

# Coupled oscillators and activity waves in ant colonies

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We investigated the phenomenon of activity cycles in ants, taking into account the spatial structure of colonies. In our study species, *Leptothorax acervorum*, there are two spatially segregated groups in the nest. We developed a model that considers the two groups as coupled oscillators which can produce synchronized activity. By investigating the effects of noise on the model system we predicted how the return of foragers affects activity cycles in ant colonies. We tested these predictions empirically by comparing the activity of colonies under two conditions: when foragers are and are not allowed to return to the nest. The activity of the whole colony and of each group within the colony was studied using image analysis. This allowed us to reveal the spatial pattern of activity wave propagation in ant colonies for the first time.

**Keywords:** ants; activity cycles; coupled oscillators; mathematical model; image analysis; social insects

## 1. INTRODUCTION

Social insects are the product of one of the major evolutionary transitions from solitary to collective organization (Szathmary & Maynard-Smith 1995). Of all the social insects, ants have the greatest ecological success in terms of the number of species, the variety of habitats colonized and biomass (Wilson 1971). The secret of this success is that colonies often act as a social unit, exhibiting an efficient and flexible division of labour (Tofts & Franks 1992; Bourke & Franks 1995; Gordon 1996) and problem solving beyond the scope of the individual (Franks *et al.* 1991).

Complex collective behaviour performed by ant colonies includes foraging (Beckers *et al.* 1990), building behaviour (Franks *et al.* 1992) and flexible task allocation (Gordon 1995). Such collective behaviours might be regulated either by a centralized control mechanism (for example, in honeybees and *Polistes* wasps the queen has a dominant role during certain activities (Reeve & Gamboa 1987; Winston & Slessor 1992)) or a distributed control where the local interactions between the individuals determine the collective behaviour (Deneubourg & Goss 1989; Adler & Gordon 1992). The activity cycles which occur within ant colonies of certain species, especially *Leptothorax*, are an example of distributed control (Franks & Bryant 1987; Franks *et al.* 1990a; Cole 1991; Cole & Hoeg 1996; Cole & Cheshire 1996). Workers tend to be active together and inactive together and there is no evidence that any particular individual acts as a pacemaker. Synchronicity arises because active ants can activate inactive ants through physical contact (Cole

1991). Synchronized bursts of activity, which in *Leptothorax acervorum* occur approximately every 20 min, may promote the efficiency of task allocation within the colony by mutual exclusion (Hatcher *et al.* 1992).

In all previous work on activity cycles, workers have been considered to have a homogenous spatial distribution within the nest. It is known, however, that ant colonies, including those of many *Leptothorax* species, have a high level of spatial organization, for example brood sorting (Franks & Sendova-Franks 1992) and worker spatial fidelity (Sendova-Franks & Franks 1993, 1994). One form of heterogeneity in colonies of *L. acervorum* is that there are two spatially separate aggregates of workers inside the nest; one is found near the nest entrance and the other near the brood pile in the middle of the nest (figure 1). The influence of these aggregates on activity is the focus of this paper.

Systems of coupled oscillators are a suitable approach for studying rhythmic behaviour at many levels of biological organization, from populations of molecules to populations of organisms (Winfrey 1980; Goldbeter 1996). Cole (1991) regarded an ant colony exhibiting activity cycles as a population of coupled oscillators: individual ants oscillate between activity and inactivity and coupling occurs due to the ability of ants to activate inactive neighbours. In this paper we regard the two spatial groups of workers within the nest as coupled oscillators. This will be the case if the frequency of interactions and, hence, behavioural coupling between individuals within a group is greater than that among individuals belonging to different groups. If no intergroup interactions were to occur, each group would behave as an independent oscillator. At the other extreme, if there were little or no spatial organization within the nest, the colony would behave as a single oscillator. *L. acervorum* is likely to lie somewhere between these extremes, with the movement of ants between the groups allowing a degree of coupling

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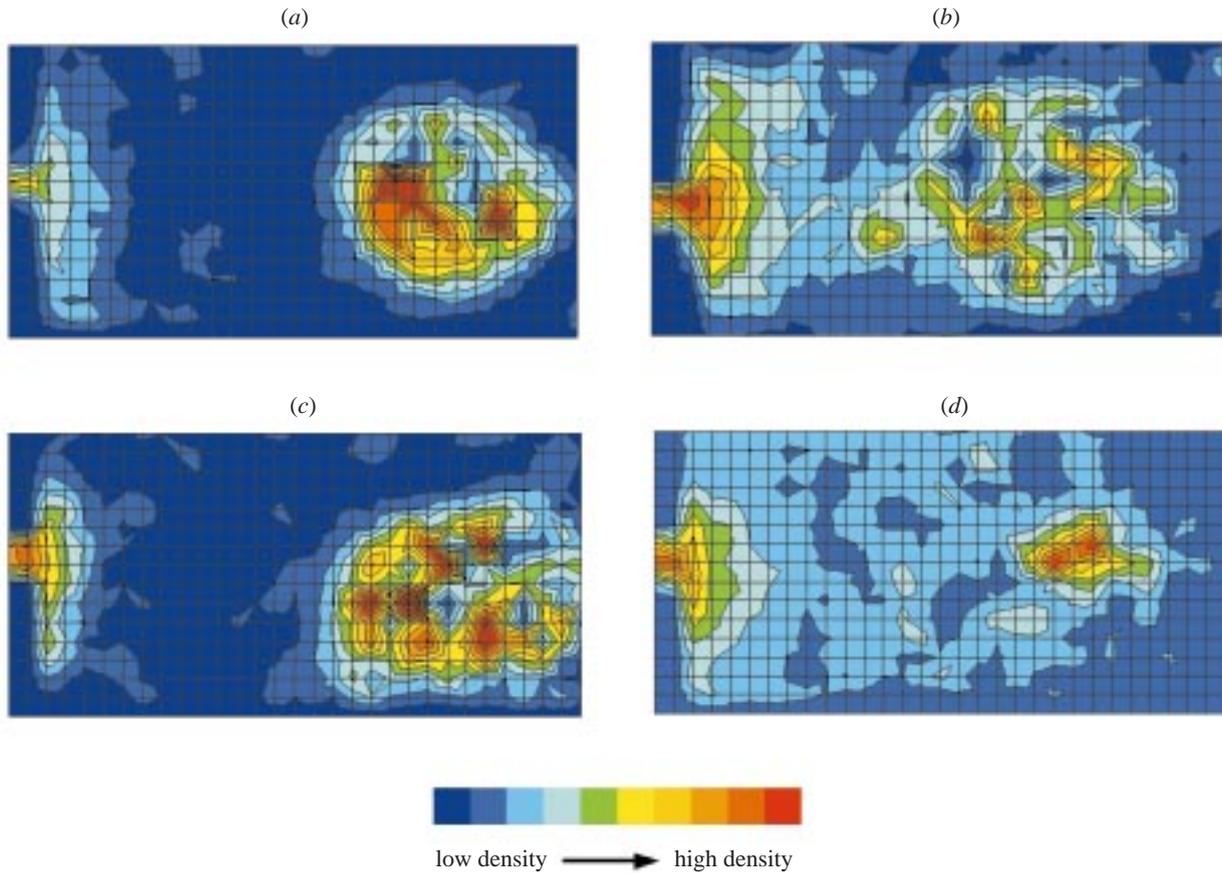


Figure 1. The density of ants in the four nests (*a–d*) recorded by image analysis software, in each case summed over 6 h periods. The nest entrance is on the left of each graph. Two main aggregations of ants were present in all colonies. These aggregations were persistent throughout the experiments.

of group activity levels. We examined this using image analysis. We also investigated the effect of workers leaving and returning to the nest. When foragers leave the nest they become much more isolated and their coupling with pulses of activity within the nest is lost. For this reason, workers will return from periods of foraging and exploration at intervals that bear little or no relation to patterns of activity within the nest. We explored the influence of these individuals on the rhythmical activity within the nest. To do this we developed a mathematical model which makes new predictions and we tested these predictions empirically by preventing foragers from returning to the nest.

## 2. THE MODEL

A number of different types of mathematical model have been developed to explain how activity cycles in lepto thoracine ants occur: differential equations (Hemerik *et al.* 1990), process algebra (Tofts *et al.* 1992) and mobile cellular automata (Miramontes *et al.* 1993; Cole & Cheshire 1996) including fluid neural networks (Solé *et al.* 1993).

Here we develop a model, based on a system of ordinary differential equations, structurally similar to that of Hemerik *et al.* (1990). It describes the state of three groups of workers, named solely on the basis of their spatial location: ‘brood pile workers’ and ‘nest entrance workers’ inside the nest and ‘foragers’ outside

the nest. Workers inside the nest have two possible states, active (indicated as  $N_a$  for the nest entrance workers and  $B_a$  for the brood pile workers) or inactive (indicated as  $N_i$  for the nest entrance workers and  $B_i$  for the brood pile workers), while foragers outside the nest have a generic ‘foraging’ state ( $F_o$ ). The total number of brood pile workers,  $B = B_i + B_a$ , is constant. Individuals in the nest entrance group may leave the nest to become foragers and vice versa. The total number of nest entrance workers and foragers,  $F = N_i + F_o + N_a$ , remains constant. Each group inside the nest oscillates between the two states. They are coupled by parameters ruling the influence of the oscillators on one another. This represents workers moving to and activating workers in the other group.

The system is composed of five differential equations. Equations (1) and (2) constitute the oscillator for the nest entrance group, equations (4) and (5) constitute the oscillator for the brood pile worker group, and equation (3) describes the non-oscillatory behaviour of the outside forager group

$$\frac{dN_a}{dt} = g(E)f(N_a, B_a)N_i - (l - s)N_a + aF_a, \quad (1)$$

$$\frac{dE}{dt} = N_a h(N_a, B_a) - wE, \quad (2)$$

$$\frac{dF_o}{dt} = lN_a - aF_a, \quad (3)$$

$$\frac{dB_a}{dt} = g_1(H)f_1(N_a, B_a)B_i - s_1B_a, \quad (4)$$

$$\frac{dH}{dt} = B_a h_1(N_a, B_a) - zH. \quad (5)$$

The functions  $f$  and  $f_1$  model the activation of inactive ants, either spontaneously or through interactions with active ants. In accordance with Hemerik *et al.* (1990), we chose a nonlinear dependence between active and inactive ants, which implies an autocatalytic effect of active workers (Goss & Deneubourg 1988). By varying the parameters in functions  $f$  and  $f_1$  we are able to regulate the degree of coupling between the two oscillators.

The functions  $g$  and  $g_1$  are decreasing functions of the variables  $E$  and  $H$ , respectively. These variables determine the probabilities of transition from the inactive to the active state of nest entrance workers and of brood pile workers, respectively. The variables  $E$  and  $H$  increase with the number of interactions that have recently occurred between active ants and  $g(E)$  and  $g_1(H)$  are a measure of the ants' reduced probability of activation having been active. This is similar, in probabilistic terms, to including a refractory period after activity.

Active ants become inactive with a constant probability;  $s$  for nest entrance workers and  $s_1$  for brood pile workers. Moreover, active nest entrance workers ( $N_a$ ) leave the nest to become outside foragers at rate  $l$  and outside foragers re-enter the nest to become nest entrance workers according to parameter  $a$ .

We tested the behaviour of the model in two cases. When parameter  $a=0$  (no foragers return to the nest), the system of coupled oscillators inside the nest is isolated from the non-oscillatory compartment outside the nest. When  $a=r(F_o)$  (foragers return to the nest), the non-oscillatory compartment can interact with the system in the nest. We assume, in accordance with our experimental data, that the foragers return to the nest at random times (modelled by the random function  $r$ ).

The model predicts three possible behaviours depending on the degree of coupling between the two worker groups. When coupling between the oscillators is low (representing little movement of ants and, consequently, little interaction, between groups), they can exhibit different periods. Under these conditions the introduction of noise disturbing one of the oscillators has little or no effect on the other. When coupling is high, the oscillators synchronize (figure 2*a*) and a disturbance to one causes a disturbance to the other. At an intermediate level of coupling, the oscillators can synchronize and disturbance to one results in a minor disturbance to the other (figure 2*b*).

By determining empirically which of these three behaviours best describes the effect of foragers returning to the nest, we can assess the level of coupling between the two worker groups.

### 3. MATERIALS AND METHODS

Colonies of *L. acervorum* (Fabricius) were collected in February 1998 from fallen tree branches in sites on the Dorset–Hampshire border in southern England. They were housed in artificial nests that allow the complete colony to be observed in

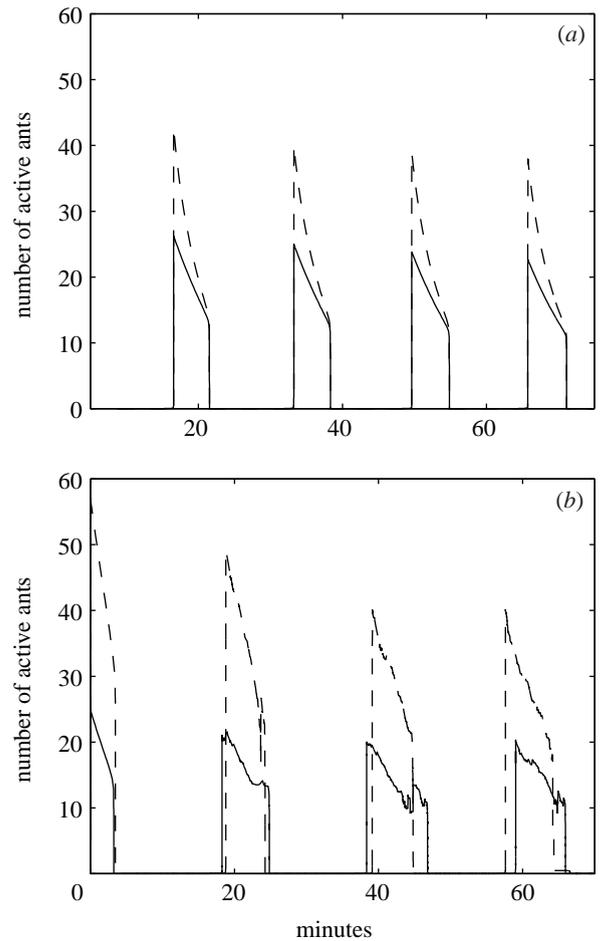


Figure 2. The number of active brood pile workers (dotted line) and nest entrance workers (solid line). (a) Dynamics of the system with coefficient  $a=0$  and a strong level of coupling: the two groups oscillate synchronously. (b) Dynamics of the system with  $a=r(F_o)$  and an intermediate level of coupling: the random return of foragers produces noise in the oscillations of the nest entrance group and a lower level of noise in the brood pile group. The plotted data have been obtained with functions

$$f(N_a, B_a) = [c + j(dB_a^2 + eB_a) + k(dN_a^2 + eN_a)],$$

$$f_1(N_a, B_a) = [c_1 + j_1(dB_a^2 + eB_a) + k_1(dN_a^2 + eN_a)],$$

$$g(x) = (b + x)^{-1},$$

$$h(N_a, B_a) = (mN_a + nB_a),$$

$$h_1(N_a, B_a) = (m_1N_a + n_1B_a).$$

The coefficients have been evaluated experimentally.

the laboratory. Nests consist of two  $7.6 \text{ cm} \times 5.1 \text{ cm} \times 0.1 \text{ cm}$  glass microscope slides held apart by a cardboard frame that was shaped to provide a chamber ( $5 \text{ cm} \times 3 \text{ cm}$ ) with a short, narrow passage to a foraging arena (Franks *et al.* 1990*a*). The nests were housed in  $10 \text{ cm} \times 10 \text{ cm}$  Petri dishes. They were supplied with food and water *ad libitum* and kept at a constant temperature of  $20^\circ \text{C}$  in continuous artificial light (see Franks *et al.* 1990*a*; Cole 1991; Cole & Hoeg 1996). Four colonies were chosen for this study, each having between 40 and 100 workers with two to three queens.

We collected data under two different experimental conditions. In the first, colonies had normal movement of foragers into and out of the foraging arena and the nest was filmed for 12 h. In the second, to test the effect of the return of foragers, the same colonies were filmed for 6 h during which all the ants

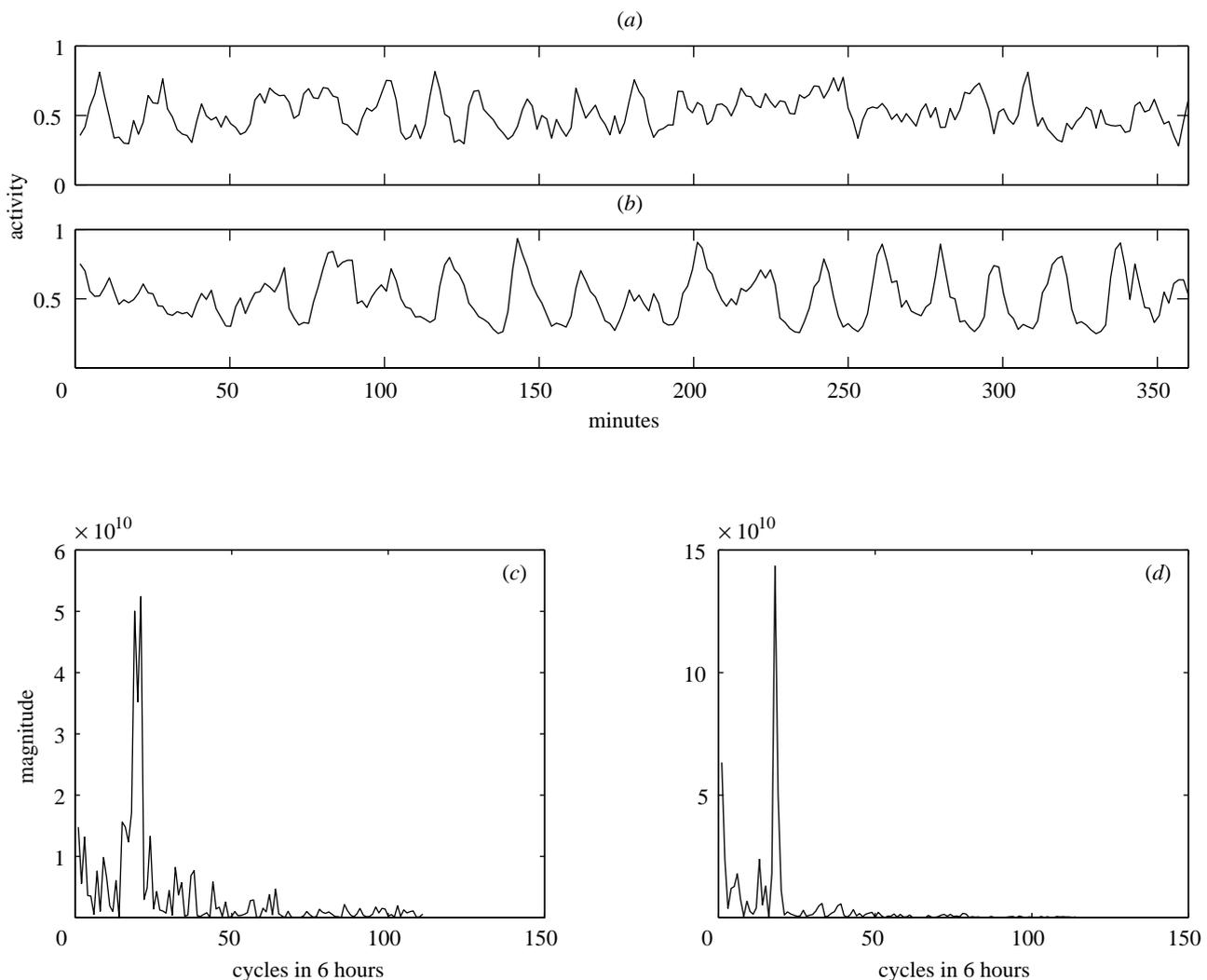


Figure 3. Time-series for whole nests when foragers (a) were and (b) were not allowed to return. Associated periodograms to (a) and (b) are shown respectively in (c) and (d).

that left the nest were removed until the end of filming. This period is sufficiently short to avoid starvation of the colony (Franks *et al.* 1990a).

Both experiments were repeated 12 times over a five week period (three replicates per colony).

The colonies had similar ratios of number of brood items to total number of workers. The mean ratio was 1.75. In experiments where foragers were removed this ratio increased to 2.8. Under both experimental conditions, however, the ratio of brood to brood pile workers was on average 2.5 with a total variation of only 8% between and within replicates.

Colonies were placed under a video camera and allowed to acclimatize for at least 1 h before recording began. We used a Panasonic S-VHS NV-SX30B video camera and a Panasonic S-VHS AG-TL700 video recorder in 12 h time-lapse mode.

The videotapes were analysed to extract spatio-temporal activity using software similar to that used by Cole (1991) and Stickland & Franks (1994) where the movement of ants was evaluated by measuring the change in pixel values between successive frames. Images were captured and analysed at a rate of one frame every 1.2 s. Each image was partitioned into a grid of 1860 squares and the activity level was summed for each square allowing spatial changes in activity to be detected. The

activity values were summed for every 60 frames to maximize the accuracy of movement detection. By dividing these activity levels by the total area occupied by the ants (in pixels) we could record what percentage of the ants in the nest were active.

The image analysis software also allowed us to record the density of ants within the nest. Figure 1 shows the two distinct groups of ants which are present in all nests; one near the nest entrance (which we refer to as the 'nest entrance' group) and one near the brood pile (which we refer to as the 'brood pile' group). This spatial distribution persisted over the experimental duration. Ants outside the nest are termed 'foragers'. Note that in this study ants are classified on the basis of their spatial location. Consequently, a brood pile worker that moves near the nest entrance becomes a nest entrance worker and so on. In the earlier modelling it was assumed that the total number of brood pile workers was constant. This is a good approximation because the number of individuals in the brood pile group remained fairly constant throughout the experiments. In other words, the number of ants leaving this group and entering this group must have been similar. By spatial partitioning of the images, we have been able to assess the activity levels of the two groups of workers inside the nest.

The data have been plotted in time-series and analysed for periodicity by Fourier spectral analysis. We plotted a

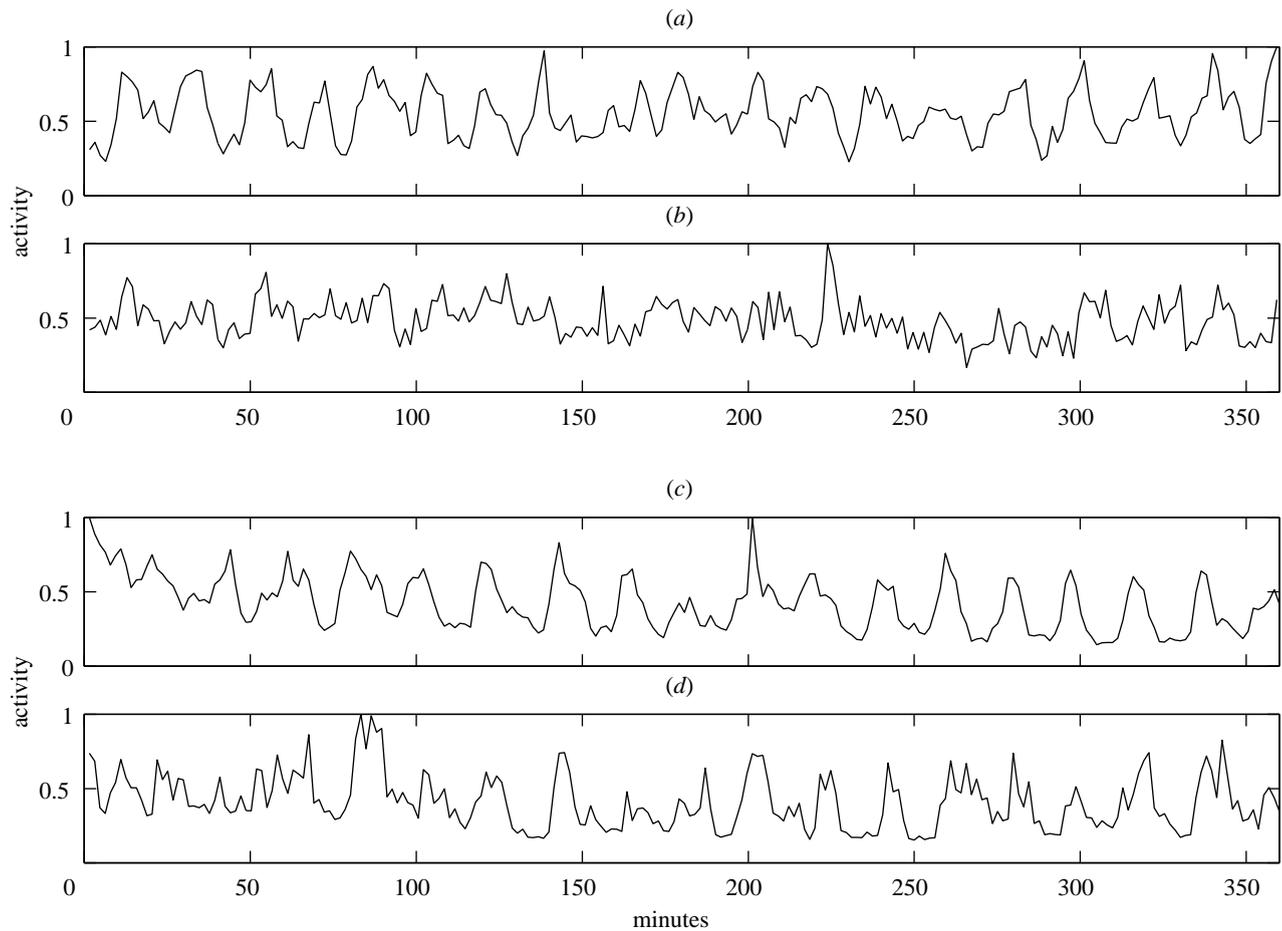


Figure 4. Time-series for the brood pile and nest entrance groups with a return of foragers, (a) and (b), respectively, and in the nest in which foragers have been removed, (c) and (d), respectively.

periodogram to evaluate the fitting of the sinusoidal waves of various frequencies to the time-series. Where periodicity is present the periodogram shows a peak at the corresponding frequency.

#### 4. RESULTS

To test the predictions of the model, we studied the activity patterns using digital image analysis. We compared the activity level of each worker group and of the whole colony under two experimental conditions.

- (i) In colonies with a normal flux of foragers in and out of the nest.
- (ii) In isolated colonies where the foragers that left the nest were prevented from returning.

We evaluated the effect of the returning foragers on the whole colony by comparing the periodicity of the activity cycles in cases (i) and (ii). The periodicity of each worker group was then considered separately to assess their role in the generation of activity cycles within the colony. Analysis of the spatial aspect of the activity data allowed us to visualize, for the first time, the generation and propagation of waves of activity within the colony.

##### (a) Periodicity of whole colonies

In nests where no foragers were allowed to return (figure 3b), the time-series show oscillations of activity that are more regular than those produced by colonies

where foragers were allowed to enter and leave the nest (figure 3a).

We analysed the periodicity of all time-series by spectral analysis. The periodograms corresponding to the time-series in figures 3a and 3b are shown in figures 3c and 3d, respectively. For both experimental conditions the activity patterns have a strong periodic component as shown by the large peaks at the frequency corresponding to 20 min. In the periodogram corresponding to the experiment where foragers were able to return there are other peaks at frequencies different to the main one. This suggests a less constant period length. In order to quantify this difference we standardized the magnitude of the periodograms, expressing it as a proportion of the magnitudes of the first 220 Fourier components (Brokwell & Davis 1993). We compared the variances of the periodograms using the  $F$ -test. This confirmed that the variance in nests when foragers were removed was significantly lower ( $p < 0.025$ ).

These data suggest that returning foragers disrupt the activity cycles within the nest and this is the experimental confirmation of the prediction of the model (figure 2).

##### (b) Periodicity of nest-worker and potential forager groups

The more regular periodicity evident where foragers were not allowed to return to the nest may be due to one of the following.

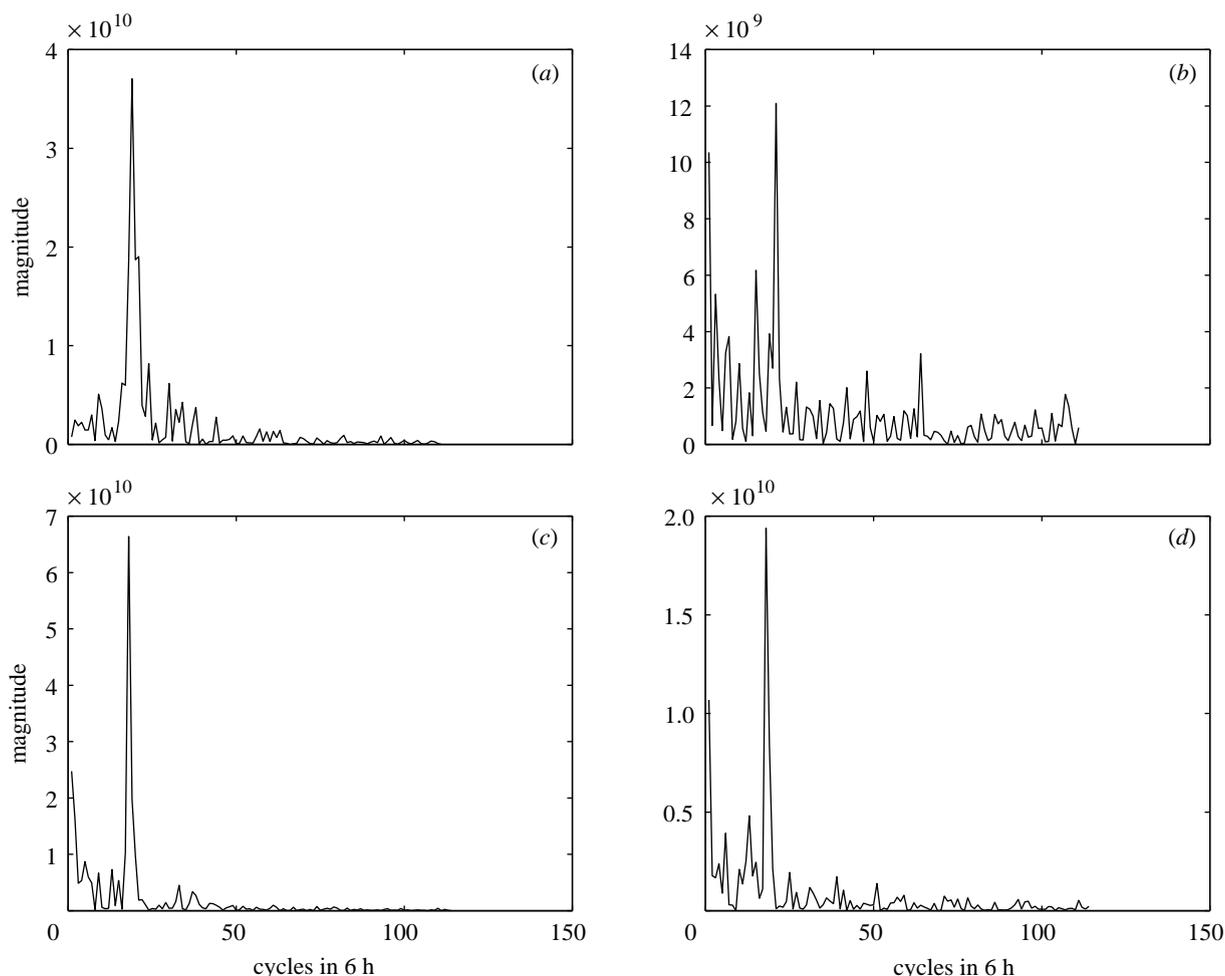


Figure 5. Periodograms for the brood pile and nest entrance groups with return of foragers, (a) and (b), respectively, and in the nest in which foragers have been removed, (c) and (d), respectively.

1. A decreasing number of non-periodic individuals in the nest.
2. The removal of the disruption to the periodicity caused by the return of foragers to the nest (assuming such return is non-synchronized).

To distinguish between these two cases we analysed the behaviour of the nest entrance group and the brood pile group separately.

The time-series depicted in figure 4 show typical behaviour under the experimental conditions where foragers were either allowed to leave and return to the nest (figure 4*a,b*) or where foragers were removed (figure 4*c,d*). Where foragers were allowed to return, the brood pile group shows clear periodic oscillations (figure 4*a*), but the nest entrance group has a very noisy time-series (figure 4*b*). Where foragers are not allowed to return to the nest both groups show clear periodic oscillations (figure 4*c,d*). This is confirmed by the periodograms in figure 5 and by an *F*-test.

The clear periodicity in the nest entrance group when foragers are prevented from returning to the nest allows us to dismiss hypothesis 1 that these workers are intrinsically non-periodic. Instead, their relative lack of periodicity under normal circumstances can be attributed to the non-synchronous activation of these ants by the returning foragers. The brood pile group seems to be less affected

by this disturbance. This may be because there is often a spatial gap between the nest entrance group and the brood pile group that may partially filter out the disturbance caused by the returning foragers.

### (c) *Spatial analysis*

To investigate further the role of the two groups in the generation of periodic activity, we examined the spatial pattern of activity within nests. When foragers are not allowed to return, distinct waves of activity propagate throughout the nest. The pulses start near the brood pile and diffuse outwards at a speed of *ca.*  $0.01 \text{ cm s}^{-1}$ . This is followed by a period of extremely low activity. An interesting feature is that the wavefronts generally propagate isotropically (being similar in all directions) (figure 6) as predicted by the mobile cellular automata model of Miramontes *et al.* (1993) under certain parameter conditions. The isotropic movement of the activity waves cannot be well represented in two dimensions, however, and is much more conspicuous when the spatio-temporal pattern is animated. The patterns within the nest when foragers were allowed to return are more complicated. Pulses of activity may arise near the brood pile or within the nest entrance group. Sometimes activity begins within both groups almost simultaneously. As the activity waves propagate the wavefronts usually become less defined preventing the detection of points of contact. Under our

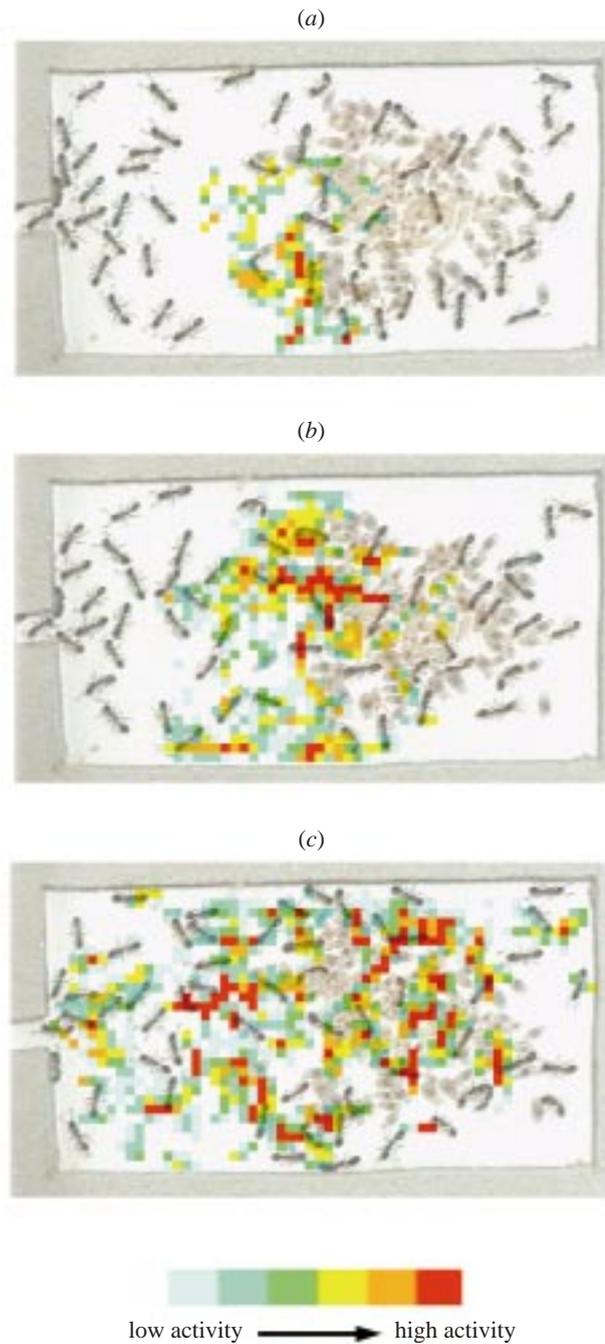


Figure 6. Three successive single frames from an animation produced by the image analysis software, showing a colour grid representing spatial activity levels summed over 6-min periods: (a) 0–6 min, activity typically starts near the brood pile; (b) 6–12 min, a roughly circular wave of activity spreads across the colony; (c) 12–18 min, most of the colony is active. Each grid is superimposed over a still image of the nest at the end of each period.

experimental conditions foragers returned non-periodically. Upon returning they first meet and often activate members of the nest entrance group by physical contact. These individuals may then leave the nest or may remain active within the nest, stimulating individuals within the brood pile group and altering the regularity of the activity cycle within this group.

## 5. DISCUSSION

*L. acervorum* colonies exhibit periodicity whether or not foragers are allowed to return to the nest. The spatial organization of the nest is, however, very important. This has been revealed by the dissection of nest dynamics using image analysis. The brood pile group always exhibits cycles of activity with a strong periodic component. The nest entrance group, however, only exhibits similar periodicity when foragers are not allowed to return. When foragers are allowed to return the periodicity of this group is significantly disrupted.

These results are consistent with the predictions of the model that treats the two groups as a coupled oscillator under an intermediate level of coupling. The strength of coupling between the groups will depend in large part on the spatial distribution of ants in the nest: where aggregates form, leaving gaps between them, interactions among ants within an aggregate are likely to be more frequent than those between aggregates. The return of foragers to the nest acts as noise disrupting the periodicity in the group of nest entrance workers. The effect of returning foragers on the periodicity of the brood pile group is much less evident. This is likely to be a result of the spatial separation and, hence, relatively weak coupling between these groups.

Hatcher *et al.* (1992) proposed that activity cycles may have a functional role in distributing ants evenly during care for brood items. Physical mutual exclusion of brood carers would lead to a uniform distribution of work if combined with temporally synchronized activity bouts. The efficiency of information transfer and energy use within ant colonies may also be increased through synchronous behaviour: ‘Long periods of inactivity may conserve energy, but unless the relatively short activity bouts of workers are synchronized, only a few could interact at any one time, and the information they exchange would tend to be both inaccurate, due to small sample sizes, and out of date’ (Franks & Bryant, p. 123, 1987). If activity cycles are adaptive, we expect that the colony would provide a homeostatic system to maintain this rhythm. It is possible to interpret the spatial separation of the two groups of workers in the nest as a simple but effective mechanism to buffer those workers near the brood pile from the disruptive effect of returning foragers.

Although we have shown that the separation of worker groups into aggregates can minimize the disruption of temporal patterns of activity, it is unlikely that these spatial aggregations have evolved solely for this reason. For example, in other *Leptothorax* species it has been shown that workers have spatial fidelity zones in the nest, potentially allowing them to specialize in tasks that occur in particular parts of the nest (Sendova-Franks & Franks 1993, 1994). Understanding the relationship between temporal and spatial organization within social insects is likely to be a particularly rewarding area for investigation in the future.

*Leptothorax* ant colonies have some of the simplest nests among all of the social insects, for example many colonies have only a single nest chamber and a single entrance (Franks *et al.* 1992; Franks & Deneubourg 1997). Many ant colonies, however, have nests with tens or hundreds of interconnected small chambers. Nests of this form are

often associated with distinct distributions of brood and worker populations (Hölldobler & Wilson 1990). This study suggests that the complex spatial structure present in many ant colonies may have major implications for temporal patterns of activity within these colonies.

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