

Is animal behaviour chaotic? Evidence from the activity of ants

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SUMMARY

Chaotic dynamics have been implicated in several biological phenomena including epidemics (Olsen & Schaffer 1990), population dynamics (Schaffer & Kot 1985; Sugihara & May 1990), electroencephalograms (Mayer-Kress & Layne 1987) and certain physiological rhythms (Glass & Mackey 1988). In this paper I show that animal behaviour may also be chaotic. The attractor of the movement activity of single, isolated *Leptothorax allardycei* ants has a small, non-integer dimension characteristic of low-dimensional chaos. The activity of entire colonies of ants yields an integer dimension that is consistent with periodicity in activity. First-return maps of the activity of single ants are highly non-random suggesting that the interpretation of determinism in these activity patterns is realistic. By contrast the first-return maps of whole-colony activity records show no pattern, a fact consistent with the interpretation of noisy periodicity in colony activity rhythms.

1. INTRODUCTION

Animal behaviour is among the most complex of biological processes. Variation in behaviour is due to an intricate outcome of genetic, developmental, neural and physiological processes as well as to environmental effects. Whereas this complexity presents us with a rich variety of phenomena, it also often limits our understanding of the evolution and operation of behaviour. Attempts at a theoretical description of a behavioural process may involve not only enormous numbers of variables but interactions among them. In organisms that live in social groups interactions among group members produce an additional level of complexity in behaviour. We can exploit this higher level of behavioural organization to explore the consequences of interactions between individuals for the behaviour of both individuals and groups.

Complex systems, with many non-linear interactions, such as those which produce behaviour, are precisely those which may exhibit complicated dynamics including chaos. They are also the sort of systems that would most benefit from simplification. If we could discover chaos in complex animal behaviour it would simplify the task of describing the dynamics of behaviour because many complex variables and interactions may be reduced to a more tractable number that are sufficient to describe the dynamics. This would improve our understanding of the operation and evolution of behaviour in at least two ways: first, by showing the type of models that are adequate to describe behavioural changes, and second by guiding the collection of data suitable for the models.

It can be difficult to examine behavioural data for

evidence of chaos because of the problems of obtaining long sequences of suitable data. To characterize behaviour or a behavioural phenotype it is often both appropriate and convenient to average the measurement of a behavioural character over some time interval. If the behaviour has a substantial stochastic component it must be averaged over some relatively large interval in order to discern whatever order exists. However, for behaviour that varies temporally this procedure will obscure any short-term pattern. In this paper I shall examine the complex temporal pattern of movement activity in individuals and groups of a social species, the ant *Leptothorax allardycei* (Mann).

Data are acquired by an automatic digitizing camera that produces a 640×128 pixel image, and counts the number of differences between successive images of the camera (Cole 1991*a, b*). The number of pixel differences is a measure of the activity in the image; measurements on images of motionless ants fall to the instrumental noise level, whereas a high level of activity produces large number of pixel differences.

Activity records of single ants and colonies of ants and their spectrograms are shown in fig. 1. Single ants have patterns of activity characterized by isolated, spontaneous bursts of activity followed by relatively long periods of inactivity. In colonies of ants there are rhythmic episodes of activity. The spectrograms illustrate that individual ants show no clear spectral peaks, whereas intact colonies have peaks of power at distinct frequencies (the height of the highest peaks are highly significant by Fisher's test, $p \ll 0.001$, Shimshoni (1971)). The activity cycles of colonies of ants are sustained and show a typical period of approximately 25 min. These cycles are similar to those observed in

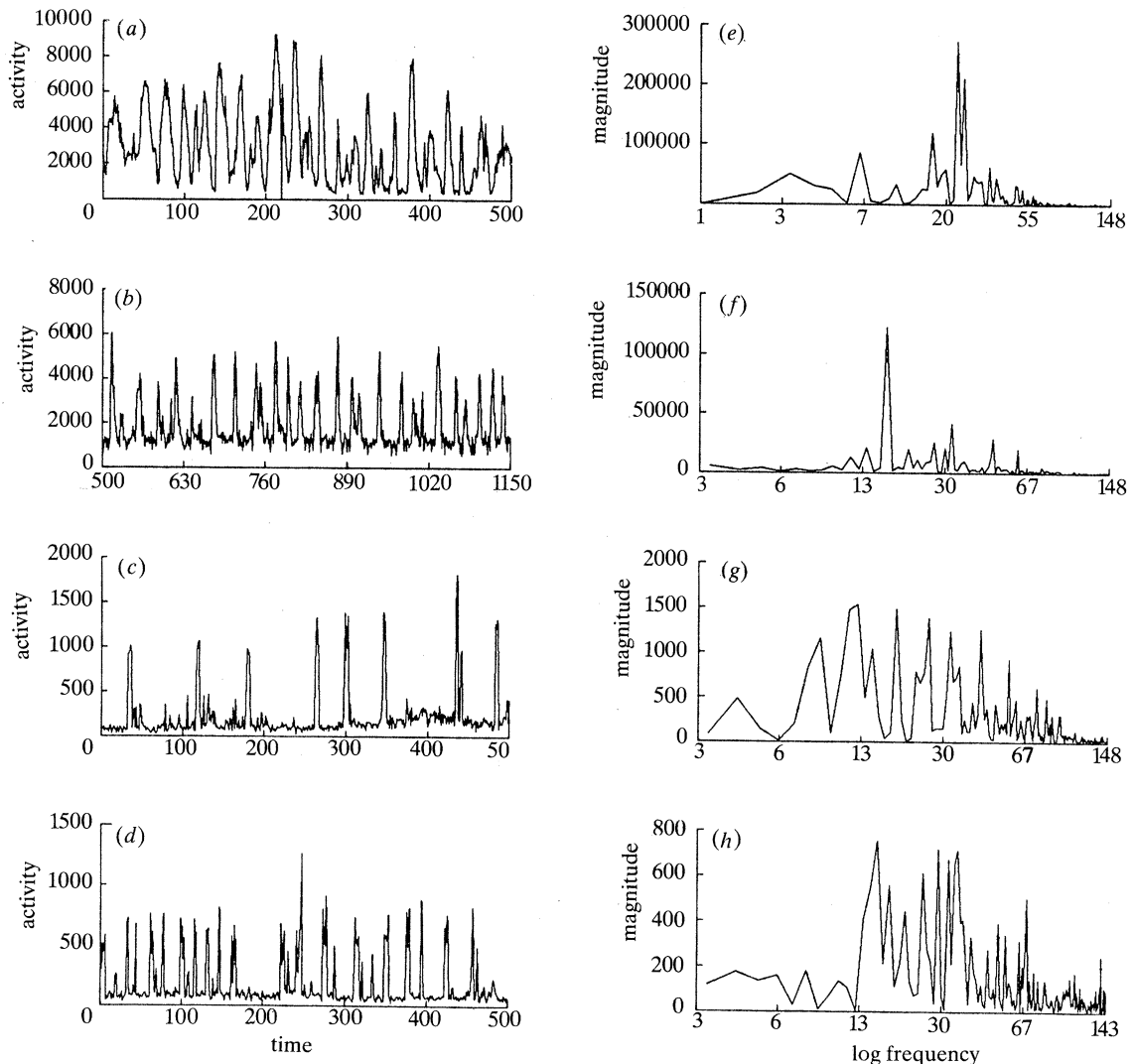


Figure 1. (*a, b*) Activity records for two intact colonies. Each time unit represents 30 s in all activity records. The measure of activity is the number of pixels in a MicronEye image that have changed during the interval. (*e, f*) Power spectra for the colony activity records. (*c, d*) Activity records for two single ant activity records. (*g, h*) Power spectra for these two single ant activity records.

L. acervorum (Franks *et al.* 1990). As larger numbers of ants are included in an aggregate, the synchrony of activity among individuals increases.

2. MEASURING THE DIMENSION OF THE ATTRACTOR

Chaotic systems are deterministic ones which are constrained to an attractor. Purely random fluctuations, by contrast, are not constrained to a low-dimensional surface, but are space filling. Finally, periodic or quasiperiodic trajectories evolve on surfaces of integer dimension. We can reconstruct the attractor of movement activity and measure its dimension.

The measurement of the dimension of an attractor is frequently made by using the method of Grassberger and Procaccia (see, for example, Olsen & Schaffer (1990); Schaffer & Truty (1988)). Although the method is in widespread use and gives reliable results for certain types of data, it can give misleading results for other types of data. Some of the pitfalls of using the Grassberger–Procaccia algorithm have been detailed

elsewhere (for examples, see Albano *et al.* (1988); Möller *et al.* (1989); Sugihara & May (1990)). One of the situations in which using Grassberger–Procaccia can give misleading results is when the data are too noisy. When the signal to noise ratio (SNR) of the data record is less than about 20 dB (measured as: $10 \log_{10} [\text{var}(\text{signal}) \div \text{var}(\text{noise})]$), then Grassberger–Procaccia is inapplicable (Hediger *et al.* 1990) because there is not a well-defined scaling region in the calculations of the correlation integral. There is instrumental noise associated with the measurement of ant activity. For the activity records of intact colonies, I have estimated the SNR to be about 35 dB, or well within the range of what Grassberger–Procaccia can tolerate. However, the SNR of individual ants is in the neighborhood of 10 dB. This level of noise makes it inappropriate to use Grassberger–Procaccia.

Other techniques for measuring dimension have been developed. To measure the dimension of the attractor of individual ants I shall use the Local Intrinsic Dimension (LID) method of Hediger *et al.* (1990). Their procedure, as does Grassberger–

Table 1. Dimension calculations for ant activity records

	number of estimates	dimension estimate	2 s.e.	SNR db	method
whole colonies	10	3.09	0.24	35	Grassberger–Procaccia
single ants	10	2.43	0.30	12	local intrinsic dimension

Procaccia, begins by lagging the data against itself in some number of embedding dimensions. The embedding dimension must be greater than $2m + 1$, where m is the dimension of the attractor to ensure that the properties of the attractor are preserved (Takens 1981; Broomhead & King 1986). One estimates the dimension as the number of orthogonal directions along which the data are arrayed in the local neighborhood of a randomly selected point. The mean of a number of such points around the attractor is the LID. If the embedding dimension is r , then we take some number, n , closest neighbours of a randomly chosen point (n is typically three times the embedding dimension, Albano *et al.* 1988; Hediger *et al.* 1990). The matrix of the coordinates of the n points in r dimensions forms the data matrix, \mathbf{M} . The eigenvalues of the standardized variance–covariance matrix, $(\mathbf{M}^{-1}\mathbf{M})$, are related to the fraction of variation that occurs along principal axes. The contribution of Hediger *et al.* (1990) was to use a result from signal processing which makes use of an information theoretic criterion, the Minimum Description Length (MDL, Wax & Kailath 1985) to estimate which of the axes are associated with the signal and which are associated with noise. In other words, the variation along the first several axes are associated with the dispersion of data around the attractor, the remaining axes are associated with random variation around the attractor. The MDL criterion of Schwarz (1978) and Rissanen (1978) has been found to give the best results. It involves finding the value k that minimizes the quantity:

$$L(k) = -\ln \left\{ \left(\prod_{i=k+1}^r u_i^{1/(r-k)} \right) \left(\frac{1}{(r-k)} \sum_{i=k+1}^r u_i \right)^{(r-k)q} \right\} + (kr - k^2/2 + k/2 + 1) \frac{\ln q}{2},$$

where u_i is the i th eigenvalue of the variance–covariance matrix. One then repeats this procedure for many points. The mean of the values for a number of points approximates the dimensions of the attractor. Hediger *et al.* show that this procedure gives a good estimate of the dimension of several well-studied chaotic systems. The important advantage of the LID technique is that it can be used even when the SNR in the system is as high as 5 dB, i.e. when the noise is as much as 30 times as great as can be tolerated by Grassberger–Procaccia. The method will overestimate the dimension of the attractor when the SNR exceeds about 15 dB as the method concludes that more of the axes are ‘real.’

Because the SNR of the activity records of ant colonies is high enough to be analysed by Grassberger–Procaccia, and is too high to be analysed by LID, I have calculated the correlation dimension using the im-

plementation of Schaffer *et al.* (1988) and the multi-dimensional tree-searching algorithm of Bingham & Kot (1989). The values obtained are summarized in table 1. Because it is difficult to obtain any sort of estimate of the error of any particular Grassberger–Procaccia estimate, I have used the replicate estimates of the correlation dimension of a number of ant colonies to estimate the distribution of the correlation dimension. The dimension of colony activity records (mean = 3.09 ± 0.24) is not significantly different from a value of three dimensions ($t = 0.24$, d.f. = 9, $p > 0.4$). The activity of colonies is consistent with nearly periodic motion about a toroidal attractor.

The dimension calculations for single ant activity records are summarized in table 1. To obtain a reliable estimate of dimension using the LID method, it is necessary to have a high density of points around the attractor. This is required because, if one uses an embedding dimension of 10, it is necessary that the 30 nearest points to a chosen point be in the local neighborhood of that point of interest. If the data density is low about the attractor, the 30 nearest points will be some distance away, and the cloud of points will not be locally linear. This will result in an overestimate of the dimension of the attractor. The data for single ant activity records are substantially longer (6 h versus 4 h) and involve larger numbers of data points (about 7200 points per record). For each single ant activity record I embed the record in ten dimensions. The lag interval, t_1 , that I use is 33 time units; each time unit represents 3 s. The time window of any particular data point is $t_w = (r-1)t_1$, where r is the embedding dimension. The length of the time window that should be used is a matter of some discussion (Broomhead & King 1986; Mees *et al.* 1987; Albano *et al.* 1988), but one guideline is to use a value of 2–3 times the correlation time, t_c , the time of the first zero of the autocorrelation function. The autocorrelation function reaches the first zero for these single ant activity records at a lag of approximately $t_c = 100$ –150. The lag interval that I use gives a time window of 300.

The dimension calculations are robust to variation in the lag used in the LID method. In figure 2 I show the estimated dimension over a range of lag intervals, from $t_1 = 25$ –45 (which corresponds to a time window of 225–405) for three individual ant activity records. The estimates are standardized so that the estimate at $t_1 = 33$ is one. Over a broad range, the estimate of the dimension does not change any systematic manner. The standard errors on these points have been omitted from the figure for clarity, but none of the estimates change as a function of time lag.

The mean dimension of the attractor of single and activity records is 2.43 ($\pm 0.30 = 2$ s.e.). This value is significantly different from the integer values of either

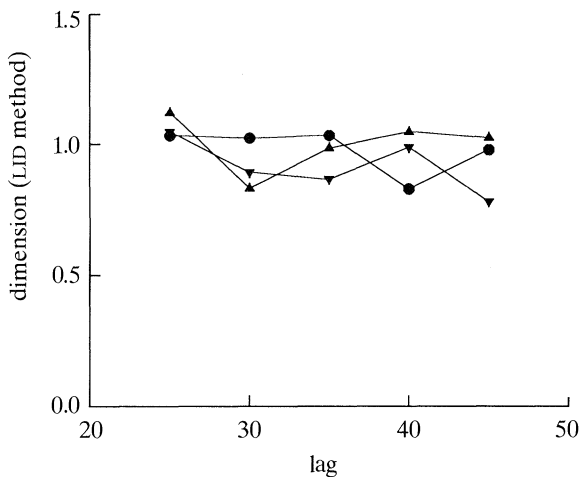


Figure 2. The Local Intrinsic Dimension calculated from three single ant activity records (inverted triangles, S5323; upright triangles, S2912; circles, S113) over a range of time lags. The dimension estimates that are summarized in table 1 use a time lag of 33 time units. The values in the figure are standardized to the estimate obtained from $t_1 = 33$. Although the standard deviations are omitted from this figure for clarity, none of the estimates differ from one another across the range of time lags. Because the estimates are based on embedding the data in ten dimensions, the time window ranges from 225–405 time units.

two ($t = 2.90$, $p < 0.01$, one-tailed) or three ($t = 3.84$, $p < 0.005$, one-tailed) as well as significantly different from that of colony records ($t = 3.49$, d.f. = 18, $p < 0.01$).

3. CONSTRUCTION OF RETURN MAPS

Prediction of the long-term course of a chaotic process is not possible due to the fact that nearby trajectories diverge exponentially with time. However, it may be possible to make short-term predictions about the dynamics of a chaotic system by constructing a first-return map of successive excursions about the attractor. The return map of a chaotic process will typically show a non-random pattern. Observation of a non-random pattern does not guarantee the presence of chaos, but in combination with other evidence, such as the non-integer dimension of the attractor, is strongly indicative. Poincaré sections are produced from the reconstructed attractor by cutting through the attractor with a plane. The plot of successive values of the trajectory against one another as they pass through this plane is the first-return map. Poincaré sectioning of the attractor, embedded in three dimensions, is illustrated in figure 3 for two single ant activity records (the return maps for these sections are shown in figure 5*a, b*). In figure 4 I show two first-return (Poincaré) maps of two activity records of intact colonies. The return maps show no indication of pattern in successive peaks. This is expected from noisy periodicity. However, the first-return maps of single ant activity records (e.g. figure 5) seem to show clearly non-random patterns.

Although a pattern may appear to be non-random,

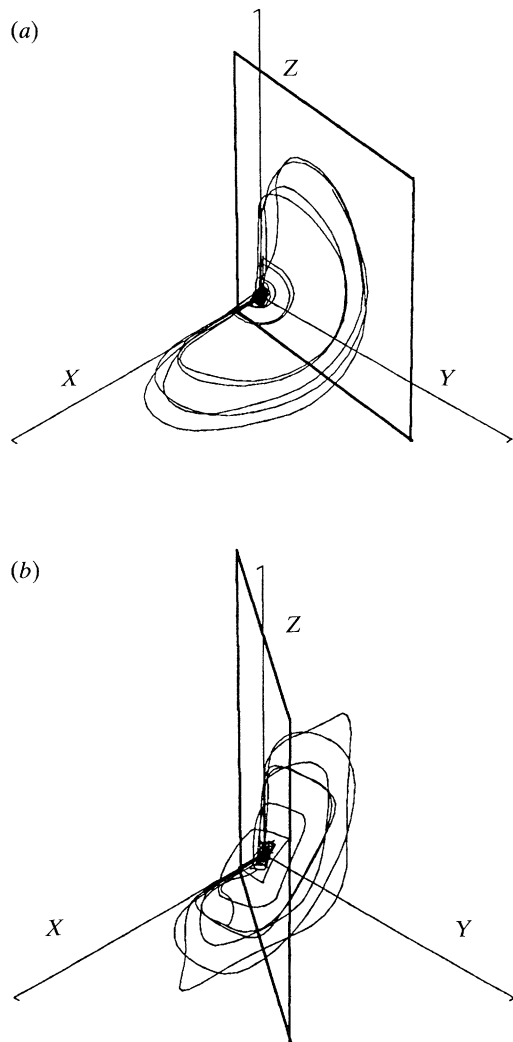


Figure 3. (*a, b*) Two reconstructed attractors from single ant activity records. The data set (X) is lagged against itself to produce a trajectory embedded in three dimensions ($X, Y = X + t, Z = X + 2t$, where t is the time lag). The intersection of the trajectory with the illustrated planes (the Poincaré sections) are used to produce the return maps shown in figures 5*a, b*, below.

it is important to recognize that pattern can be apparent in random sequences and therefore to determine whether the apparent non-randomness is significant. Quantifying the extent of the non-randomness is not straightforward. There are at least two reasons for this difficulty. The first is that the return map has an unspecified form. Therefore, the null hypothesis against which the data are to be tested is not known in advance. Second, the expected form of the return map will likely not have an integer dimension. This makes standard curve-fitting meaningless. Several methods were used to test for patterns in the return maps. The methods were all based on randomizations and do not exhaust all the possibilities. The first, following a suggestion by W. Schaffer, is to use as a test statistic, the sum of the product of the x - y coordinates of the points of the return map. This statistic is tested against a randomized distribution. The null distribution is formed by randomizing the x -coordinates (equivalent to randomizing the successive

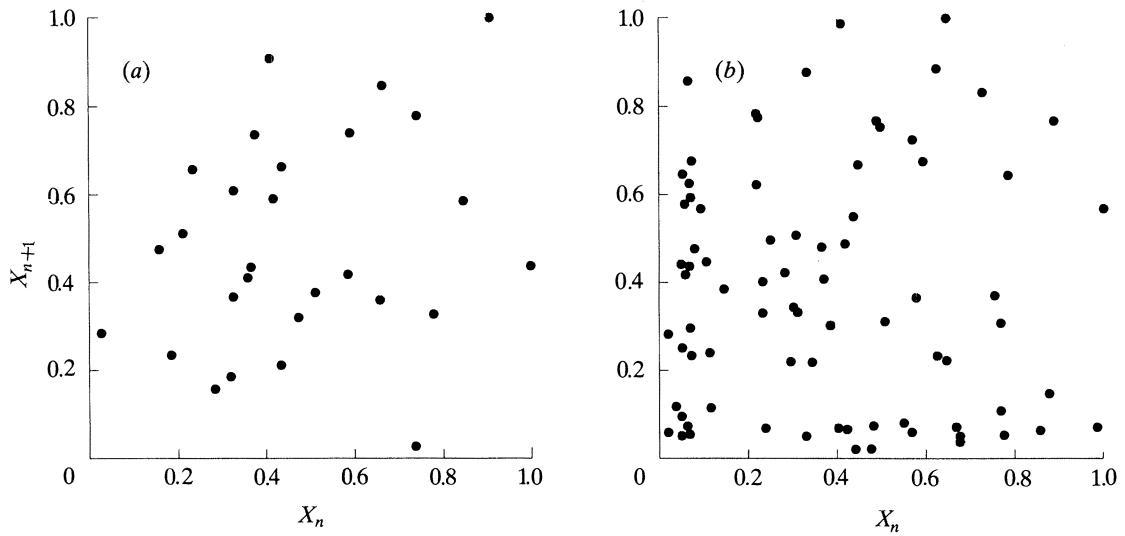


Figure 4(a, b) First-return maps from Poincaré sections of whole colony activity records embedded in three dimensions. The points are plotted on a relative scale with the largest value set equal to one. The value of the trajectory in the Poincaré section is plotted against the next value of the Poincaré section. The pattern of successive points is random.

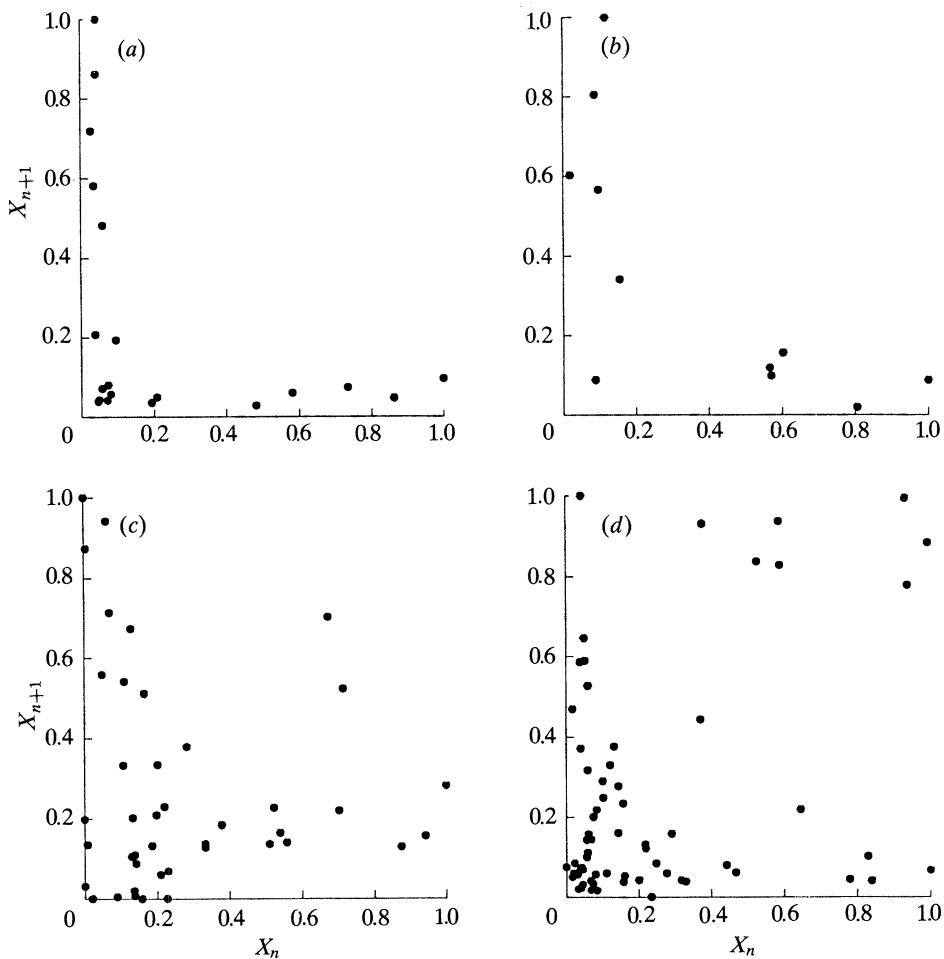


Figure 5(a-d) First-return maps from four single ant activity records. In each case the return map can be shown to have a non-random pattern. The axes and scale are as in figure 4.

passes through the Poincaré section), creating the randomized return maps and calculating the statistic. This procedure is sensitive to either an approximately

hyperbolic return map (figure 5a, b), or to a return map in which large excursions around the attractor frequently succeed one another (figure 5d).

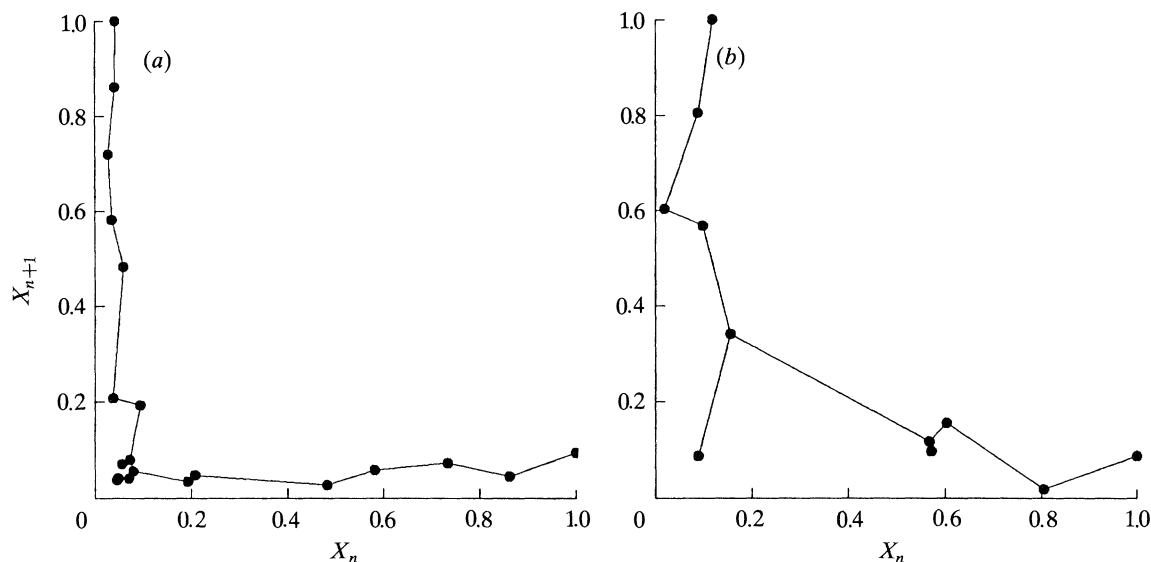


Figure 6 (*a, b*) Minimum spanning trees of the first-return maps given in Figure 3 *a, b*. The length of these minimum spanning trees is significantly less than that expected from randomized data. The axes and scale are as in figure 4.

Table 2. *Results of statistical test for non-randomness in the return maps shown in figure 3*

The entries are the estimated significance levels from the randomization tests described in the text. 'Zero' refers to the number of squares with zero points in them; 'cumu' refers to the maximum difference in the cumulative distribution function of points per square; 'prod' refers to the sum of the products of the x - y coordinates of the return maps; 'spanning tree' refers to the length of the minimum spanning trees.)

activity record	zero	cumu	prod	spanning tree	
				length	significance
S151	0.012	0.202	< 0.001	2.0	0.02
S5333	0.144	0.04	0.3	3.31	0.068
S121	0.01	0.138	0.004	1.98	0.02
S1422	0.46	0.1	0.002	4.41	0.60

The second procedure is to form the test statistic by dividing the range of x - and y -coordinates into several intervals and to count the number of boxes with 1, 2, 3, ..., etc. points in them. The cumulative distribution of the fraction of points that are found in boxes with one point, two points, three points, etc. is found. To obtain a test distribution, a large number (e.g. 500) of randomized return maps are constructed and the expected cumulative distribution function is calculated. The test statistic I use is the largest deviation of the observed from the expected cumulative distribution. The critical values must be estimated by further randomization of the data to estimate the distribution of the test statistic.

The third method is to divide the range of x - and y -coordinates as above. Here I count the number of boxes that have no points in them. Many randomized return maps are formed and the distribution of the number of empty boxes in the randomized data is used as the null distribution to test the observation. If the

data are constrained to some portion of the potential region, the number of empty boxes will be larger in the observed data.

The fourth procedure is to use the length of the minimum spanning tree as the test statistic. The minimum spanning tree (figure 6) connects the points such that the sum of the distances is as small as possible. The order of the points is randomized and the length of the minimum spanning tree calculated. The distribution of the length of the minimum spanning trees of randomized points is used to estimate the significance of the observed statistic. In patterned data the lengths of the minimum spanning tree may be less than that in randomized data.

The results of these tests are given in table 2 for the illustrated return maps (figure 5). It is possible that a unimodal map may even provide a good initial approximation of the data of figure 5 *a, b*. Given that the estimated dimension of single ant activity is about 2.4, the first-return maps ought to be nearly one dimensional. We expect that there ought to be pattern in a two-dimensional portrait of the return map.

4. DISCUSSION

In contrast to the activity patterns of intact colonies the activity of single ants appears to be chaotic. The fractal dimension of the reconstructed attractor and the existence of non-random first return maps is highly suggestive of chaos. In order to show conclusively that behaviour is chaotic one would like to develop a model for activity that (i) is chaotic under the appropriate range of parameters and (ii) reproduces the transition from chaotic to cyclic activity when interactions among worker ants are allowed. Further, one would like to show, empirically, that cycles of activity can become chaotic when the appropriate behavioural variables are changed.

The existence of chaos in animal behaviour can have

several important implications. Variation in the temporal component of individual behaviour may not be due simply to chance variation in a stochastic world, but to deterministic processes that depend on initial conditions. Although the behaviour of an organism may appear to be quite variable both between individuals and even within an individual from one time to another, the relevant behavioural phenotype may be the geometry of the attractor which may be considerably less variable.

Chaos implies deterministic constraints. The behaviour of individual ants appears to be chaotic, whereas the behaviour of colonies of ants differs markedly in having a rhythm. The transition from the chaos of individuals to the rhythmicity of colonies presumably occurs due to interactions among the colony members. The transition from periodicity to chaos that can be observed in dynamical systems may be played out in the structure of an ant colony. The colony as a social unit may be regarded as a self-organizing structure in which order is maintained by the predictable outcome of interactions among individuals (Cole 1991*a, b*).

The perception of animal behaviour as randomly varying, noisy, or governed by uncontrollable environmental influences could be fundamentally altered by these observations. For example, the temporal pattern of other types of behaviour such as locomotion, feeding or mating may display evidence of low-dimensional chaotic processes. If some of the variation in behaviour is due to the sensitive dependence on initial conditions characteristic of chaotic processes, rather than chance variation in behavioural state or environmental conditions, it suggests that individual responses to stimuli may be generated by fundamentally different processes. This source of variation would have to be considered in our efforts to understand the evolution of behaviour.

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