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## ACCEPTED MANUSCRIPT

## Non-stationary aging dynamics in ant societies

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(Dated: April 21, 2011)

In recent experiments by Richardson et al. ((2010), PLoS ONE 5(3): e9621. doi:10.1371/journal.pone.0009621) and motion out of the nest is shown to be a non-stationary process intriguingly similar to the dynamics encountered in physical aging of glassy systems. Specifically, exit events can be described as a Poisson process in logarithmic time, or, for short, a log-Poisson process. Nouvellet et al.(J. Theor. Biol. 266, 573, (2010)) criticized these conclusions and performed new experiments where the exit process could more simply be described by standard Poisson statistics. In their reply, (J Theor. Biol. 269, 356-358 (2011)) Richardson et al. stressed that the two sets of experiments were performed under very different conditions and claimed that this was the likely source of the discrepancy. Ignoring any technical issues which are part of the above discussion, the focal point of this work is to ascertain whether or not both log-Poisson and Poisson statistics are possible in an ant society under different external conditions. To this end, a model is introduced where interacting ants move in a stochastic fashion from one site to a neighboring site on a finite 2D lattice. The probability of each move is determined by the ensuing changes of a utility function which is a sum of pairwise interactions between ants, weighted by distance. Depending on how the interactions are defined and on a control parameter dubbed 'degree of stochasticity' (DS), the dynamics either quickly converges to a stationary state, where movements are a standard Poisson process, or may enter a non-stationary regime, where exits can be described as suggested by Richardson et al. Other aspects of the model behavior are also discussed, i.e. the time dependence of the average value of the utility function, and the statistics of spatial rearrangements happening anywhere in the system. Finally, we discuss the role of record events and their statistics in the context of ant societies and suggest the possibility that a transition from non-stationary to stationary dynamics can be triggered experimentally.

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### I. INTRODUCTION

In their study of motion in Temnothorax albipennis ant colonies, Richardson et al. [1] found that ants leave their nest at a decelerating rate, and that the sequence of exit times can be modelled using a peculiar Poisson process, for short log-Poisson process, also known from record dynamics in glassy systems[2–4]. Subsequently [5], the same group experimentally demonstrated that social interactions are a prerequisite for log-Poisson behavior. Motivated by Ref. [1], Nouvellet et al.[6] performed different experiments on the motion of Pharaoh's ants within their nesting area. The results could be described by a 'null' model, where ants act independently and where the activity is described by a standard Poisson process, as fitting for a stationary and time homogeneous situation. In their reply [7], Richardson et al. stressed that the two sets of experiments were performed under different conditions and claimed that this would lead to different event statistics. For completeness, we also mention that Nouvellet et al. recently replied [8] to the comment of Richardson et al..

The discussion between the two groups raises two important theoretical issues. One is whether the observed differences simply reflect the ability of the same system (or same type of system) to display either behavior depending on some external condition or parameter, as is the case in glassy systems at high and low temperatures. The second question regards the possible interpretation of records in the context of ant dynamics, and more generally, in the context of the dynamics of social agents. The dynamics of the simple model discussed below suggests some answers.

In the model, ants move in a probabilistic fashion within a toroidal lattice, where contiguous points each represent contiguous areas of physical space. Allowed moves involve a single ant changing its position from one lattice point to one of its four neighbors. Moves are accepted or rejected with probabilities depending on the ratio of the change they entail in a utililty function E to a parameter T dubbed 'degree of stochasticity' (DS). Specifically, the DS gauges the willingness of ants to make risky choices which decrease the value of their own (and hence the whole system's) utility function. These choices are akin to investing capital for the sake of future gains. The lower the DS, the less inclined

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ants are to do so, i.e. at zero DS only moves which increase E are performed. In the opposite limit of very high T, moves are accepted regardless of the sign and magnitude of the corresponding change in E. From an algorithmic point of view, E and T play a role similar to the energy and temperature in a Monte Carlo simulation of a physical system. More importantly, the model dynamics and the dynamics of glassy systems are similar, a property which the chosen notation is meant to emphasize. Nevertheless, no relation is implied between the DS parameter T and the physical temperature of the environment in which ants move. At low DS, and for certain types of interactions but not for others, a non-stationary dynamical regime is found, in many respect similar to the physical aging regime of glassy systems. The experimental findings of Richardson et al. are reproduced in this non-stationary regime. Again to stress the connection to glassy dynamics, the latter regime will is also called 'aging' regime. It should be kept in mind, however, that in discussing the properties of the model 'aging' only refers to the gradual changes in the collective dynamical behavior of the whole colony. Correspondingly, the 'age' of the system  $t_{\rm w}$  is simply the time elapsed from the start of the dynamical process through which spatial structures emerge starting from a completely structure-less configuration. In contrast, the model does not contemplate the possibility that single ants could change their characteristic response to the same external stimuli. It hence excludes, a priori, any aging process affecting individuals. The model also features a stationary regime, where movements are well described by a standard Poisson process, similar to the findings of Nouvellet et al. We speculate at the end on how these two regimes can arise in ant colonies and on whether it is possible to trigger a change from one to the other.

### II. MODEL DESCRIPTION

Ants of N different types move on a toroidal lattice of size  $M=L^2$ , where L is the linear grid size. Here, a 'type' is only defined in terms of interactions and no other properties, e.g. size and color, are attached to it. The interactions determine, in turn, how ants move around. In the following, lattice points are indexed using typewriter order, i.e. the natural sequential ordering of letters in a text written in a western language. A configuration is then specified by the number  $n_{l,x}$  of individuals of type l located at site x, i.e. by the  $N \times M$  rectangular matrix  $\mathbf{n}$ . The interactions  $J_{ij}$  between a pair of individuals of type j and i are ordered in the  $N \times N$  square matrix J. Without loss of generality (see below), the latter can be assumed to be symmetric. Denoting matrix transposition by a superscripted dagger,  $(^{\dagger})$ , we construct the  $M \times M$  matrix

$$\mathbf{I} = \mathbf{n}^{\dagger} \mathbf{J} \mathbf{n}. \tag{1}$$

Each entry  $I_{xy} = \sum_{i,j=1}^{N} n_{ix} J_{ij} n_{jy}$  represents the interaction of all individuals at site x with all individuals at site y, irrespective of the Euclidean distance  $d_{x,y}$  separating these two sites. To weigh distance in, we finally introduce a 'damping' matrix  $\mathbf{D}$ , with entries  $D_{x,y} = \exp(-\alpha d_{x,y}^2)$ , where  $\alpha$  is a non-negative constant. Note that D is symmetric and has diagonal elements equal to one. The sum of all interactions finally produces the utility function

$$E = \operatorname{trace}(\mathbf{ID}) = \sum_{x=1}^{M} \sum_{y=1}^{M} I_{x,y} D_{y,x}.$$
 (2)

Each element of the double sum represents the interaction of individuals located at positions x and y, duly modified by the damping factor  $D_{y,x}$ . The change in utility associated to the move of an individual of type l from site f(rom) to site t(0) is correspondingly given by

$$dE_{l,t,f} = 2\sum_{x=1}^{M} \sum_{i=1}^{N} (D_{x,t} - D_{x,f}) n_{i,x} J_{l,i} + 2J_{l,l} (1 - D_{t,f}).$$
(3)

Were the matrix J not symmetric, the term  $2J_{l,i}$  in the above expression would be replaced by  $J_{l,i}+J_{j,l}$ . As anticipated, symmetric interactions can therefore be assumed from the outset with no loss of generality. Secondly, if the system only contains a single ant of type l, i.e. if  $n_{i,x}=\delta_{i,l}\delta_{x,f}$ , the change in utility associated to any move from f to t is always zero. Likewise if the interactions are independent of distance, e.g. if D has all entries equal to one. In both cases, motion is purely diffusive.

In general, the dynamics is a Markov chain generated by the Metropolis rule. In the stationary state eventually reached by the dynamics, the average value of the utility function E decreases with increasing DS, while in a physical system the average energy increases with temperature. Each update comprises the following steps: a position is randomly chosen with equal probability among all those available. A type is then chosen in the same fashion. An ant of the given type (if present) is assigned a candidate move to a randomly chosen neighboring site. The move is accepted if it increases the value of the utility function. Moves decreasing the utility function are accepted with a

probability which decays exponentially as a function of the ratio  $dE_{l,t,f}/T$  of the change in E to the value T of the DS. For T=0 the dynamics is a greedy optimization algorithm attempting to maximize the utility function. In the stationary distribution of the Markov chain just defined, the probability for configuration k is, modulo a normalization constant, equal to  $\exp(E(k)/T)$ . Whether the stationary distribution is within reach strongly depends on the DS, as further discussed below. Time evolution is gauged in terms of Monte Carlo (MC) sweeps, each sweep comprising a number of queries equal to the number of individuals in the system. In the initial configuration, the number of ants of each type which are located at a site is drawn, independently for each site and type, from a uniform distribution between 0 and 10.

To connect with ant experiments, an arbitrary site on the grid is designated 'exit', and all movements which involve this particular site are recorded as 'events'. Depending on the situation, we either consider the statistics of the waiting times  $t_k - t_{k-1}$  between consecutive events, or that of the corresponding log-waiting times  $\ln(t_k) - \ln(t_{k-1})$ . Secondly, we calculate the time dependence of the average utility function for a number of different situations. Thirdly and finally, we show that, in the aging regime, the probability of 'large' events (defined later in the text) occurring in an arbitrary time interval  $[t_w, t]$  anywhere on the grid scales as  $\ln(t/t_w)$ , modulo finite time corrections due to our time variable being restricted to integer values.

#### III. GENERAL CONSIDERATIONS

Depending on a number of choices detailed below, the model either quickly reaches a stationary state or is unable to do so within numerically accessible time scales. In the first case, the 'exit' process is a standard Poisson process. In the second, a Poisson process also describes the statistics but with the logarithm of time replacing time in its average. A logarithmic time dependence also characterizes the statistics of spatial re-arrangements occurring anywhere in the system. It does seems that the replacement  $t \to \ln t$  restores the time-homogeneity of the model dynamics at low values of T.

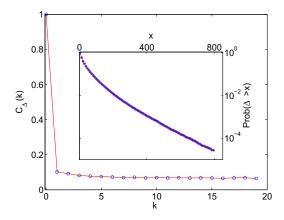
Behind the decelerating nature of aging dynamics is the gradual *entrenchment* of dynamical trajectories in more long-lived metastable configurations[3, 4]. In our model ants which attract each other tend to cluster. Starting from a random distribution, ever larger clusters get established on gradually fewer sites. As discussed below, this in turn creates growing dynamical barriers (e.g. empty sites) for ants which have not yet joined a cluster.

To investigate the issue further several choices of interactions have been considered. Our first choice is a null model lacking any metastable configurations. Ants of the same kind repel each other, while ants of different kinds attract each other. Correspondingly, the interaction matrix has diagonal and off-diagonal elements equal to -1 and 1 respectively. In this case, ants of the same type tend to maximize their mutual distance and hence spread out uniformly in space, irrespective of type. Sites end up either being empty or being occupied by ants of different types. For all T values, the dynamics quickly converges to a stationary state, where 'exit' events are (nearly) a standard Poisson process, of the sort illustrated (for a different example) in the left panel of Fig.1. For all T s, the average E relaxes in a way similar to the high T curves (T = 200 and 500) shown in the left panel of Fig. 2.

More interesting is the case where ants of the same type are indifferent to each other, while ants of different types attract each other, possibly with the exception of ants of type 1 and 2, which repel each other. Correspondingly,  $J_{ii} = 0$  for all i,  $J_{12} = J_{21} = -1$  and  $J_{ij} = 1$  for any other values of i and j. Here, the dynamical behavior strongly depends on the value of the T: stationarity is reached quickly at sufficiently high T but is unachievable at low T.

Consider first the case of two types of ants with attractive interactions. A high values of E (low T) equilibrium configuration has the two types grouped into a small number of sites and, eventually, into a single site. Starting from a random initial distribution, empty areas gradually form. Since ants belonging to two metastable cluster located at different sites can increase their utility function by a merging process which requires crossing growing empty areas, correspondingly growing dynamical barriers between metastable configurations are present in the model. As shown in Fig. 1. this model version has Poisson and log-Poisson exit statistics at high, respectively low T.

Consider now four types, with pairs of type (1-2) repelling each other, and all other pairs attracting each other. Spatially segregated domains of type 1 and 2 must gradually form, while groups of ants of type 3-4, each centered on a particular site, form within each of the two domains. Besides empty space, a domain  $d_2$  containing ants of type 2 presents an additional dynamical barrier for ants of type 1, since it either must be crossed or circumvented in order for these to join a domain  $d_1$  located on the opposite side of  $d_2$ . Also in this case, low T aging behavior is found to characterize the dynamics.



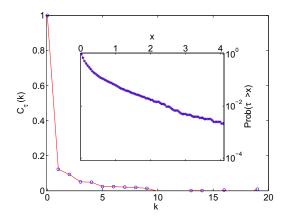


Figure 1: (Color online) Left: The correlation function  $C_{\Delta}(k)$  for the waiting times between consecutive exit events, plotted vs. k. The insert shows the cumulative distribution of the waiting times, plotted on a logarithmic vertical scale. The system contains two types of ants moving on a grid of linear size 7 with DS parameter is T=50. Right: same as above, except that the DS value is here T=5 and that the correlation and cumulative distribution are calculated using the log-waiting times rasher than the waiting times.

#### IV. DATA ANALYSIS

In all our simulations, the damping parameter is  $\alpha$  is equal to 5, i.e. interactions are strongly localized in space. The spatially averaged density of each type of ant is close to 1.8. E.g., with four types present, the system contains appr. 7.2 ants per grid site. Linear grid sizes L=5,7 and 9 were investigated for four ant systems and seen to have qualitatively similar behaviors. Linear grid size L=7 was used for systems with 2, 3, 4 and 5 ant types. The result shown are for L=7 to emphasize that a large grid size is not required to obtain aging behavior.

Figure 1 describes the exit statistics in a system where two types of ants are present. At the k' th sweep the program checks whether motion has occurred at the site dubbed 'exit' and, if so, registers the corresponding time  $t_k$ . The simulations, each running from t=5 to  $t=5\cdot(1+10^5)$ , are repeated 100 times in order to improve the statistics. The DS values used in the simulation are T=50 and T=5 in the left and right panel, respectively. The data shown are statistically very different in spite of being graphically rather similar. In the left panel the waiting times, i.e. the time differences  $\Delta_k = t_k - t_{k-1}$  are analyzed with respect to their correlation and their distribution. Since the  $t_k$ 's are integer rather than real numbers, the exit process can never be truly Poissonian. We nevertheless estimate the normalized correlation function of the  $\Delta_k$ 's, averaged over 100 independent runs. For independent entries, the latter would equal the Kronecker's delta  $C_{\Delta}(k) = \delta_{k,0}$ . We furthermore estimate the probability that  $\Delta > x$ , as a function of x. For a Poisson process this probability decays exponentially in x. The correlation and probability distribution are plotted in the main figure and the insert, using a linear and a logarithmic ordinate, respectively. We see that short waiting times, i.e.  $\Delta_k$ 's of order one are over-represented relative to the straight line representing the Poisson case. Secondly, the correlation decays to about 1/10 in a single step, but then lingers at that value. Taken together, these two feature indicate that a short waiting time is more likely followed by another short waiting time, i.e. that the motion often stretches over several sweeps.

The right panel of the figure shows data obtained as just discussed, except that logarithmic time differences  $\tau_k = \ln(t_k) - \ln(t_{k-1})$  rather than linear ones are utilized. The correlation function  $C_{\tau}(k)$  decays quickly to zero, albeit not in a single step, and the probability that  $\tau > x$  is nearly exponential. Again, short log-waiting times are overrepresented in the distribution, and since the correlation decays to near zero in k=5, they are likely to follow each other. Thus, also in this case ant at the 'exit' stretches beyond a single sweep. In summary, banning the effect of our time unit, the sweep, being too short relative to the de-correlation time of ant motion, T=50 data are, as expected in a stationary regime, well described by a Poisson process, while T=5 data are well described by a log-Poisson process.

The values of the utility function and the DS strongly affect ant motion: The first gauges the well-being of the ants or the degree to which a desirable aim is reached by the ant society. Its value could possibly be empirically quantified for agents which can be polled. The DS measures the willingness to perform unpleasant moves, or to invest accumulated capital. As high DS value signals indifference, administering suitable drugs to the ants could possibly increase the DS.

The average value of the utility function plotted vs. time provides a good overall characterization of the model dynamics. At low DS values, the statistics of the fluctuations of the utility function provides further insight on the nature of ant motion. We note that while exit events clearly reflect what happens at a given site, changes in E can occur due to motion anywhere in the system. At the level of a single trajectory, E appears most of the time to be a constant. I.e. its fluctuations, defined as differences between consecutive sweeps, are most of the time equal to zero. Correspondingly, most of the time, ants hardly move outside the area represented by a single grid point. Occasionally, a negative fluctuation is quickly followed by one or more positive fluctuations. Such events indicate motion across a barrier from one metastable configuration to another, the latter usually having a higher value of E. Positive fluctuations larger than he threshold value  $\Delta E_{\rm tr} = 0.22$  are counted as large events, irrespective of where they occur in the system. The threshold is chosen to filter our small fluctuations which could easily be reversed. The overall shape of the statistics of large events is, within bounds, insensitive to the specific choice of threshold.

Considering that, at sufficiently low T, the average E grows logarithmically in time, the typical number of large fluctuations can be expected to do the same. For  $k=0,1,\ldots 5$ , consider observation time intervals of the form  $[t_w,\frac32t_w]$  where  $t_w=800-2^k$ . Increasing k by one unit doubles the length of the interval, but the difference between the logarithm of the end-points remains in all cases equal to  $\ln(3/2)$ . If the statistics of large events were only dependent on this logarithmic difference, the probability  $P_n(t_w,\frac32t_w)$  that at least n 'large' events occur in any of the intervals would be independent of k, and probability functions obtained for different values of  $t_w$  would collapse on the same graph. This can never be exactly true: since at most one event can be registered per MC sweep, the highest number of events possible is limited by the length of the observation interval. I.e. finite time corrections to the logarithmic law can be expected.

All data presented in Fig. 2 pertain to a system with four types of ants. Its left panel depicts, on a logarithmic horizontal scale, the value of the utility function per ant, averaged over 100 trajectories, as a function of time (i.e. number of MC sweeps). For T=500 and 200, a constant value is approached which increases as the DS decreases. For T=5 and T=10 the average E is seen to grow logarithmically without approaching equilibrium. The equilibrium value would lie far above the plateau reached at T=200. If the logarithmic trend were to continue up to its asymptotic long time limit, the 'transient' would stretch over more than 10 decades. The behavior at T=30 is intermediate. Here, the curve has two knees, with a third barely visible at the end of the range. Yet, no stationary state is reached within the observation time. Consider now the two low T curves. For any fixed value of time, the mean value of the utility function increases with T. The strong non-equilibrium character of the low T dynamics is highlighted by the ordering being opposite than in the equilibrium regime.

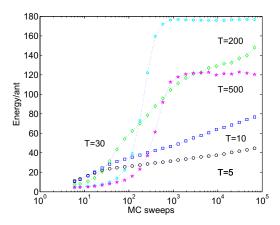
The statistics of low T fluctuations in E was investigated for T=5 and T=10, with data collected at the latter value of the DS shown in the right panel of the figure. The insert illustrates the highly intermittent nature of the fluctuations. In the main panel, the probability of large events  $P_n(t_w, \frac{3}{2}t_w]$  is plotted versus n for six different values of  $t_w$ , each twice as large as its predecessor.

Data sets belonging to different observation intervals collapse for values of the abscissa, n, smaller than the length of the observation interval. Banning finite-time effects, the global dynamics is thus well described by a process which is homogeneous in the logarithm of time. This fully agrees with the statistical properties of the exit process which describes motion at a single site, but which, on the other hand is observed over a much longer time span. We finally note that the same scaling analysis performed using data sampled at T=5 yields a near perfect data collapse, with the sole exception of data taken during the shortest and earliest observation interval [800, 1200]

## V. SUMMARY AND OUTLOOK

A stochastic model is used to explore the dynamics of groups of ants, or more generally, social agents, which move in a confined space to optimize a utility function E depending on their mutual interactions. The dynamics is stationary, respectively non-stationary for high and low values of a model parameter called 'degree of stochasticity' (DS). The latter is a measure of risk-willingness: at high DS values, agents readily perform moves which decrease their utility function, while in the opposite limit they are mainly unwilling to do so. A macroscopically quiescent system state is soon reached at high DS values, while the state slowly evolves due to the gradual emergence of new spatial structures at low values of the DS. Correspondingly, the statistics of 'exits' from the nest, i.e. movements involving a particular but arbitrary site, is either a simple Poisson process , as found by Nouvellet et al. [6] or a log-Poisson process as found by Richardson et al. [1]. At low DS values, the probability that n large changes of the utility function occur anywhere in the system in a given time interval is found to scale with the difference of the logarithms of the interval's end-points, except for finite time corrections important for short observation intervals. In conclusion, the model's low DS dynamics is in-homogeneous and decelerating when parameterized by time, but turns into a homogeneous process when the logarithm of time is used as independent variable.

The above type of logarithmic relaxation occurs in both biological and physical systems[1, 4, 9–11]. Whenever



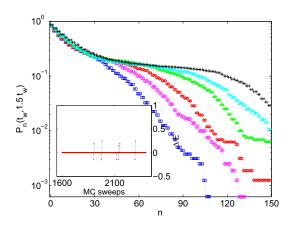


Figure 2: (Color online) All data shown pertain to a system with four ant types, with one negative and five positive interactions between different types. Left panel: the value of the utility function per ant, averaged over 100 trajectories, is plotted versus time. The initial configuration is in all cases obtained by randomly placing the ants on the grid. Right panel: The probability that the number of 'large' events (as defined in the main text) occurring in the interval  $[t_w, 3/2t_w]$  is larger or equal to n is estimated using 2500 trajectories all run at the DS value T=10. The results are plotted versus n. for sampling intervals starting at  $t_w=800$  (lowest curve) up to  $t_w=25400$  (highest curve), via intermediate values  $t_w=1600,3200,6400$  and 12800. The insert shows a sample trajectory starting at  $t_w=1600$ .

record-breaking noise fluctuations can trigger irreversible changes in configuration space its origin is linked to the mathematical properties of record-statistics [2, 12]. Our model suggests a novel interpretation of record dynamics as applied to socially interacting agents: The record sized fluctuations triggering important and irreversible dynamical changes correspond to record high investments, i.e. to a record high decrease of the utility function of the ants involved.

Returning to the findings of Richardson et al. and Nouvellet et al. which motivated this work, one can speculate on what the present model has to say on the origin of the different behaviors observed by the two groups. Firstly, both behaviors are possible. Secondly, the Poisson exit statistics seen in the stationary regime can also more simply be obtained by assuming that ants act independently of each other. The log-Poisson behavior does however require interactions. This is the case in experiments [5], where it is removed by disrupting the pattern of social interactions among the ants. In the model, it is possible to increase the value of the DS parameter in a continuous fashion. At a threshold value, the log-Poisson statistics is then replaced by a Poisson statistics. The question is whether the same controlled transition could be achieved experimentally, i.e. by gradually changing the geometry of the nest, by chemically masking the stimuli ants affect each other with, and finally, by using drugs which increase the risk-willingness of the ants, or equivalently, their indifference to external stimuli. To obtain the effect might not require too drastic interventions: A 'normal' DS value just below the threshold could be favored by evolution because it guarantees the fastest possible increase of the utility function compatible with the history dependence and memory effects which generally occur in glassy dynamics and which seem to naturally belong to an evolving biological organization.

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In a stochastic model of ant behavior, ants move in their nest to improve a utility function which depends on distance and ant-type dependent interactions. At low values of a parameter called Degree of Stochasticity (DS), the spatial organization of the society slowly changes and the utility function grows as the logarithm of time. At high values of the DS a stationary state is quickly reached. > log-Poisson and Poisson statistics of nest exit events are found in the two regimes.

