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Marginally Stable Swarms Are Flexible and Efficient

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Abstract. — A simple model of cooperative food retrieval in ants is introduced to illustrate how a many-body biological system such as a swarm can exhibit an efficient and flexible behavior if it is close to an instability, but in a region where structured patterns of activity can grow and be maintained.

Résumé. — Un modèle simplifié de fourragement coopératif chez les fourmis est introduit pour illustrer l'idée qu'un système biologique collectif tel qu'un essaim peut être à la fois flexible et efficace si les paramètres comportementaux qui le caractérisent se situent au voisinage d'une zone d'instabilité, mais dans une région où une activité structurée peut se développer et se maintenir.

1. Introduction

Since a few years, ethologists have become increasingly aware of the self-organizing properties of social insects (ants, wasps, termites and bees) [1]: cooperative phenomena taking place at the colony level result from interactions at the individual level. Such interactions may either be direct (e.g., antennation, food offering, mandibular contacts), or indirect, via modifications of the environment (transformations of the environment include, e.g., nest building, brood sorting, trail laying). The collective foraging behavior (i.e., food retrieval) of ants is of particular interest [2]: in many cases, it is mediated by trail laying and trail following, whereby individuals returning from a food source to the nest deposit a chemical substance called a pheromone and those looking for food follow pheromone gradients; but it may also be supplemented by more direct stimulations, where one single individual guides another individual or a group of individuals to the food source. The process whereby an ant is influenced towards a food source by another ant or by a chemical trail is called recruitment. Recruitment has been shown to give rise to structured spatiotemporal patterns of activity (i.e., strong trails to food sources, allowing for efficient foraging) if some behavioral parameters, such as the number of active foragers, reach critical values [1]: recruitment is an autocatalytic process in which individuals

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are all the more stimulated to forage at a given location as there already are individuals foraging at that location, owing to chemical marking of space and direct stimulation; but, because of pheromone evaporation, forgetting, task switching, and because ants may get lost, the maintenance of trails and direct stimulation requires dissipative constraints (such as a minimal number of actors) to be satisfied. If, on the contrary, the behavioral parameters do not lie in the appropriate range of values, only random patterns of activity can be maintained; in other words, food sources can only be discovered by chance and cannot really be exploited. The passage from random to structured behavior at bifurcation values can obviously be understood with tools and concepts familiar to physicists, namely those developed in the context of phase transitions.

One problem with structured foraging is that it may be too stable, because of the possibly strong autocatalytic nature of recruitment: if a better choice is offered to the colony, it may be unable to shift its activity towards that better choice. Flexibility when faced with a better opportunity can only be achieved in the vicinity of a bifurcation, i.e. a point (or a region) of instability. But, since structured foraging is more efficient than random foraging, the location of the behavioral parameters should be slightly in the "ordered" phase, in the weakly autocatalytic zone close to the bifurcation. In summary, only marginally stable swarms are both flexible and efficient (at least in the context of foraging). This is the main thesis of this paper, which will be developed in two steps: 1) A quick presentation of relevant biological data will be made, together with an intuitive interpretation of the experiments in terms of marginal stability. 2) To account for the experimental observations, a simple probabilistic cellular automaton (PCA) model of cooperative foraging will be introduced and studied along these lines.

Finally, note that this connection between phase transitions or bifurcations, and adaptability, has recently known an upsurge of interest among physicists and biologists, under the possibly misleading name of "edge of chaos" (EOC). The exact meaning of EOC crucially depends on the context within which it is used, but roughly speaking, it describes the vicinity of some zone of instability separating a region of more ordered (or less random) behavior, from a region of less ordered (or more random, or more chaotic) behavior. The relevance of the EOC has been discussed in the context of evolution [3–5], or complex ecosystems [6], where species may be "critically" influencing one another and generate events of all sizes. An important application of the EOC is to adaptive behavior: it has been suggested by several authors that a behavior at the EOC might be optimal from the viewpoint of adaptation, because efficient information transfer, storage and processing can take place at the EOC [4,7–9], especially in a spatially extended system, where marginal stability allows for the existence of coherent flows of information between different parts of the system. For example, a model of ant behavior based on mobile automate was introduced by Solé, Miramontes and Goodwin [8,9], 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 [10].

The path that shall be followed here may seem less ambitious (and to some extent less speculative). It is related to the symmetry-breaking (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 [11]. Edelstein-Keshet *et al.* [12] 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. In other words, an optimal tradeoff between exploration and exploitation can be realized in the vicinity of a SB bifurcation point. This is a conjecture I would like to develop with the example of cooperative foraging in ants. The nice thing with the

case which will be presented is that clear experimental data is available, which can be readily mapped onto a physical interpretation.

2. Experiments

2.1. EXPERIMENTAL SETUP AND RESULTS. — It may be useful to briefly describe the experiments [13] that will be discussed and modelled. 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 (respec-

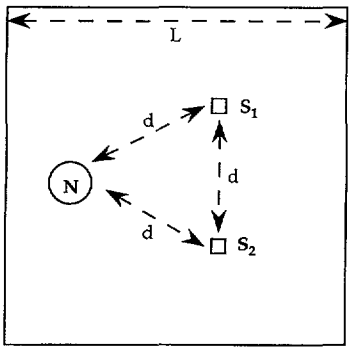


Fig. 1. — Experimental setup, comprising a nest (N) and two food sources (S_1 and S_2) located at the same distance from the nest, and forming an equilateral triangle of size d with the nest. The foraging area is a $L \times L$ square. Both L and d are adjusted to the speed of ants, and therefore depend 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 $L/2$.

tively 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 $t_1 = 0 < t_2$

In (E3), t_2 is sufficient large to allow for a stationary state to be reached with source S_1 alone before S_2 is introduced.
Three basic types of behaviors B1, B2, and B3 have been observed, depending on the species:

(B1) Colonies exhibiting behavior 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 behavior B2:

(B2i) strongly break the symmetry between the identical sources in E1,

(B2ii) clearly choose S_2 in E2, and

(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 behavior B3 exploit both sources symmetrically in all experiments.

Without going into much detail, let us mention the existence of three basic types of recruitments in ants, that we call R1 (mass recruitment), R2 (mass and group recruitment), and R3 (tandem recruitment). It has been shown [14] that the type of recruitment is highly correlated with the typical size of colonies: species using R1 have larger colonies than species using R2, which in turn have much larger colonies than species using R3. It so happens that B1 corresponds to species using R1 (e.g., *Iridomyrmex humilis* (Ih), *Lasius niger* (Ln)), B2 to species using R2 (e.g., *Tetramorium caespitum* (Tc)), and B3 to species using R3 (e.g., *Leptothorax unifasciatus* (Lu)). There is actually an intermediate type of behavior, B2' (e.g., *Myrmica sabuleti* (Ms), using R1), where the colony can switch to the richer source introduced after a delay only when the difference h between the sources is sufficiently large. All these results can be accounted for with a simple model, first introduced in a more primitive form by Deneubourg *et al.* [15], where the number of foragers N is the relevant parameter, by assuming that the intensity of trail laying can be modulated as a function of source quality (a phenomenon observed in several species, see [16]).

2.2. Interpretation of Experimental Observations. — There are clues allowing us to suggest that colonies exhibiting flexible behavior (B2) in the two source experiment are certainly close to a point of instability, as can be seen from the simple argument depicted in Figure 2. 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 (down 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 behavior 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. For example, an Ising system can be described by its magnetization M whose thermal average value varies with $\mu = 1/kT$. One very simple normal form (see e.g., [17]) displaying a critical bifurcation at $\mu = \mu_c$ is the noiseless overdamped relaxation of a particle in a potential $U = (\mu - \mu_c)\frac{M^2}{2} + \frac{M^4}{4}$. $\partial_t M = (\mu - \mu_c)M - M^3$. 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 Figure 2a, 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 modifying U: $U = -(\mu - \mu_c)\frac{M^2}{2} + \frac{M^4}{4} - hM$, so that the normal form becomes that of an imperfect bifurcation

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

the corresponding bifurcation diagram for fixed h being that of Figure 2b. (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). We see in particular that system A cannot be in the same state as in Figure 2a 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.

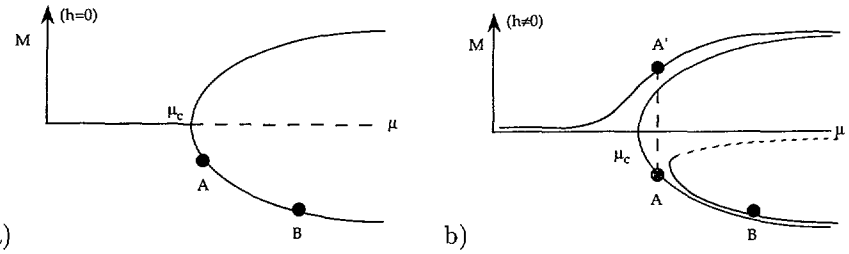


Fig. 2. — a) Sketch of a bifurcation diagram in the absence of external field; A and B are characterized by $\mu_c \leq \mu(\mathrm{A}) \ll \mu(\mathrm{B})$, and are both on the same branch of stable solutions for the order parameter M. b) Sketch of a bifurcation diagram in the presence of an external field; B remains on its branch, while A is attracted towards the more favorable state.

To make contact with the previously described experiments, let X_1 (respectively X_2) be the number of individuals foraging at source S_1 (respectively S_2), and N_1 (respectively N_2) the average asymptotic value of X_1 (respectively X_2). Then, the quantity $N_2 - N_1$ plays the role of the "order parameter" M of Figure 2. A and B correspond to two species with two different foraging habits, equation (1) would describe the dynamical evolution of the macroscopic or colony-level quantity M in the presence of two sources whose quality difference is h. The set of behavioral parameters, embodied in μ (e.g., $\mu = N$ = number of foragers), determines the colony's ability to adapt.

3. Model

We shall see that the combination of the number of active foragers and of the ability to modulate the trail laying rate (or more generally the recruitment rate) can predict whether or not the colony is able to switch, with an extension of the simple model of Deneubourg *et al.* [15]. Let α be the recruitment rate, i.e. the probability of success of a forager when

trying to stimulate a potential recruit, δ the fraction of ants encountered by an individual within a coarse grained unit of time, so that $\delta\frac{X}{N}$ 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. α integrates the foraging area, individual speeds, turning rates (i.e., rates of U-turns), while δ gives a picture of the physiological state of the colony (i.e., satisfaction or starvation: it is well known to experimenters that to study foraging, a few days of starvation is required for the colony to be willing to look for food!). $a = \alpha\delta$ therefore plays the role of an effective recruitment rate. 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: a fraction $\frac{X}{g+X}$ of recruited foragers reach the food source, and this corresponds to the reliability of trail-following, or alternatively, in the case of tandem or group recruitment, to the reliability of the guide [15]; we see that this reliability increases as X grows. This is a reasonable assumption provided the timescale of pheromone's variations is of the same order as variations of the number of foragers. Saturation of the reliability of trail following is neglected because it corresponds to pheromone concentrations almost never relevant in normal conditions (saturation has been observed only in laboratory experiments involving artificial trails; this is to be contrasted with the models of Millonas [18], and Rauch *et al.* [19], which rely heavily on saturation effects). Finally, let $1/b$ be the average time that an ant spends foraging at a given source. In what follows, N will play the role of the control parameter μ of Figure 2. 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, not speaking of the full spatiotemporal complexity of colony behavior. 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.

The probabilistic cellular automaton (PCA) model is composed of N individuals that can take either one of four states:

state 0: at nest,

state 1: foraging at source 1,

state 2: foraging at source 2,

state 3: lost (lost ants have in fact an adaptive effect, since they can find new sources).

The transition probabilities $T_{m\to n}$ between these states are given by:

$$\begin{aligned} T_{0\to i(i=1,2)} &= a_i\frac{X_i}{N}\frac{X_i}{g+X_i} \\ T_{0\to 3} &= \sum_{i=1}^{2} a_i\frac{X_i}{N}\left(1-\frac{X_i}{g+X_i}\right) \\ T_{0\to 0} &= 1-\sum_{i=1}^{2} a_i\frac{X_i}{N} \end{aligned} \tag{2}$$

where a_i is the effective recruitment rate to source i. A higher value of a_i corresponds to a higher-quality source. I shall make the simplifying assumption that only a_i (and not g) is

affected by source quality, but simulations show that this does not qualitatively modify the results. The difference between the sources is expressed in the following form:

$$a_i^- = (1 - \Delta) a_i^+ \tag{3}$$

where a_i^- (resp. a_i^+) is the effective recruitment rate to the poorer (resp. richer) source ($h \equiv \Delta$).

$$\begin{aligned} T_{i(i=1,2)\to 0} &= b \\ T_{i\to i(i=1,2)} &= 1 - b \end{aligned} \tag{4}$$

$$\begin{aligned} T_{3\to 0} &= p \\ T_{3\to i(i=1,2)} &= c \\ T_{3\to 3} &= 1 - 2c - p \end{aligned} \tag{5}$$

where $1/p$ is the time taken by explorers before returning to the nest if they do not find any source, and c the probability that a source is found by chance by an explorer. All these transition probabilities reflect what has been said previously; they define a mean-field, global coupling. All parameters have been tuned to experimentally suggested values [15]. Let $E = N - X_1 - X_2$ be the number of lost or exploring ants.

A simple stability analysis of the mean-field equations, obtained straightforwardly by writing down the master equation corresponding to the transition rates:

$$\begin{aligned} \partial_t X_i &= a_i (X_i/N)(X_i/g_i + X_i) \left(N - E - \sum_{i=1}^{2} X_i \right) + cE - bX_i \\ \partial_t E &= \left(\sum_{i=1}^{n} a_i (1 - (X_i/g_i + X_i))(X_i/N) \right) \left(N - E - \sum_{i=1}^{2} X_i \right) - 2cE - pE \end{aligned} \tag{6}$$

shows that the null state ($X_1 = X_2 = E = 0$) is a linearly stable 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, $c > \frac{1}{2} \frac{bp}{a - b}$, 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 and/or, once again, if the colony is willing to forage. Note that a "Ginzburg-Landau" equation similar to (1) can in principle be obtained from (6) for $M = X_2 - X_1$. It has been found that results averaged over many simulations coincide nicely with the direct numerical integration of the mean-field equations (6): this shows that an equation similar to equation (1) can closely describe the macroscopic behavior of the (mean-field) PCA introduced in this section.

In all the simulations, the initial conditions contained either slightly more individuals foraging at source 1 than at source 2 (E1 and E2), or only individuals foraging at source 1 (E3: source 2 is introduced after stationarity has been reached with a single source); each point of the curves or surfaces has been obtained from averaging over 100 simulations of 10^5 steps each (1 step=1 global update), but a stationary state is reached much more rapidly, after a few hundreds of steps. In real ants, one step would correspond to a few seconds or a minute. Let us first study the simulation of experiment E1 (that is, $\Delta = 0$ and $t_1 = t_2 = 0$). It is important to emphasize that, owing to the nonlinearity of problem, embodied in the transitions rates (2),

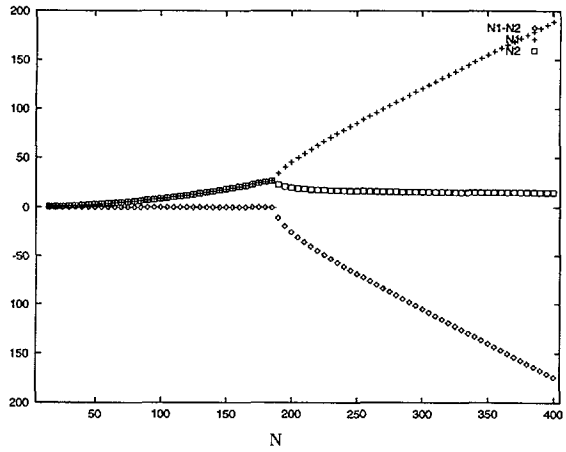


Fig. 3. — Simulation of experiment E1 (see text): N_1, N_2, and $M = N_2 - N_1$ as a function of N, with $a_1 = 0.03$, $a_2 = 0.03$, ($\Delta = 0$), $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

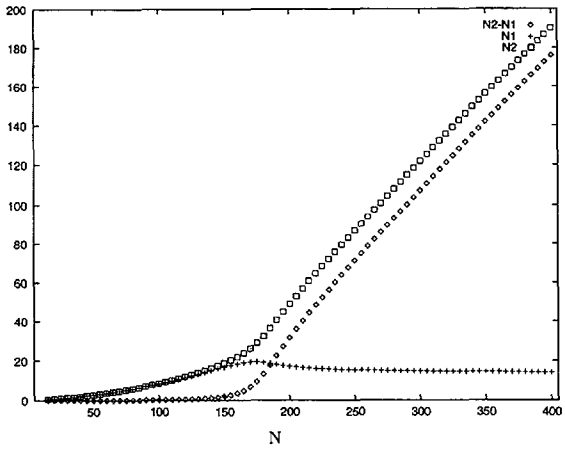


Fig. 4. — Simulation of experiment E2: N_1, N_2, and $M = N_2 - N_1$ as a function of N, with $a_1 = 0.0297$, $a_2 = 0.03$, ($\Delta = 0.01$), $b = 0.017$, $c = 0.018$, $g = 25$, p=0.15.

the number N of particles in the system is a relevant parameter and not merely a scale factor: N plays here the role of the control parameter μ of equation (1), while $M \equiv N_2 - N_1$ is the associated order parameter. The results (N_1, N_2, and M as a function of N) are presented in Figure 3. 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 Figure 4 (similar to Fig. 3, 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 Figure 2. As a further test of

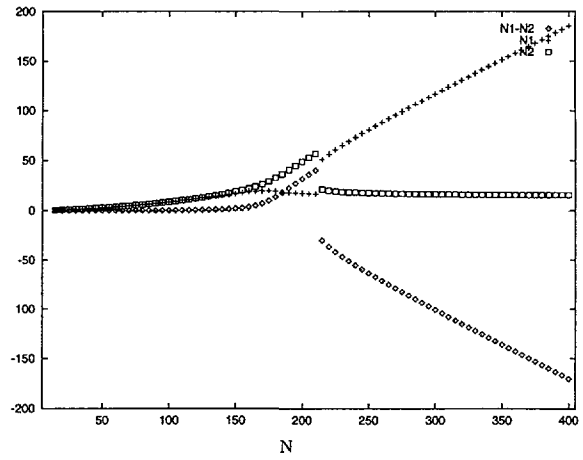


Fig. 5. — Simulation of experiment E3: N_1, N_2, and $M = N_2 - N_1$ as a function of N, with $a_1 = 0.0297$, $a_2 = 0.03$, $(\Delta = 0.01)$, $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

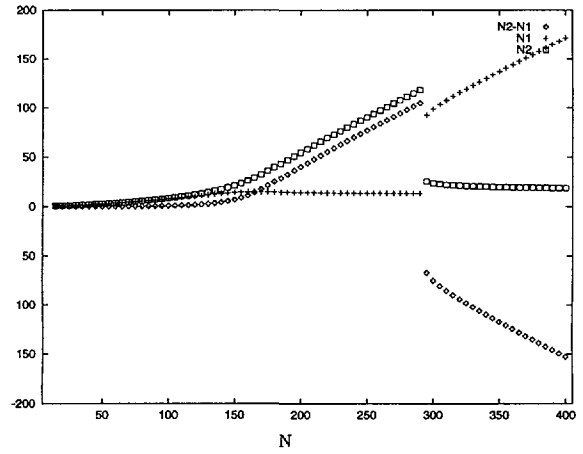


Fig. 6. — Simulation of experiment E3: N_1, N_2, and $M = N_2 - N_1$ as a function of N, with $a_1 = 0.0291$, $a_2 = 0.03$, $(\Delta = 0.03)$, $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

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 Figures 5 and 6, with $\Delta = 0.01$ and $\Delta = 0.03$, respectively. As can be seen, if the "external field", represented by 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 behaviors: B1 corresponds to a large number of active foragers (say, $N > 350$), B3 to a small number

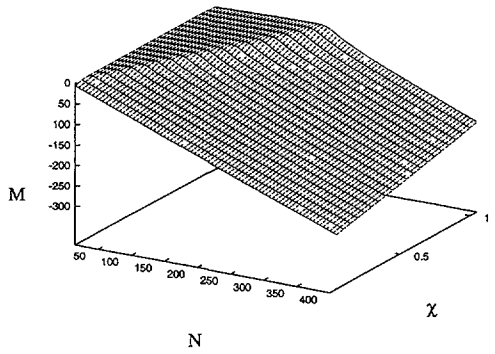


Fig. 7. — Simulation of experiment E1: x-axis: N varies from 10 to 400; y-axis: χ varies from 0 to 1; z-axis: $M = N_2 - N_1$; $a_1 = 0.03$, $a_2 = 0.03$, ($\Delta = 0$), $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

(say, $N < 100$), and *the adaptable behavior 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.

It is now necessary to test the robustness of this model by including several biologically relevant extensions. For instance, 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:

$$\frac{X_i}{g + X_i} \rightarrow \frac{Y_i}{g + Y_i}$$
$$Y^{t+1}_{i(i=1,2)} = (1 - \chi)Y^t_i + X^t_i \tag{7}$$

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 $\tau = \dfrac{1}{\log(1 - \chi)}$). The longer lifetime of pheromone certainly gives rise to more strongly marked trails, and therefore to less flexible behavior over a wider range of behavioral parameters. The results for E1 are presented in Figure 7 (M) for χ varying from 0 to 1. The essential modification with respect to Figure 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 Figures 8 (order parameter M), 9 (average number of foragers $\langle \chi_2 \rangle$ at source S_2), and 10 (proportion of individuals foraging at source 1, $\left\langle \dfrac{X_1}{X_1 + X_2} \right\rangle$).

We see with Figures 8 and 9 that the region where a colony can be adaptable is the "top of a wave" (or the bottom of a valley in Fig. 10) 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 Figure 11, for $\chi = 0.05$: we see that the size S of the adaptive region increases with increasing Δ, which is not surprising. It is also interesting to measure how S varies with the external field. The result is shown in Figure 12: S scales with

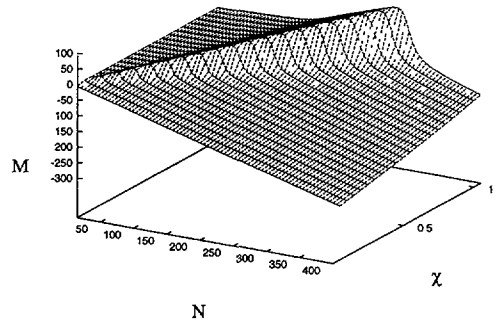


Fig. 8. — Simulation of experiment E3: x-axis: N varies from 10 to 400; y-axis: χ varies from 0 to 1; z-axis: $M = N_2 - N_1$; $a_1 = 0.0297$, $a_2 = 0.03$, $(\Delta = 0.01)$, $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$.

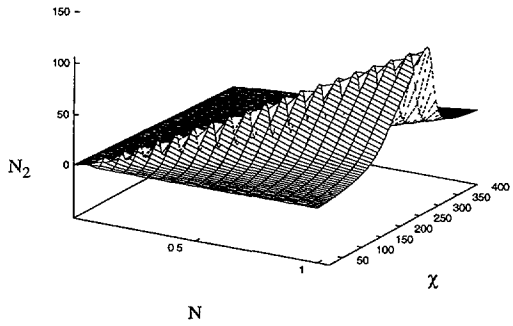


Fig. 9. — Idem as Figure 8, but with z-axis: $N_2 = \langle X_2 \rangle$.

Δ as $\Delta^{1/\delta}$, $\delta = 0.85 \pm 0.02$. 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 $c\left(1 - e^{-\chi^{Y_i}}\right)$. The addition of this factor does not qualitatively

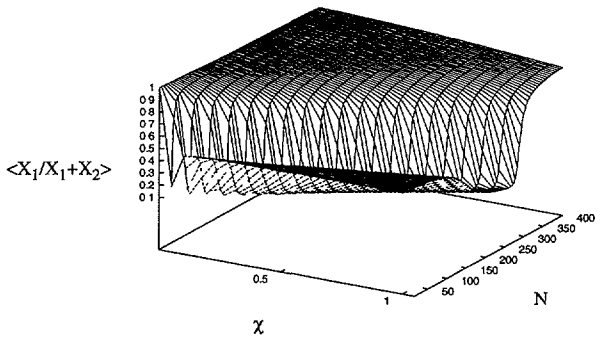


Fig. 10. — Idem as Figure 8, but with z-axis: $\left\langle \dfrac{X_1}{X_1 + X_2} \right\rangle$ (i.e., proportion of individuals foraging at source 1).

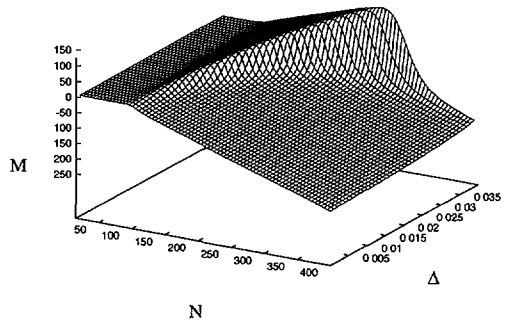


Fig. 11. — Simulation of experiment E3: x-axis: N varies from 10 to 400; y-axis: Δ varies from 0.005 to 0.035; z-axis: $M = N_2 - N_1$; a_1 ranges from 0.02895 to 0.02985, $a_2 = 0.03$, $b = 0.017$, $c = 0.018$, $g = 25$, $p = 0.15$, $\chi = 0.05$.

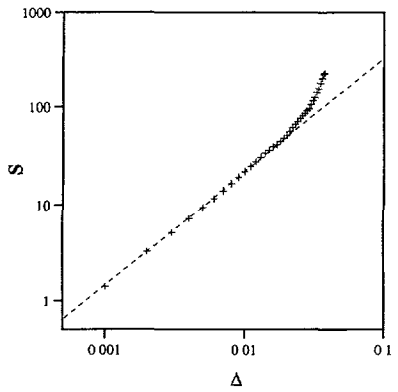


Fig. 12. — Simulation of experiment E3: log-log plot of size S of adaptive region (y-axis) vs. Δ (x-axis); same parameters as Figure 11. S scales with Δ as $\Delta^{1/\delta}$, $\delta = 0.85 \pm 0.02$. Dashed line indicates slope $1/\delta \approx 1.175$.

modify the results, as Figure 13 shows ($\Delta = 0.02895$ and $\chi = 0.05$).

In summary, although this model is simple and does not reflect the full complexity of real ant colonies, it does contain some important ingredients and the essence of the argument: whatever the relevant behavioral parameters may be, it has been shown that colonies exhibiting behavior B2 are close to a point of instability in a zero external field, yet slightly in the ordered phase, and are 1) flexible owing to the vicinity of the bifurcation, and 2) efficient because they lie in the ordered phase, where structured patterns of activity can be sustained. It would be unreasonable to say that this is true for an arbitrary collective biological system, but it is tempting to confer some degree of generality to this principle.

4. Related Work and Discussion

Millonas [18] developed in the same context an interesting physics-inspired formalism to deal with collective decision making from individual activities, where ant-particles are nonlinearly coupled to a pheromonal field; phase transitions are observed as the degree of determinism

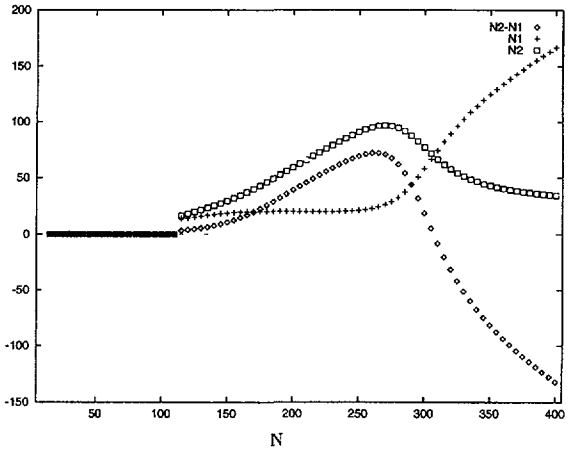


Fig. 13. — Simulation of experiment E3: N_1, N_2, and $M = N_2 - N_1$ as a function of N, with $a_1 = 0.02895$, $a_2 = 0.03$, ($\Delta = 0.035$), $b = 0.017$, $c_i = 0.018(1 - e^{-\chi Y_i})$, $g = 25$, $p = 0.15$, and $\chi = 0.05$.

(or conversely, the error level) in trail-following is varied. Rauch *et al.* [19] recently studied a spatiotemporal version of this model by means of simulations, which allowed them to explore the structures of the trail networks that may form. They concluded, in agreement with the present paper, that ordered behavior is important for structured, efficient trails to exist, but that this behavior should not be too stable in order to allow for flexible responses; an optimal combination of these two conflicting tendencies is realized close to instabilities. However, their model does not describe any particular experiment, but simply ants wandering around, laying pheromone and following trails; it is thus hard to speak of adaptivity. The approach followed in the present paper chose to ignore complex spatiotemporal features to concentrate on a specific example, for which well-defined experiments have been performed and adaptability has a clear meaning. Let us mention another promising path, followed by Edelstein-Keshet *et al.* [12], who are currently systematically exploring the effects of all relevant parameters on foraging dynamics (a useful job pointing to the need for more experimental data).

The focus of this paper was 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, all the more as the various behavioral parameters characterizing a colony are very likely to fluctuate. Let us briefly consider again normal form (1), which applies qualitatively to the present case through equations (6). The more complex picture of a whole set or hierarchy of bifurcations can be obtained, at least qualitatively, directly from this simple case. We may now assume quite naturally that the environmental field is time dependent, i.e., $h = h(t)$. h is likely to be a random process, such as a Poisson process describing the appearance of seeds in a foraging patch; U will be minimum if the state M of the colony corresponds to foraging in a region where a large amount of seeds just arrived. Finally, it is usual to add some noise term to equation (1), accounting for the random component in individual behavior:

$$\partial_t M = (\mu - \mu_c)M - M^3 + h(t) + \xi \tag{8}$$

where, e.g., ξ is a Gaussian process with $\langle \xi_t \rangle = 0$ and $\langle \xi_t \xi_{t'} \rangle = D\delta(t - t')$. In fact, owing to parameter fluctuations, the noise term might as well be multiplicative. The question of adapt-

ability can now be expressed in simple terms: given some set of random processes $h(t)$, how can the system be in the most adapted state as often as possible, with as few reorganizations as possible? (One seeks to minimize, e. g., $\int U(M(t))\mathrm{d}t$ and $\int |\partial_t M|\mathrm{d}t$ simultaneously). It has been argued in this paper that one possibility is to have a system with $\mu = \mu_c + \varepsilon$, where $\varepsilon > 0$ is small. But another, somewhat more robust solution is to allow the system to cross its critical region as often as required, or to maintain it in the vicinity of the point of instability, with a time-dependent, and possibly state-dependent, μ.

1) μ may more or less randomly fluctuate: 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 μ to have a state-dependent variance with more intense fluctuations when the current state is particularly not satisfactory.

2) The system may be periodically driven by external factors, such as temperature or light, or exhibit 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* [20], *Leptothorax allardycei* [21], *Pheidole hortensis* [20], where the timescale is of the order of 30 minutes, or in *Myrmecina graminicola* and *Messor capitata* [22] on a larger timescale, of the order of a day or so. 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 [23]: 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. There is also 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 setup *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 setup.

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 behavior: 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 behavior 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 (SOC) [24], although it is not clear to me how the optimal coupling of the environment and the control parameter can be obtained. This mechanism would in any case satisfy the requirement that only minimal reorganizations should take place, a constraint that is also crucial, but very difficult to handle. Sornette [25] argued along the same lines that most examples of SOC can be characterized by a feedback mechanism, involving a retroaction of the order parameter on the control parameter which allows the system to maintain itself at the critical state. Fraysse *et al.* [26], drawing an analogy with "smart materials" [27], further suggested that this feedback mechanism might allow the system to *optimize* its response to a perturbation, very much in the spirit of the present paper.

4) The noise term ξ, which can very well be sufficient to induce a shift of the system in a multistable potential, has been so far ignored. It is well known that if $h(t)$ is periodic with a long period, there is an optimal noise intensity for which the signal/noise ratio is maximum [28]. We may therefore guess that any signal containing only low frequencies will also induce stochastic

resonance (although there will not be a single peak in the noise spectrum). Here again, one parameter, namely the noise intensity D, has to be tuned; but it is quite natural to think of ants as getting more and more excited (noisy) if they are not satisfied. This could constitute yet another tuning mechanism.

References

[1] Deneubourg J.-L., Pasteels J.-M. and Verhaeghe J.-C., *J. Theor. Biol.* **105** (1983) 259; Deneubourg J.-L. and Goss S., *Ethol. Ecol. Evol.* **1** (1989) 295; Bonabeau E. and Theraulaz G., Intelligence Collective (Paris, Hermès, 1994).

[2] In some species, usually characterized by small colonies, foraging may be purely individual.

[3] Kauffman S.A. and Johnsen S.J., *J. Theor. Biol.* **149** (1991) 467.

[4] Kauffman S.A., The Origins of Order (New York, Oxford University Press, 1993).

[5] Bak P. and Sneppen K., *Phys. Rev. Lett.* **71** (1993) 4083; Flyvbjerg H., Sneppen K. and Bak P., *Phys. Rev. Lett.* **71** (1993) 4087; Chau H.F., Mak L., and Kwok P.K., *Physica A* **215** (1995) 431; Ray T.S. and Jan N., *Phys. Rev. Lett.* **72** (1994) 4045.

[6] Kaneko K. and Ikegami T., *Physica D* **56** (1992) 406; Solé R.V., Lopez D., Ginovart M. and Valls J., *Phys. Lett. A* **172** (1992) 156; Solé R.V. and Manrubia S.C., *J. Theor. Biol.* **173** (1995) 31; *Phys. Rev. E* **51**(1995) 6250.

[7] Crutchfield J.P. and Young K., *Phys. Rev. Lett.* **63** (1989) 105; Langton C., *Physica D* **42** (1990) 5; PhD Dissertation, University of Michigan (1991); Vastano J.A. and Swinney H.L., *Phys. Rev. Lett.* **60** (1988) 1773; Jørgensen S.E., *J. Theor. Biol.* **175** (1995) 13.

[8] Solé R.V. and Miramontes O., *Physica D* **80** (1995) 171; Miramontes O., Solé R.V. and Goodwin B.C., *Physica D* **63** (1993) 145.

[9] Goodwin B., How the leopard changed its spots. The evolution of complexity (New York, Charles Scribner's Sons, 1994).

[10] Adler F.R. and Gordon D.M., *Am. Nat.* **140** (1992) 373; Gordon D.M., Paul R.E. and Thorpe K., *Anim. Behav.* **45** (1993) 1083.

[11] Haken H., Synergetics (Berlin, Springer Verlag, 1983).

[12] Edelstein-Keshet L., *J. Math. Biol.* **32** (1994) 303; Edelstein-Keshet L., Watmough J. and Ermentrout G. B., *Behav. Ecol. Sociobiol.* **36** (1995) 119.

[13] Beckers R., Deneubourg J.-L. and Pasteels J.-M., *Actes Coll. Ins. Soc.* **4** (1989) 219; Beckers R., Deneubourg J.-L., Goss, S. and Pasteels, J.-M., *Ins. Soc.* **37** (1990) 258; de Biseau J.-C., Deneubourg J.-L. and Pasteels J.-M., *Psyche* **98** (1991) 323.

[14] Beckers R., Goss S., Deneubourg J.-L. and Pasteels J.-M., *Psyche* **96** (1989) 239.

[15] Deneubourg J.-L., Aron S., Goss S., Pasteels J.-M. and Duerinck G., *Physica D* **22** (1987) 176; Pasteels J.M., Deneubourg J.-L. and Goss S., in: Law of Nature and Human Conduct, I. Prigogine and M. Sanglier Eds. (Brussels, Cordes, 1987); Pasteels J.M., Deneubourg J.-L. and Goss S., *Experientia Suppl.* **54** (1987) 155.

[16] Cammaerts M.-C., Proc. of 8th Intnl. Cong. of Intnl. Union for the Study of Social Insects (Wageningen, 1977) 294; Cammaerts M.-C. and Cammaerts R., *Behav. Proc.* **5** (1980) 251; Hangartner W., *J. Ins. Physiol.* **15** (1969) 1.

[17] Manneville P., Structures et Instabilités, C. Godrèche Ed. (Paris, Les Éditions de Physique, 1986).

[18] Millonas M., *J. Theor. Biol.* **159** (1992) 529.

[19] Rauch E.M., Millonas M.M. and Chialvo D., submitted to *Phys. Lett. A* (1995).

[20] Franks N.R., Bryant S., Griffiths R. and Hemerik L., *Bull. Math. Biol.* **52** (1990) 597; Hemerik L., Britton N.F. and Franks N.R., *Bull. Math. Biol.* **52** (1990) 613.
[21] Cole B.J., *Am. Nat.* **137** (1991) 244; *J. Ins. Behav.* **4** (1991) 129; *Proc. R. Soc. Lond. B* **244** (1991) 253.
[22] Goss S. and Deneubourg J.-L., *Ins. Soc.* **35** (1988) 310.
[23] Berridge M.J. and Rapp P.E., *J. Exp. Biol.* **81** (1979) 217.
[24] Bak P., Tang C. and Wiesenfeld K., *Phys. Rev. A* **38** (1988) 364; Bonabeau E., *Physica A* **208** (1994) 336.
[25] Sornette D., *J. Phys. I France* **2** (1992) 2065.
[26] Fraysse N., Sornette A. and Sornette D., *J. Phys. I France* **3** (1993) 1377.
[27] Whittle M. and Bullough W.A., *Nature* **358** (1992) 373.
[28] Stochastic resonance, *J. Stat. Phys.* **70** (1993) 1-514.