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Phase-ordering kinetics of cemetery organization in ants

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The clustering of dead bodies by ants is simulated, using a cellular automaton model, the rules of which are carefully derived from experiments. Starting from a random spatial distribution of corpses, a cemetery organizes itself into clusters of corpses. The dynamics of clustering can be compared to the phase-ordering kinetics of a bidimensional idealized magnetic system with a scalar conserved order parameter. In particular, scaling relations are found for the structure factor and the dynamics of cluster growth, which can be compared with those predicted by the theory of phase-ordering kinetics. Observed exponents are consistent with those expected in early stage phase-ordering kinetics. [S1063-651X(98)03104-3]

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A phase-ordering phenomenon is observed after a temperature quench from a homogeneous phase into a two-phase region [1]. Conserved fields are particularly interesting, because interfaces cannot move independently and their dynamics is nonlocal. In the diluted case, when one of the phases occupies only a negligible volume fraction, the theory of Lifschitz and Slyozov [2] predicts, among other things, that the characteristic size $\langle R(t)\rangle$ of the minority phase clusters grows at late times as $t^{1/3}$ in space dimension $d>2$ for a conserved scalar field. This result has been argued to extend to $d=2$ [3,4], with possible logarithmic corrections, and to cases where none of the phases' volume fractions is infinitesimal [1]. Corberi, Coniglio, and Zannetti [5] showed, by means of numerical simulation of a Ginzburg-Landau equation, that the early stage of coarsening may be characterized by $\langle R(t)\rangle \propto t^{1/4}$ for a conserved scalar order parameter. The structure factor $S(k)$ is also predicted to exhibit late stage scaling (or more complicated ''multiscaling'') behavior [1,6]: $S(k)\propto k^4$ for $k<k_m$, and $S(k)\propto k^{-3}$ for $k>k_m$ (Porod tail, indicating the existence of sharp interfaces), where k_m is the peak wave vector. Castellano and Zanetti [6] showed that the observation of this behavior depends on the initial fluctuations of the order parameter: when initial fluctuations are strong, the k^4 behavior takes a long time to build up. $1/k_m$ is expected to vary as $t^{1/3}$, but $1/k_m \propto t^{1/4}$ is often observed [7,8]; when initial fluctuations are strong, the exponent 1/3 or 1/4 for $1/k_m$ is approached from below [6].

In the present paper, we study a model of cemetery organization in ants [9] that appears to exhibit many of the properties of the phase-ordering kinetics of an idealized two-dimensional magnetic system with a scalar conserved field. Our approach is ''behavioral'' by nature, that is, we simulate the observed behavior of ants and do not try to build a ''physical'' model of it with an explicit Hamiltonian. This peculiar system can be seen as a model experimental system for studying phase ordering outside the domain of physics. There exist numerous examples of many-body phenomena in the animal kingdom, including aggregation, flocking [10] or schooling [11], the formation of living chains or bridges [12], collective hunting [13–15], etc. In such examples, it is interesting to draw a parallel between the behavior of the biological system and the behavior of a corresponding physical system, the properties of which are well known. Such properties may include, for example, scaling exponents at phase transitions or dynamic scaling laws.

An ordering phenomenon is observed in some species of ants when corpses of dead ants are spread in the colony's two-dimensional foraging area: ants pick up dead bodies or dead items and deposit them some time later; picking up occurs with high (respectively, low) probability when items are isolated (respectively, surrounded by many other items), and, conversely, deposition occurs preferentially in regions with a high density of items. This behavior at the level of individual ants leads to the formation of macroscopic clusters. Figure 1(a) shows 4000 corpses randomly located in a two-dimensional experimental arena used to study clustering in the ant *Pheidole pallidula*, and Fig. 1(b) shows clusters of dead bodies that have appeared after 68 h. Because ants tend to perform random walks before and after picking up or depositing an item, this clustering process is slow. The scalar field is the spatial density of dead items, which is obviously globally conserved by the reorganization performed by the ants; this reorganization is similar to a spin exchange dynamics.

We use a two-state mobile cellular automaton model, carefully derived from experiments, which is a modified version of a model previously introduced by Deneubourg *et al.* [9]. A site r_j containing a dead body item at time t (an item may be a part of a corpse, such as the thorax or the abdomen [16]) is represented by $S(r_j,t)=1$, and an empty site by $S(r_j,t)=0$. Each agent, representing an ant, performs a random walk on the lattice, and, if unloaded, picks up an item located at a given site with some probability. When loaded, the agent continues to perform a random walk until it decides to drop it at an empty site. Let $X_i(t)$ be the site occupied by agent i at time t, and Y_i the state of agent i at time t: $Y_i=0$ if the agent is unloaded, and $Y_i=1$ if the agent is carrying an item. The probability of dropping an item was studied

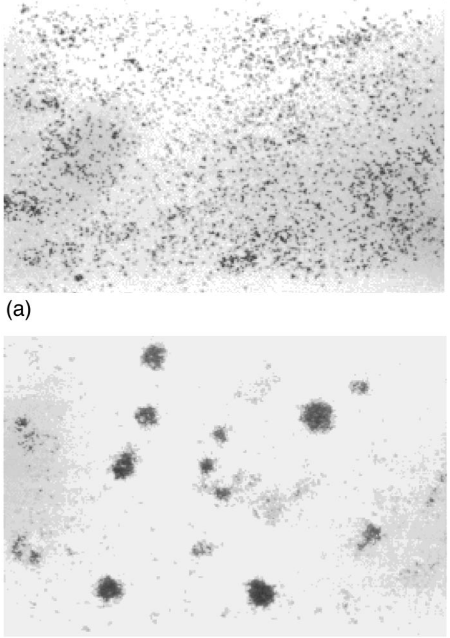

FIG. 1. (a) 4000 dead bodies are randomly placed on an experimental $50\times 50\text{-cm}^2$ arena where *Pheidole pallidula* workers are present. The surface of a dead item being of the order of $0.015\,625\ \text{cm}^2$, the surface fraction occupied by dead items is of the order of 0.025. Modified from Ref. [9]. (b) Experimental arena after 68 h. Modified from Ref. [9].

experimentally by Chrétien [16] in the ant *Lasius niger*: the probability that an ant drops an item next to an n cluster can be approximated by $p_d(n)\propto 1-(1-p)^n$, for n up to 30, where p is a fitting parameter. But ants cannot precisely evaluate the size of a cluster: a local mechanism is required to allow them to perform this evaluation. Observation of the clustering process suggests that the size of a cluster is evaluated through a temporal integration: as a loaded ant walks on a cluster, she is hampered in her walk because the item she is carrying tends to cling to other items, requiring an effort on the part of the ant, who gives up her item in an empty slot after some time. It is very likely that deposition takes place when the temporally integrated effort becomes large. In order to reproduce this feature, each agent is endowed with a short-term memory, where the states of the last m encountered sites are stored. m is adjusted so that actual cluster size in the simulations corresponds roughly to the number $\overline{n}$ of memorized occupied sites (here $m=30$). Then, the perceived cluster size $\overline{n}$ is used to define the probability of depositing an item in the vicinity of the cluster,

$$P_d(\overline{n})=0.7[1-(1-p)^{\overline{n}}], \tag{1}$$

if $S(X_i)=0$ [$P_d=0$ if $S(X_i)=1$], with $p=0.01$. Note that $P_d=0$ when $\overline{n}=0$, which is consistent with the fact that an ant extremely rarely deposits an item where it would be isolated. The picking up behavior is more easily modeled, as it seems to rely more on the direct perception of the neighborhood of an item: an item surrounded by many other items is likely to be entangled with them, requiring a larger effort to pick up than an isolated item. The required effort is an increasing function of the number of neighboring items. Although the probability of picking up an item was not precisely measured in Chrétien's experiments [16], it was reported [9,16] that it is low when the item is surrounded by other items, and substantially higher when the item is isolated. The following procedure has been implemented: the picking-up probability P_p is given by a threshold function

$$P_p=\left(\frac{0.1}{0.1+f}\right)^2 \tag{2}$$

if $S(X_i)=1$ [$P_p=0$ if $S(X_i)=0$], where f is the fraction of the neighboring sites of X_i occupied by an item. Because there are eight neighboring sites in our simulations, f can take its value in $\{0,\frac{1}{8},\frac{1}{4},\ldots,\frac{7}{8},1\}$. New experiments seem to confirm Eq. (2) [17].

It must be emphasized that a very large arena was necessary in Deneubourg *et al.*'s [9] experiments to obtain ''bulk'' clusters: in effect, ants are attracted toward the edges of the experimental arena if these are too close to the nest, resulting in clusters almost exclusively along the edges. Any heterogeneity in the environment serves as an aggregating device. The simulations reported below correspond to the case of a very large arena. Because very large arenas require an enormous number of freshly dead individuals, these experiments could not be done more than once, and only three pictures of the arena were taken at three different times by Deneubourg *et al.* [9], which is obviously insufficient to make reliable statistics. The behavior of ants, however, has been recorded for smaller arenas, and the respective probabilities of picking up and depositing a dead body could be computed. Our simulations use these experimentally determined parameters, and generalize them to very large arenas. A square grid of linear size $L=200$ is used for the Monte Carlo simulations, with periodic boundary conditions, $n=1000$ items (the fraction of the surface occupied by dead items is 0.025, which can be considered as a relatively diluted system), and $N=5$ agents. At each time step, every agent moves to an adjacent site. Each agent performs a random walk and picks up or deposits items according to the probabilities given by Eqs. (1) and (2). Because L^2 (not necessarily all different) lattice sites are visited every $L^2/N=8000$ time steps by all agents, we define by convention a Monte Carlo step (MCS) as corresponding to 8000 time steps. Obviously, it takes more time for all sites to be visited, as agents are performing random walks, which, again, makes the phase-ordering process very slow. Figure 2 shows a pattern obtained after 5000 MCS's with this model. We find a good qualitative agreement between the experimental and simulated spatial patterns, which indicates that we have a plausible description of the phenomenon, especially given the few ingredients needed to specify the model.

The average cluster size $\langle R(t)\rangle$, the maximum cluster size $R_m(t)$, and the normalized structure factor, defined by

$$S(\mathbf{k},t)=n^{-1}\left\langle \left|\sum_j S(r_j,t)e^{i\mathbf{k}\cdot\mathbf{r}_j}\right|^2\right\rangle, \tag{3}$$

where $\mathbf{k}=(k_x,k_y)=(2\pi/L)[m_1-(L/2),m_2-(L/2)]$ $(m_1,m_2=0,1,\cdots,L)$, have been measured. $S(k=|\mathbf{k}|,t)$ is obtained by spherical averaging over the $(k,\ k+\delta k)$ shell in k space. The first moment $k_1(t)$ of the structure factor, defined by

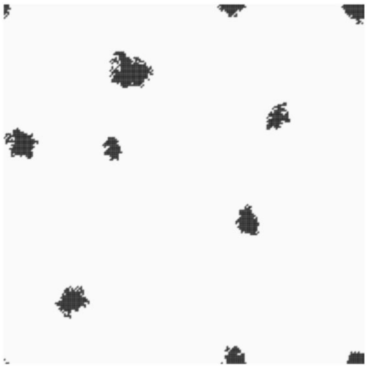

FIG. 2. Configuration obtained from simulation (see text) after 5000 MCS with $N=5$ agents. $n=1000$ items are initially randomly placed in the 200×200 simulated arena. The fraction of the surface occupied by dead items is 0.025.

$$k_1(t)=\frac{\sum_k kS(k,t)}{\sum_k S(k,t)}, \tag{4}$$

can be calculated more accurately than the peak wave vector $k_m(t)$, and is expected to have similar temporal properties [7]. Figure 3 shows a double logarithmic plot of $\langle R(t)\rangle$ and $R_m(t)$ as a function of t: the behavior of both $\langle R(t)\rangle$ and $R_m(t)$ is consistent with a growth proportional to $t^{1/4}$, as would be expected in early stage ordering [5]. The $\frac{1}{4}$ exponent is approached from below. Figure 4 shows a double logarithmic plot of $S(k,t)$ as a function of k for different values of t: whereas a k^{-3} tail can be observed for $k>k_m$ after some time, no k^4 behavior is observed for $k<k_m$ within simulation time. Such a behavior would be consistent with the early stage ordering of a system with strong initial order parameter fluctuations [6]. Finally, Fig. 5 shows a double logarithmic plot of $1/k_1(t)$ as a function of t, the temporal growth of which is consistent with $1/k_1(t)\propto t^{1/4}$, with the exponent $\frac{1}{4}$ being approached from below, which, again, would be consistent with a system with strong initial order parameter fluctuations [6].

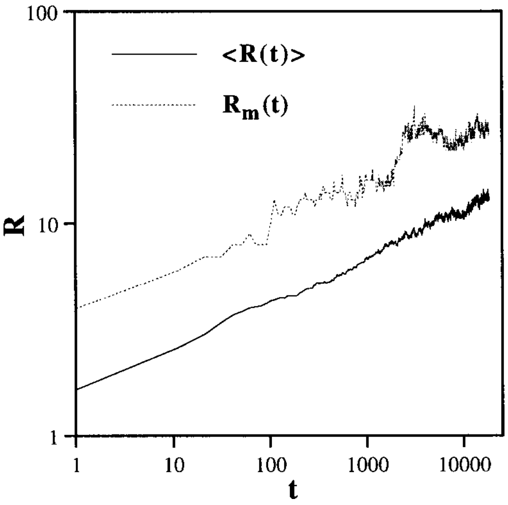

FIG. 3. Double logarithmic plot of $\langle R(t)\rangle$ and $R_m(t)$ as a function t (in MCS), consistent with a $t^{1/4}$ growth at late times. The exponent $\frac{1}{4}$ is approached from below.

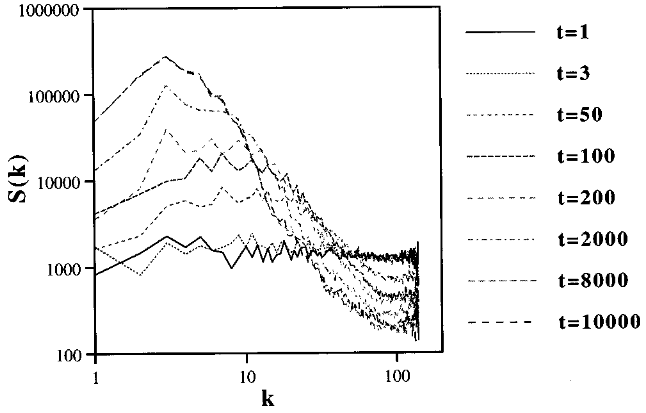

FIG. 4. Double logarithmic plot of $S(k,t)$ (averaged over five simulations) as a function of k at different t (in MCS). A k^{-3} Porod tail can be observed for $k>k_m$ after some time, but no k^4 behavior is observed for $k<k_m$ within simulation time.

In conclusion, we have introduced a plausible model for the clustering of dead bodies by ants, the dynamic scaling properties of which seem to be consistent with predictions from theories, or other simulations, of phase-ordering kinetics. The slowness of the clustering process may explain why our observations are consistent with other results obtained in the *early stage* of phase ordering [5]. That our results seem to be similar to those obtained with strong initial order parameter fluctuations is more difficult to explain. There are a few features of the model that might contribute to these observations. For example, our agents perform random walks, which are obviously correlated. Moreover, time is ill defined, because ‘‘spin’’ exchanges take variable amounts of time: a laden agent may perform a random walk for a varying number of time steps before unloading its item. Finally, in experiments, the number of ants participating in the clustering process may fluctuate, making it in principle more difficult to compare time varying quantities with predictions, but simulations with a fluctuating number of agents generate the same

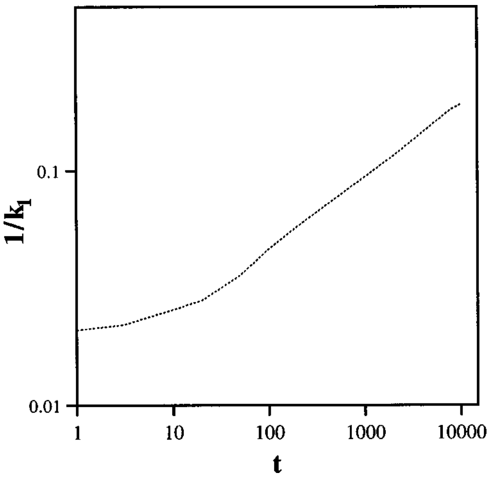

FIG. 5. Double logarithmic plot of $1/k_1(t)$ as a function of t (in MCS), the temporal growth of which is consistent with $1/k_1(t)\propto t^{1/4}$, with the exponent $\frac{1}{4}$ being approached from below.

scaling properties. It should therefore be possible to test the predictions in future experiments.

In a related problem, Glazier and co-workers [18] applied a modified version of the large-Q Potts model to the description of the rearrangement of biological cells through differential adhesion. Some ant species (e.g., *Leptothorax unifasciatus* [9,19]) do not only cluster dead bodies, but also sort their brood: larvae are gathered into a large cluster containing all the brood, with small larvae in the center and large larvae in the periphery. Although larval sorting and dead body clustering certainly rely on different physicochemical mechanisms, the behavioral dynamics at the level of individual ants appears to be quite similar. Sorting larvae into several categories according to their sizes is, however, more complex than clustering them: this process is similar to cell sorting, and actually requires that some kind of ‘‘differential adhesion’’ be implemented in the behavior of individual ants. The most relevant description of larval sorting by ants would not be the large-Q Potts model, but rather a simple extension of the model presented in this paper, where differential adhesion would be reflected in differential probabilities of depositing items depending on the number of items belonging to each category encountered in the recent past [9].

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