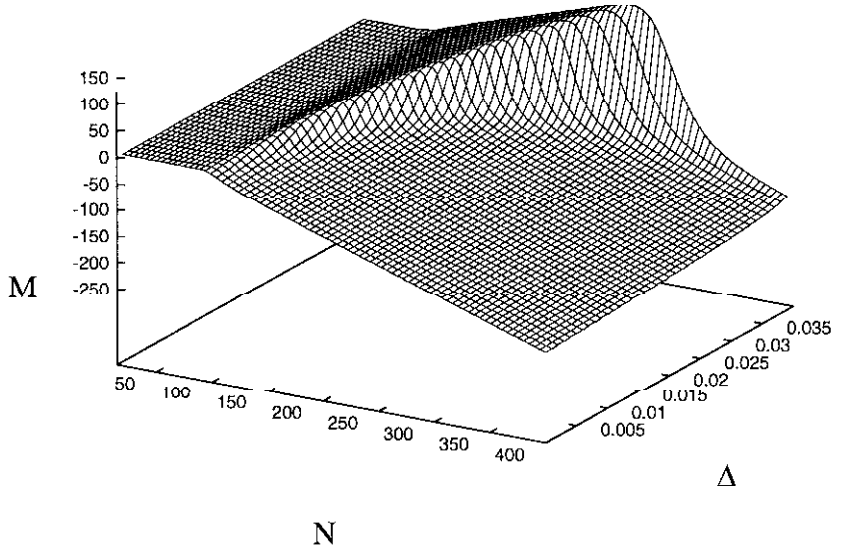


Fig. 11. Simulation of experiment E3: x-axis: N varies from 10 to 400; y-axis: Δ varies from 0.005 to 0.035; z-axis: $M = N_2 - N_1$; a_1 ranges from 0.02895 to 0.02985, $a_2 = 0.03$, $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$, $\chi = 0.05$.

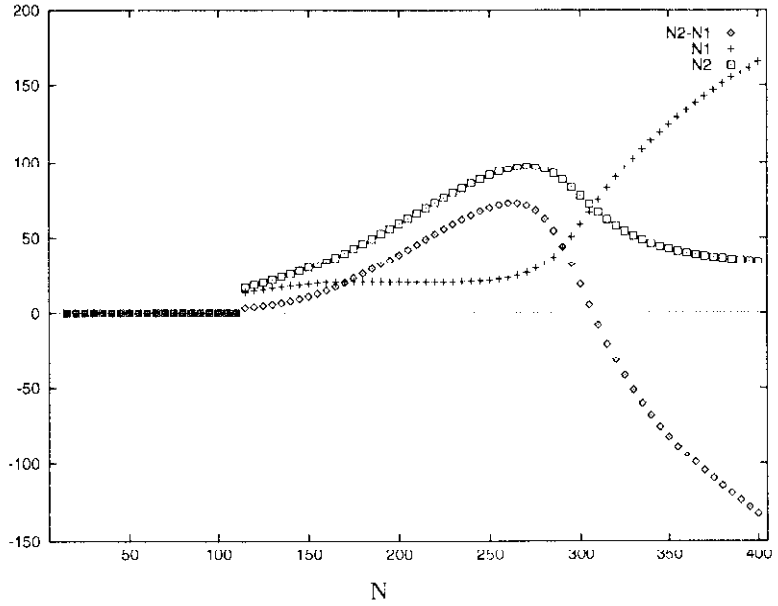


Fig. 12. Simulation of experiment E3: N_1, N_2, and $M = N_2 - N_1$ as a function of N, with $a_1 = 0.02895$, $a_2 = 0.03$, ($\Delta = 0.035$), $b = 0.017$, $c_i = 0.018(1-e^{-\chi Y_i})$, $g = 25$, $p = 0.15$, and $\chi = 0.05$.

of Fig. 8 is not as clear as it might first appear. This uncertainty points to the need for (clear) experimental data on the physico-chemical properties of pheromonal substances (e.g., how, and over what timescales do they diffuse and evaporate?). In any case, I shall make the simplifying assumption that the number of active foragers can be considered as an 'effective' control parameter that gives a reasonably good image of how the colony's behaviour is controlled.

The results for E1 within this context are presented in Fig. 9 for χ varying from 0 to 1. The essential modification with respect to Fig. 4 is that bifurcation points are shifted as χ varies. E2 yields essentially the same results as before; as a test of the imperfect bifurcation, simulations have been performed with many more individuals at source 1, and led to a selection of source 1. The results for E3 are presented in Fig. 10. We see that the region where a colony can be adaptable is the 'top of a wave' of a rather small width in parameter space, close to the point of instability of the unperturbed system with $h = 0$, i.e., $\Delta = 0$. The effect of varying Δ on case E3 is shown in Fig. 11, for $\chi = 0.05$: we see that the size S of the adaptive region increases with increasing Δ, which is not surprising. Finally, the probability for a lost ant to find a source by chance certainly depends on the length of trails leading to that source. To include this effect, c can be replaced, e.g., for source i, by $c_i = c\left(1-e^{-\chi Y_i}\right)$. The addition of this factor does not qualitatively modify the results, as Fig. 12 shows ($\Delta = 0.02895$ and $\chi = 0.05$).

2.5 Model (C)

The models presented in the previous subsections were simple models derived from an original suggestion by Deneubourg *et al.* (1987a) and Pasteels *et al.* (1987a, 1987b). Let us now consider a more recent model introduced by Beckers *et al.* (1990) to account more explicitly for the differences that exist between group and mass recruitment. They suggest that the degree of precision of trail following is given by $F = \frac{g+X^2}{h+X^2}$ (where $g < h$ are two parameters which depend on the quality of the food source and characterize the efficiency of the trail at the beginning of recruitment) in the case of mass recruitment. In the case of group recruitment, $F = k$ is a constant depending only on the quality of the food source. A given combination of group and mass recruitment can then be characterized by a coefficient β such that $F = (1-\beta)k+\beta\frac{g+X^2}{h+X^2}$, where $\beta \in [0,1]$. In the mean-field equations of motion (2), F_i should now be replaced by

$$F_i = (1-\beta)k_i+\beta\frac{g_i+X_i^2}{h_i+X_i^2} \qquad (4)$$

The results of the numerical integration of the equations with this form of F_i, in the case of experiment E3, are depicted on the bifurcation diagram of Fig. 13, where the asymptotic difference between the number of foragers at source 2 minus the number of foragers at source 1 (i.e., $M \equiv \lim_{t\to\infty}(X_2-X_1)$), is represented as a function of both β (x-axis) which varies from 0 to 1 and N (y-axis) which varies from 10 to 400. All other parameters have been assigned (biologically relevant or measurable) values suggested by Beckers *et al.*

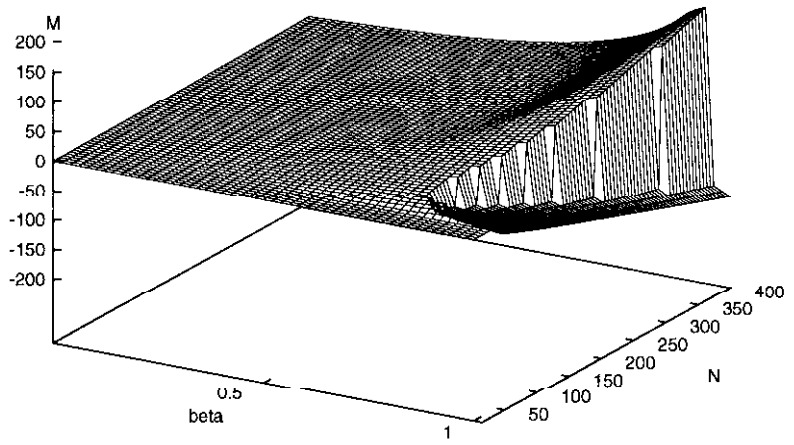


Fig. 13. Numerical integration of equations (1). $M = \lim_{t\to\infty}(X_2 - X_1)$ is plotted (z-axis) as a function of β (x-axis) and N (y-axis), with $a_1 = 0.028$, $a_2 = 0.03$, $b = 0.017$, $c = 0.018$, $h_1 = 37$, $h_2 = 35$, $g_1 = g_2 = 25$, $k_1 = 0.58$, $k_2 = 0.6$, $p = 0.15$. β varies from 0 to 1, and N from 10 to 400.

(1990). As can be seen from Fig. 13, complete mass recruitment is never flexible, while some finite amount of exploring ants allows the colony to switch to the better quality source when group recruitment is used. The most efficient exploitation of the richer source is realized 'at the edge' of the surface, close to the line of instability, where there is a brutal decrease of the number of foragers at source 2 (around $\beta \approx 0.8$). Therefore, if the proportion and/or the influence of group recruitment, which is represented by β in the present model, lies in this particular region, flexibility is assured.

3. 'TUNING' MECHANISMS

In the previous sections, the focus was on the adaptability exhibited by a system close to a point of instability. It remains to know how such a system can maintain itself in a position where it can break symmetries. The aim of the present section is to propose some candidate 'tuning' mechanisms which drive the system towards its threshold of instability. I shall consider here only the simple case of a single instability crossed by the system as some parameter is varied. The more complex picture of a whole set or hierarchy of bifurcations can be obtained, at least qualitatively, directly from this simple case. I see several possible ways (the list is not exhaustive):

(1) The control parameter is more or less randomly fluctuating (F is a random process which can be considered to be independent of E): this may be the case for instance of the recruitment rate which varies as a function of the physiological states of the individuals. A more plausible situation would be for F to have a state-dependent variance with more intense fluctuations when the current state is particularly not satisfactory.

(2) The system is periodically driven by external factors, such as temperature or light, or exhibits bursts of synchronized activity owing to more internal factors, such as starvation and satisfaction, which directly depend on the colony's activities. Indeed, oscillatory

phenomena on various timescales have been reported in several species of ants such as *Leptothorax acervorum* (Franks *et al.*, 1990; Hemerik *et al.*, 1990), *Leptothorax allardycei* (Cole, 1991a, 1991b, 1991c), *Pheidole hortensis* (Calabi *et al.*, 1983), where the timescale is of the order of 30 minutes, or in *Myrmecina graminicola* and *Messor capitata* (Goss & Deneubourg, 1989) on a larger timescale, of the order of a day or so. The fact that there are not more instances of synchronized activity in ants stems from difficulty of discovering the phenomena, which may much more widespread than current knowledge suggests. The candidate mechanisms that can generate synchronized activity are numerous (the literature on coupled oscillators is abundant in physics). Moreover, oscillatory phenomena have been found in many biological systems, and it has been argued that oscillations are common in regulatory systems (Berridge & Rapp, 1979): this could be the case precisely because parametric oscillations allow a system to reset its state below a point of symmetry-breaking instability where it can break the symmetry differently. Moreover, there is a general advantage to being synchronized as compared to a fluctuating parameter: in effect, bursts of synchronized activity that drive the system beyond a critical number allow it to set-up *structured patterns of activity*, that could possibly not exist if the system had an average activity below the minimum level for the structures to be set-up.

Maybe one of the clearest examples of 'oscillatory' symmetry-breaking is the case of the playlike territorial behaviour of two male fish *Barbus oligolepis* in a tank (Kortmulder, 1986; Kortmulder & Feuth-de Bruijn, 1993). This example is also described in (Goodwin, 1995) in the same context as the present paper. The observed phenomenon is a succession of synchronized 'heatings and quenches', whereby the aggressiveness of both fish increases and decreases more or less periodically in time. One occurrence of this behaviour results in one part of the tank, say part A, being inhabited by one fish (say fish 1), while part B is inhabited by the other fish (fish 2). When there is a sequence of such behaviours, fish 1 chooses A, then B, and B again, and then A again, etc., with an apparently random pattern of spatial preferences. The other part of the tank is selected by the other fish, "in agreement" with fish 1. It is not possible, on the sole basis of the observations reported in (Kortmulder, 1986; Kortmulder & Feuth-de Bruijn, 1993), to determine the origin of the synchronized behaviour of the fish in the tank. But the overall behaviour is reminiscent of periodic oscillations, possibly generated by some combination of synchronization processes, that make the system (fish 1 + fish 2) cross its critical surface regularly. Once again, the adaptive advantage of this kind of behaviour is to be looked for in the possible modifications of the environment that took place within the time scale of one oscillation.

(3) A third possibility, related to the previous idea, is to have bursts of synchronized activity whose sizes are distributed according to some law. In effect, we have dealt so far with simple situations, simple symmetries, and simple driving mechanisms, but more complex situations may correspond to, say, hierarchies of symmetries. It is likely that not all environmental modifications require drastic changes in the system's behaviour: large reorganizations should be rarer than smaller ones, but should still have a non-zero probability of occurring. This suggests a powerlaw size distribution of the bursts of synchronized activity. To achieve this refined mechanism, the distributed behaviour of the system should have a feedback effect on the global parameter μ so as to modify it exactly by the required amount. One candidate mechanism is self-organized criticality (Bak *et al.*, 1988), although it is not clear to me how the optimal coupling of the environment and the control parameter can be obtained.

Such a behaviour has recently been observed in a toy (shape space) model of the

immune system (Bonabeau, 1994) comprising B cell metadynamics and network dynamics only, where a microscopic (local) perturbation due to the presence of a long-lived molecule of the self propagates through the network and may lead, *only if necessary*, to a macroscopic (global) reorganization of the pattern so as to integrate the perturbing molecule and therefore produce tolerance. The ability to reorganize at any scale in response to a perturbation is the signature of criticality. A more realistic description of the immune system should include many more features. But experimental observations (Forni *et al.*, 1980; Lundqvist *et al.*, 1989) suggest that indeed the immune system's dynamics comprises a "complex mixture of oscillatory modes which would give access to a wide array of possible configurations" (Varela & Coutinho, 1991).

4. SUMMARY

In conclusion, I have presented evidence that regions of marginal stability, or using a more fashionable vocabulary, the edge of chaos, may offer more flexibility to collective biological systems. This feature is particularly advantageous in a changing environment (although this may depend on the particular ecological niche in which the system is embedded). The robustness of this argument has been demonstrated with several models developed in the context of cooperative foraging in ants, where experiments carried out on several species with various behavioral parameters show that only specific parameters allow for flexibility. Models show that such parameters are precisely those characterizing the edge of chaos. Because regions of marginal stability may be small, it is unreasonable to think that biological systems reliably operate in the vicinity of bifurcation points: several possible tuning mechanisms have been suggested, that would allow a system to maintain itself at, or to come back regularly to, the edge of chaos. We can also speculate (Edelstein-Keshet, 1994), that evolution may have driven species of trail followers towards behavioral parameters inducing flexibility.

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