



## Activity cycles in ant colonies: worker interactions and decentralized control

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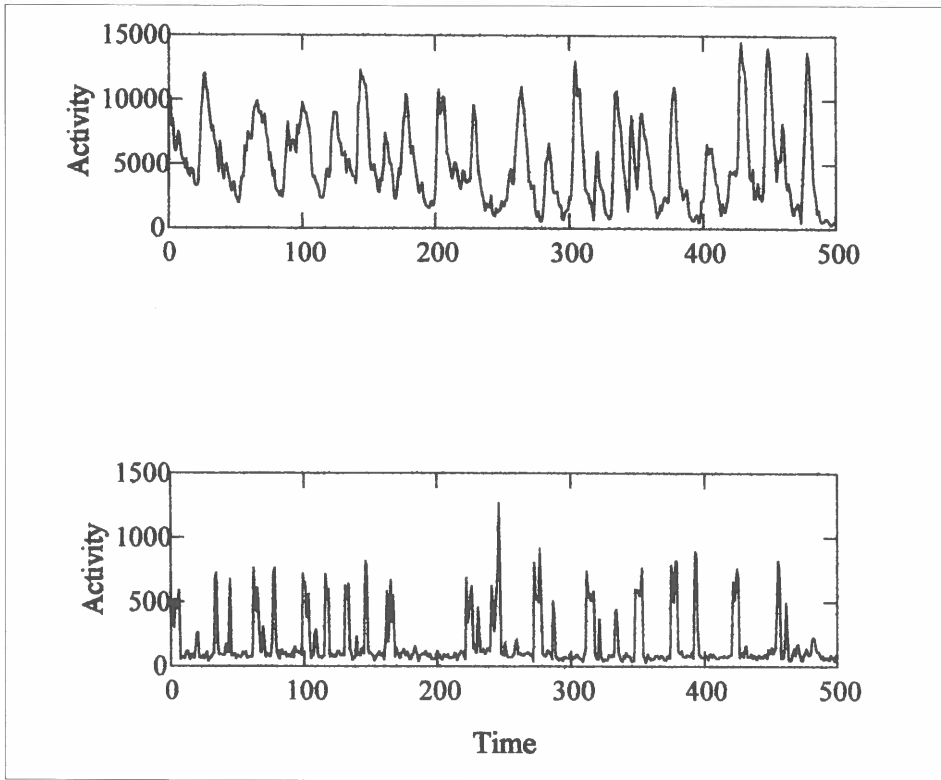
### Summary

In this chapter we look at the phenomenon of periodic activity cycles in ant colonies. Although most of the information on activity cycles in ant colonies is available for *Leptothorax*, it seems to be a phenomenon that occurs widely. Cycles of activity that last approximately one-half hour occur in colonies, with their occurrence being a function of the number of individuals that are in an aggregate or a colony. The presence of brood has an important influence on activity cycles, increasing the degree of periodicity, though brood are neither necessary nor sufficient for the production of periodic activity. We discuss models for the production of activity cycles and divide the models into two basic groups, those that require global colonywide variables that influence each colony member and those which are based on local interactions with no global connections among workers. We find that the local models, which have explicit spatial structure, are more realistic and have greater predictive power even though they are often more cumbersome to use. Finally, we consider the functional basis for periodic activity in ant colonies. There is essentially no information about the function or possible adaptive significance of this widespread, colony-level phenomenon.

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### Introduction

One of the most intriguing questions about the organization of social insects is the means by which the actions of individuals produce colonywide phenomena. Successful integration of individual effort enables efficient foraging, nest construction and brood care. How do the independent actions of workers produce such large-scale effects? What sort of coordination and control mechanisms



**Figure 1** The activity pattern of an intact colony of *Leptothorax allardycei* (top) and an isolated worker of *L. allardycei* (bottom)

The y-axis is activity measured in pixel changes between successive images [1, 3], and the x-axis is time in 30-s intervals.

iments that illustrate the relationship between the activity of individual workers and the activity patterns of colonies. We shall discuss the mechanism of interaction among individuals, and other important correlates of activity cycles such as colony hunger, worker age and the presence of brood.

### Periodic activity of colonies

The pattern of activity in colonies of *Leptothorax* ants has a periodic component. In some cases the periodic signature is extremely strong. Fourier analysis is used to analyze periodicity in the data record. Any temporal data record can be

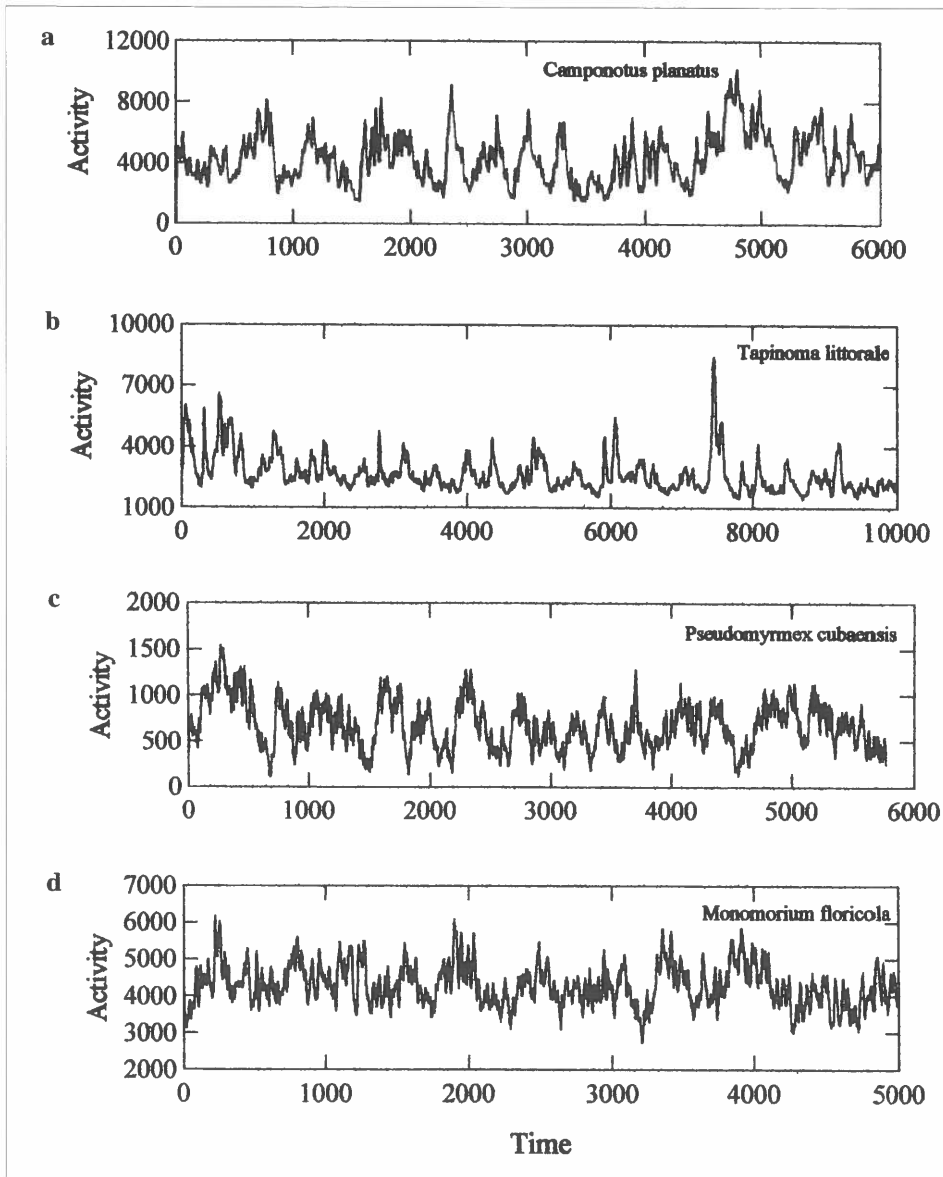
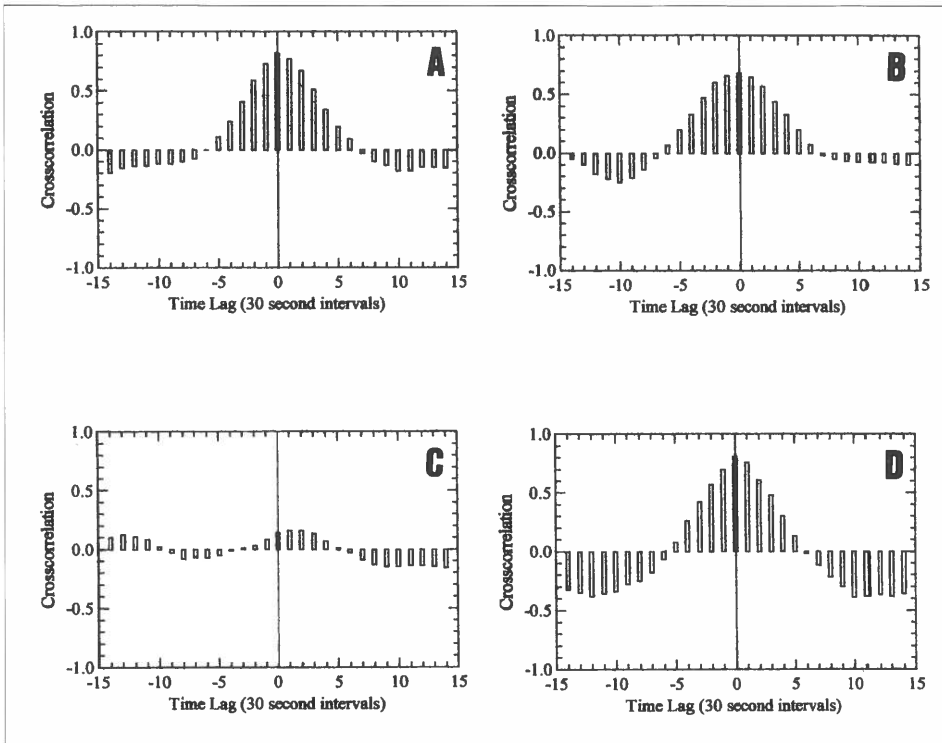


Figure 2 Activity patterns for four species of ants: (a) *Camponotus planatus*, (b) *Tapinoma littorale*, (c) *Pseudomyrmex cubaensis*, and (d) *Monomorium floricola*. The axes are as in Figure 1 with the time scale in five second intervals.



**Figure 3** Cross-correlation functions for split colony experiments

(A) Cross-correlation in activity [2] between two portions of a nest before the experiment demonstrating synchrony. (B) Cross-correlation between two portions of the nest on the same side of a double-screened partition, demonstrating synchrony. (C) Cross-correlation between two portions of the nest on opposite sides of a double-screened partition (which allows air flow, but no physical contact among ants), demonstrating no synchrony. (D) Cross-correlation between these sectors after the double-screened partition has been removed, showing that synchrony is reestablished.

If colonies of *L. allardycei* characteristically show periodic activity, individual workers do not show any evidence of periodicity (Fig. 1b). An isolated worker becomes active spontaneously, remains active for a relatively short interval (typically about 5 min) and becomes spontaneously inactive. The interval between episodes of inactivity has a negative exponential frequency distribution (Fig. 4), suggesting that there is no periodic recurrence to the activity of an isolated individual. Cole [5, 6] has argued that the activity pattern of individual workers shows deterministic chaos. Although the interval between episodes of

Aggregates that had 15 workers had the same degree of periodicity as intact colonies, and there was a nearly linear trend to become more periodic with larger numbers of workers. There is not a threshold number of workers that results in periodicity, nor is there any evidence that there are special individuals that govern the oscillation; activity cycles are a property of the aggregate.

The presence of brood also influences the production of activity cycles [1, 3, 4]. Cole and Hoeg [4] showed that different types of brood are differentially effective in producing this change. They used four group sizes (1, 3, 7 and 15 workers) and 20 pieces of four types of brood, eggs, small larvae, large larvae or pupae. The results were that eggs, small larvae and large larvae all had identical effects, and they increased the level of periodicity, whereas in the presence of pupae workers were no more periodic than workers without brood. Although brood influence activity cycles, they are neither necessary—large aggregates without brood show cycles of activity, nor sufficient—small aggregates in the presence of brood do not show activity cycles.

Although this experiment controlled for the number of brood, the ratio of workers to brood was not controlled. Even in the largest aggregates, the number of brood per worker was greater than 1. Hemerik et al. [9] suggest that there is a threshold brood:worker ratio, above which brood can produce activity cycles, and below which activity cycles cannot be produced. An experiment by Tofts et al. [10] did look at the brood:worker ratio and found no difference between activity cycle characteristics and this ratio.

The feeding status of a colony influences the production of activity cycles in *L. acervorum* [1]. During starvation, a larger proportion of the workers become foragers and cycles seem less prominent.

Active ants affect the activity states of other ants. When an active ant encounters an inactive ant, the inactive ant will become active sooner than if it does not encounter an active ant. In *L. allardycei* there is a “phase advance” in the inactive ant whose amount depends on the timing of the interaction [11]. In *L. acervorum* active ants are effective in stimulating inactive ants to become active [1]. In *L. allardycei*, when two active ants encounter one another, they tend to lengthen the time that each will spend in the active state [3]. The effect is to double the amount of time that is spent active after an interaction.

nation of a positive feedback mechanism, such as stimulation, and a post-activity latency period can be sufficient.

Cole [8] elaborated on these models to include several types of stimulation, including type 1 and type 0 phase resetting in the periodic activity of isolated workers. In type 0 resetting ants would become active after stimulation regardless of when, during the inactive phase, they are stimulated. In type 1 resetting, the phase change does not always result in activity, but is a function of the phase of stimulation. These models have less current validity since individual ants are known not to have periodic activity. All of these models are formally identical to epidemic models in which the “disease” being transmitted is activity and individuals move through infective, recovered but immune and susceptible stages [13].

Tofts et al. [10] present a different formalism of the Goss and Deneubourg model. The model has many of the same elements, although they are treated using a WSCCS (weighted synchronous calculus of communicating systems) description. In this model ants remain inactive for a fixed period, and then become wakeable. If they wake up, they wake up all other wakeable ants, then they immediately become inactive. The activity of colonies of such ants rapidly synchronize and remain synchronized. The length of the cycle is primarily a function of the length of the inactive period.

## The energy model

The energy model developed by Hemerik et al. [9] is an analytical model that focuses more directly on how physiological factors might regulate activity cycles in ant nests. Goss and Deneubourg’s autocatalytic model assumes that the phenomenon is driven by a combination of stimulation and a fixed post-activity latency period; the energy model is based on a threshold time for the digestion of food. The model demonstrates that the overall energy level in the colony coupled with the number of active ants is sufficient to produce synchronized, cyclic behavior in the nest. The energy model is mathematically similar to a number of models that have been proposed for the regulation of other physiological processes [14].

In order to model the interaction between colony nutrition and colony activity, they assume that the energy level in the nest is the total energy level of food

## Mobile cellular automata models for activity

The spatially explicit models that are described in this section are direct descendants of the probabilistic model of Goss and Deneubourg [12]. The essential components of the probabilistic models, that ants are in different activity states and they interact with one another to change each other's activity are the same. The essential difference is that there is an explicit spatial component and interactions occur only locally. This is much more realistic and produces substantial differences in the behavior of the models.

These models are designed specifically to examine the behavior of *Leptothorax*, but are not limited to *Leptothorax* ants, ants in general or even social insects. We will first present the rationale for the modeling approach, then describe the model and define the conditions under which the model shows periodic behavior.

Mobile cellular automata (MCA) models were developed by Solé and co-workers [15]. Subsequently these models were elaborated and modified by Miramontes and co-workers [16], Solé and Miramontes [17] and Cole and Cheshire [3]. They are spatially explicit models in which the ants (the mobile automata) are allowed to move on a lattice representing the nest. An ant's level of activity can range from some maximum to some minimum. The behavioral state of an ant is active if its activity level exceeds some threshold, typically zero. An active ant may move one step on the lattice; an inactive ant remains in its current location. If an ant is inactive, there is a small probability that it can become active spontaneously. If an ant does not interact with another ant, its level of activity declines until it reaches zero.

An ant can interact with others if they are in close proximity, that is, the eight nearest lattice points. Rules for permissible interactions are based on the behavioral states of the ants involved. Since each ant is either active or inactive, and may have a neighbor that is either active or inactive, there are four types of pairwise interactions. If an interaction between two ants is allowed, it changes the focal individual's state; the activity of an ant in the next time step is a function of the activity of its neighbors and its current activity.

Solé and co-workers [15] showed that this MCA system exhibits oscillations that are similar to the activity cycles of *Leptothorax* ants. They examined several rule sets, but concentrated primarily on models where all possible interactions were allowed. Cole and Cheshire [3] looked systematically at the behavior that

state variable. In the autocatalytic model the state variables are the proportion of workers that are active, refractory and inactive but susceptible. Since the probability that any ant becomes active is a function of the global fraction of ants that are in each of the three possible states, and each ant, in whatever activity state, is capable of interacting with ants in any other activity state, each ant is connected to each other ant. The necessity of writing a simple, differential form for the model, necessitates postulating global connection among ants, and global variables.

The MCA models are fundamentally different in this regard. There are no global variables. Instead, spatial structure is an integral part of the model. While this has some advantages in terms of realism and simplicity of construction, there are some disadvantages as well. The most prominent disadvantage is that it is no longer possible to write down a simple set of differential equations that can be solved by inserting them into widely available numerical integrators. Because MCA models do not have the history of differential equations, there are not widely available flexible techniques for model construction. As this sort of model becomes more widely used, the availability of simulation packages for their development can be expected to make such models easier to use for a larger number of investigators.

Although the spatial structure of a cellular automata model makes modeling more dependent on computer simulation, it has the advantage of being more realistic. The data for *L. allardycei* show that direct, physical interactions among ants are required for activity to spread and for synchrony of activity. Had there been a pheromone which produced activity within the colony (or alternatively, a metabolite that when produced inhibited activity), then the actions of one worker in one part of the nest could influence the actions of a worker in distant portions of the nest as easily as it influenced nearby ants. Such a globally connected colony could make use of global colony state variables. If the pattern for *L. allardycei* is general, this is not an accurate description of the phenomenon.

Because the phenomenon has spatial properties, it seems essential to use a model that assumes the spatial properties, whatever other disadvantages it may have. The MCA models are quite similar to the autocatalytic model in another regard; they assume that ants move through states of activity and inactivity (although refractory periods are not essential). In this sense the MCA models can be viewed as an individual-based version of the autocatalytic models. Here autocatalysis proceeds only at the level of a local neighborhood; the colony state is



chronous workers could result in a nonlinear increase in productivity. In fact, the exponent that describes the nonlinear increase in efficiency only needs to be greater than 1. We are aware of no data that address this issue.

Synchrony may also help to ensure that worker activity is uniformly distributed throughout the nest. Hatcher et al. [18] argue that if individual brood care workers randomly choose which brood to tend, some may remain untended for a substantial period of time, with a negative effect on growth and survivorship. When activity is synchronized, a more uniform distribution of care results from information exchange via the mutual exclusion of workers from brood that are already being cared for, forcing those workers to find other, currently untended, brood [18]. This also has the advantage of preventing unnecessary task repetition. Simultaneous activity (rather than periodicity *per se*) is advantageous because it reduces the overlap in brood tending. The quiescent periods that occur between bouts of activity in *Leptothorax* colonies may be a consequence of synchrony, reducing energy expenditure during routine periods. Recent work with *Solenopsis invicta* by Cassill and Tschinkel ([19] and this volume) has shown that workers feed larvae in discrete time units; all larvae are fed for the same length of time, but hungry larvae are fed more frequently than sated larvae. This fact is consistent with the mutual exclusion hypothesis of Hatcher et al. [18]; however, Cole and Cheshire [3] demonstrate that although brood has an effect on the amount of periodicity, it is more dependent on the addition of more workers than on the addition of brood. It must be noted that if the brood:worker ratios are critical, there have been no experiments that directly manipulate this factor. It is the number of workers, not the number of larvae that regulates synchrony and periodicity in *L. allardycei*. This does not mean that there is no relationship between brood and activity cycles, only that brood is not necessarily the cause. However, the presence of brood does tend to enhance periodicity [3, 4]; thus brood may exert some direct influence.

Alternatively, synchrony and periodicity may not have any direct adaptive significance. No one has demonstrated that synchrony is functionally more efficient, so while it is possible that it enables more coordinated behavior in ant colonies, it is also possible that the simultaneous activity of numerous individuals may result in colonial inefficiency due to interference between workers. In fact, there is no experimental evidence that activity cycles have any adaptive value. It has been argued that the existence of activity cycles is an epiphenomenon that is not itself adaptive, but is the by-product of interactions among individuals [2, 8].

- 539–547
- 5 Cole BJ (1991) Is animal behavior chaotic? Evidence from the activity of ants. *Proc R Soc Lond B* 244: 253–259
  - 6 Cole BJ (1994) Chaos and behavior: the perspective of nonlinear dynamics. In: L. Real (ed): *Behavioral mechanisms in evolutionary ecology*. University of Chicago Press, Chicago, 423–443
  - 7 Liebovitch L, Toth T (1991) A model of ion channel kinetics using deterministic chaotic rather than stochastic processes. *J Theor Biol* 148: 243–267
  - 8 Cole BJ (1992) Short-term activity cycles in ants: age-related changes in tempo and colony synchrony. *Behav Ecol Sociobiol* 31: 181–188
  - 9 Hemerik L, Britton NF, Franks NR (1990) Synchronization of the behavior within nests of the ant *Leptothorax acervorum* (Fabricius). I. Modeling the phenomenon and predictions from the model. *Bull Math Biol* 52: 613–628
  - 10 Tofts C, Hatcher M, Franks NR (1992) The autosynchronization of the ant *Leptothorax acervorum* (Fabricius): theory, testability and experiment. *J Theor Biol* 157(1): 71–82
  - 11 Cole BJ (1991) Short-term activity cycles in ants: a phase response curve and phase resetting in worker activity. *J Insect Behav* 4: 129–137
  - 12 Goss S, Deneubourg JL (1988) Imitation as a source of autocatalytic synchronized rhythmical activity in social insects. *Insect Soc* 35: 310–315
  - 13 Bailey NTJ (1964) *The elements of stochastic processes with applications to the natural sciences*. John Wiley, New York
  - 14 Murray JD (1989) *Mathematical biology*. Springer, New York
  - 15 Solé RV, Miramontes O, Goodwin BC (1993) Oscillations and chaos in ant societies. *J Theor Biol* 161: 343–357
  - 16 Miramontes O, Solé RV, Goodwin BC (1993) Collective behavior of random-activated mobile cellular automata. *Physica D* 63: 145–160
  - 17 Solé RV, Miramontes O (1995) Information at the edge of chaos in fluid neural networks. *Physica D* 80: 171–180
  - 18 Hatcher MJ, Tofts C, Franks NR (1992) Mutual exclusion as a mechanism for information exchange within ant nests. *Naturwissenschaften* 79: 32–34
  - 19 Cassill DL, Tschinkel WR (1995) Allocation of liquid food to larvae via trophallaxis in colonies of the fire ant, *Solenopsis invicta*. *Anim Behav* 50(3): 801–813



Periodicity may be an incidental consequence of selection acting on the interaction of individual ants with nest mates.

Selection acts on the colony phenotype by changing the actions of individuals. What sort of selection on colonies may result in the production of activity cycles as an indirect effect? Here it is useful to mention the result of one further set of simulations using the MCA model. Recall that one of the features of the MCA model was that certain types of interactions could be permitted or forbidden. The essential interaction that results in periodic activity is the effect that an active ant has on another active ant. The type of interaction that has the greatest effect on the total amount of activity in simulated colonies is the ability of an active ant to influence an inactive ant. However, model colonies with both types of interaction have the highest total activity level; the other interactions do not matter. Colonies in which active ants stimulate the activity of both active and inactive ants have the highest total activity. They will also have periodic activity.

The ability of active ants to stimulate the activity of inactive ants [1, 2, 11] may not be important to the establishment of periodicity, but it may be the single most important factor determining the overall activity level in colonies. Therefore, selection on colonies for higher activity levels should inevitably result in production of colony activity cycles.

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## References

- 1 Franks NS, Bryant R, Griffiths R, Hemerik L (1990) Synchronization of the behavior within nests of the ant *Leptothorax acervorum* (Fabricius). I. Discovering the phenomenon and its relation to the level of starvation. *Bull Math Biol* 52: 597–612
- 2 Cole BJ (1991) Short-term activity cycles in ants: generation of periodicity by worker interaction. *Amer Naturalist* 137: 244–259
- 3 Cole BJ, Cheshire D (1996) Mobile cellular automata models of ant behavior: movement activity of *Leptothorax allardycei*. *Amer Naturalist* 148: 1–15
- 4 Cole BJ, Hoeg L (1996) The influence of brood type on the periodic activity of *Leptothorax allardycei*. *J Insect Behav* 9:

not directly relevant. A consequence of using a spatially explicit model, without global connections, and of considering the types of interactions that can occur between individuals leads to a nonintuitive conclusion: cyclic behavior of colonies is due solely to the influence that active ants have on other active ants. This social facilitation effect is necessary and sufficient for the production of cycles in sufficiently large aggregates. The stimulus of activity in inactive ants (the sort of interaction assumed by the autocatalytic and energy level models) is not necessary and in fact retards the production of activity cycles [3].

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## The significance of activity cycles

Although we know a certain amount about the phenomenon of activity cycles and there is also a considerable body of theoretical work that can be applied to the subject, there is little information on the significance of activity cycles. This is in stark contrast with the situation in the other chapters in this section in which the importance of recruitment, nest construction or swarming is transparent. In this section we will discuss hypotheses for the functional significance of activity cycles. There are two classes of hypotheses, those that ascribe a functional significance to activity cycles and those that suggest that cycles are an epiphenomenon produced by other selective pressures.

The existence of synchronized activity pulses in *Leptothorax* colonies may be adaptive if this organization improves the efficiency with which colonies perform tasks that either conform to a cyclic pattern or else coincide with rhythmic stimuli. Several authors have discussed circumstances under which synchrony may enable workers to coordinate their activities more efficiently, particularly when tasks require interactions between workers [10, 12, 18].

Goss and Deneubourg [12] illustrate how synchronous activity may be more efficient than uniform activity under such circumstances. If  $A$  represents a colony's total amount of worker activity, and this is uniformly distributed over a period of  $T$  minutes, then the average level of activity is  $A/T$ . Likewise, if  $A$  occurs during a single minute, the average activity level is also  $A/T$ . However, if workers interact with one another such that efficiency is related to the square of the number of active workers, then efficiency becomes  $A^2/T$  for uniform activity, but  $A^2$  for synchronous activity. Thus, synchronous activity is  $T$  times more efficient. It seems perfectly plausible to suppose that interactions between syn-

is produced by each possible rule set. By allowing or forbidding each of the four types of potential interactions, 16 rule sets were produced that enumerated all possibilities. An interaction matrix,  $\mathbf{J}_{ij}$ , is defined to indicate the effect that a neighbor,  $j$ , has on ant  $i$ , where  $i$  and  $j$  are either active or inactive. For example, if  $\mathbf{J}_{11} = 1$ , an active neighbor is allowed to influence the activity of the active focal ant; if  $\mathbf{J}_{11} = 0$ , then an active neighbor is forbidden from influencing the behavior of the active focal ant.

The essential result of Cole and Cheshire is that a single rule was essential to produce cycles of activity in these models:  $\mathbf{J}_{11}$ , the effect that an active ant has on another active ant. When  $\mathbf{J}_{11} = 1$ , the models show cyclic activity patterns. The degree of periodicity increases with increasing numbers of ants. When  $\mathbf{J}_{11} = 0$ , the models did not show periodicity with any number of ants. If an active ant causes another active ant to remain active longer, then cycles of activity will emerge as more ants are added to the aggregate. If active ants do not mutually reinforce each other's activity, then there will be no activity cycles. Active workers of *L. allardycei* reinforce one another's activity.

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## The relation of the theories

The autocatalytic model is the simplest model of those that have been proposed for the production of colony activity cycles. It shares a number of similarities both with the energy model and with the cellular automata models. The autocatalytic model and the energy model can both easily be written in the form of differential equations. While the solution to the equations cannot be as easily written, the models can be numerically integrated, and a periodic solution may exist. The existence of a periodic solution does not verify the models' accuracy, only that it is possible for such models to produce the appropriate behavior. A set of differential equations can be produced for a colony because both models assume the existence of global parameters, and global connections among the workers. By this we mean that the behavior of individuals is a function of the aggregate state of colony. This is most conspicuous in the energy model, because a state variable, the energy level of the colony, describes something that is a property of the colony as a whole. Furthermore, each worker responds to changes in this state variable: colony energy level dictates change in another state variable, the probability that ants activate. Each ant is connected to every other ant through this

both in the nest and within the adults and larvae. As in the autocatalytic model, individual ants are considered to be either active or inactive. The digestive process that is at the foundation of the energy model is expressed as exponentially decreasing with time, whereas the rate of increase of energy level in the colony is proportional to the total number of active ants within the nest. The assumption is thus that only active ants are able to provision the nest.

In this model, the rate at which active ants become inactive is a constant, such that the rate of change in the number of active ants is proportional to the number of active ants. The rate at which inactive ants become active is a decreasing function of colony energy, such that activity is stimulated by low energy level. This feature is built into the model because of the observation that starved colonies show more activity. Active ants are also able to activate inactive ants. Thus, the rate of increase in the number of active ants must also increase as the number of active ants increases. This is a point of similarity between the autocatalytic and energy models.

The energy model predicts that manipulation of colony energy levels will change the number of active ants. The validity of the model could be tested by examining the results of simulations under two conditions (starvation and increased brood:worker ratio). Franks et al. [1] found that after prolonged starvation, the proportion of active ants in a nest is at a higher and more constant level. The energy model also demonstrates that the proportion of active ants remains at a constant level that is greater than the maximum proportion that are active normally. When the brood:worker ratio is increased or decreased, there is a similar response in the rate of change of the colony energy level. When brood:worker ratio is high, the model predicts that fewer ants are synchronously active and that periods of activity are shorter, but occur more frequently.

The model assumes that there is a positive relation between the number of ants active and the number of ants that become active. It requires a quadratic term relating the rate of increase of active ants to the number of active ants in order to produce a rhythmic pattern of activity. Versions which only used the linear term resulted in a stable equilibrium. This is in keeping with the activation assumption of Goss and Deneubourg's [12] autocatalytic model, and the observation of Franks et al. [1] that individual *L. acervorum* workers become active significantly more often when contacted by other ants.

## Models for the production of activity cycles

There have been several attempts to model the production of colony activity cycles. The models take different approaches and make different assumptions. The purpose of this section is to categorize the different models and to point out the essential differences and similarities in the underlying organization, if not the approach. Then we shall use the results summarized above to see which models have empirical support and which seem less likely given the data available.

### The autocatalytic model

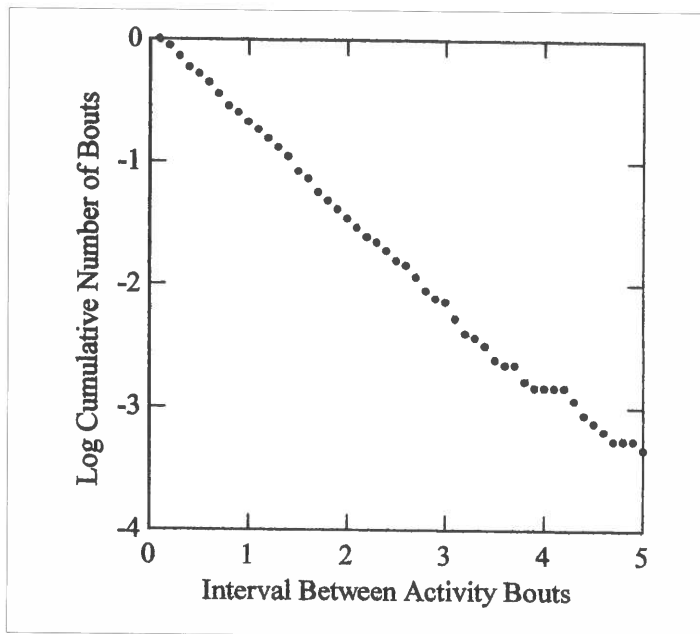
The first model to explain the processes underlying the existence of activity cycles in insect colonies was the autocatalytic model developed by Goss and Deneubourg [12]. They demonstrated that activity cycles, such as those that had been observed in the ant *L. acervorum*, could be generated by a population of individuals without an exogenous driver.

The model consists of three core assumptions. At each time step there is a fixed probability (following an exponential distribution) that a currently active worker will become inactive. Once a worker becomes inactive, it experiences a refractory period of fixed duration during which it cannot be reactivated. Thereafter, the now susceptible ant can become active, either spontaneously at a low, fixed probability during each time step, or alternatively, through stimulation by the activity of any active worker that encounters it. The greater the current number of active workers in the colony, the greater the likelihood that an inactive worker will become active.

At each time step, individuals are randomly paired, and any inactive but susceptible ant that is paired with an active ant also becomes active. This process soon results in synchronous bouts of activity with a period between activity peaks that is approximately equal to the refractory period. However, the model does not produce synchronous activity in simulations where the refractory period is too short relative to the duration of activity, or when the ability of an active ant to stimulate an inactive ant is too low.

The fundamental outcome of the autocatalytic model is the demonstration that synchronous, periodic patterns similar to those produced by ant colonies can be generated without the need for an external pacemaker mechanism. The combi-





**Figure 4** The cumulative distribution of intervals between activity bouts

The linear relationship on this log-linear plot indicates a negative exponential frequency distribution.

activity is not predictable over long intervals, the magnitude and timing of activity is predictable over a short interval. The activity pattern of a single ant has the characteristics of a chaotic switch [7]. Franks et al. [1] demonstrate that the distributions of the duration of activity bouts and interbout intervals for single workers within colonies of *L. acervorum* do not suggest periodic individuals either.

Age influences the amount of activity of individual ants. Cole [8] suggested that activity declines as a function of worker age, and the probability that a worker becomes spontaneously active decreases with age. Although the situation is somewhat more complicated, it is a function of age. The degree of activity of an isolated ant (measured as the fraction of time active) first increases for the first several months of life and then declines. There is a highly significant quadratic term ( $P < 0.001$ ) in the regression of activity on age. It is only during the latter half of the life of the worker in the lab that activity declines monotonically.

The degree of periodicity increases with the number of workers in the aggregate. Cole and Cheshire [3] used aggregates of 2, 3, 5, 7, 11 and 15 workers.

Most data collection runs have been for 4–8 h, but there have been longer observations runs of >24 h. During these longer runs, the period of the oscillation can occasionally change, rather abruptly. This blurs the periodicity, over the entire data record. If one looks at a sliding window, one can see the presence of a single period, the appearance of a second periodic component and the fading out of the first periodic component. These results suggest that a simple oscillator, governing the production of periodicity, is unlikely to be the cause of colony activity cycles. Rather, it is consistent with the interpretation that this is a decentralized, group phenomenon that emerges through the interaction of workers.

There are two further results from intact colonies that give information about the mechanism of spread of activity and the rate at which activity spreads. The activity record of an intact colony of *L. allardycei* was separately recorded in 16 separate grid squares ( $4 \times 4$ ). The activity of regions in two halves of the nest was synchronous (shown by the peak in the crosscorrelation function in Fig. 3a). A double screen partition was inserted into the nest into two portions that had air connections, but did not permit physical contact among ants. Separate regions on the same side of partition were still synchronized (Fig. 3b), whereas regions on opposite sides of the screen partition were not (Fig. 3c). Although they continued to oscillate, they did so with different periods. Finally, when the screen partition was removed, synchrony between the two halves of the nest was reestablished (Fig. 3d). Direct physical contact among workers seems to be required for synchronous activity. By comparing the activity records at two portion of the nest, and measuring the time required for activity at one location to spread to another location, it was established that activity traveled through the nest at the rate of about .8 mm/s. Both of these experiments suggest that it is the movement of workers themselves that transmits activity, not the diffusion of a pheromone.

### Assembling activity patterns

In this section we shall describe the activity of workers and the interactions that lead to periodic activity and factors that influence activity cycles. We shall examine the activity patterns of isolated workers, small groups of workers, and the interactions among workers. This information exists only from *L. allardycei*. We shall also describe some of the complications of activity patterns including the effect of age, brood and feeding status.

decomposed into Fourier components that describe the contribution of sine waves of period  $(1, 2, \dots, n/2)$  time intervals where  $n$  is the number of measurements that are made in the record. When added together, the Fourier components reconstruct the data record. Because the sum of the coefficients is related to the variance of the data record, a Fourier analysis is similar to an analysis of variance where the size of the coefficients of the Fourier decomposition is proportional to the fraction of variance in the data record that is due to oscillations at that frequency. If a data record consists of the sum of several perfectly sinusoidal components, the coefficients of the Fourier decomposition that correspond to these components will be quite large. If there is oscillation with noise, there will be large Fourier components that correspond to the frequency of the signal, but also components that correspond to the pattern of noise. If there is a sloppy oscillation, with a tendency to drift in frequency, there may be one or more peaks of power, and the peaks will probably be broader. All biological oscillations, from heartbeats to circadian rhythms, have noise to one extent or another, and some may drift in period or amplitude.

Strong periodic components occur in the colony activity rhythms of ants, but they are never purely periodic [1–5]. How periodic are the activity rhythms? There is variation among colonies and preparations. The degree of periodicity can be measured by looking at the fraction of the variation in the data record that is due to periodic oscillations at the largest Fourier component. Cole and Cheshire [3] and Cole and Hoeg [4] report that in intact colonies about 33% of the variation is due to a single frequency component.

While most of the data has been collected from *Leptothorax* species, ants from a number of other genera have also been observed to measure activity patterns. Colonies of *Camponotus planatus* (Fig. 2a), *Tapinoma littorale* (Fig. 2b), *Pseudomyrmex cubaensis* (Fig. 2c) and *Monomorium floricola* (Fig. 2d) all show periodic components in activity. Additionally, periodic activity has been found in *Leptothorax pastinifer*, *L. isabellae*, *Pseudomyrmex elongatus*, *P. sp.*, *Zacryptocerus varians*, *Solenopsis picta* and *Xenomyrmex floridanus*. The broad representation of species from at least four subfamilies indicates that periodic activity cycles are not restricted to particular taxonomic groups. Additionally, *T. sessile* has repeatedly failed to show any substantial periodic components to behavior. Unfortunately, the comparative data are not sufficient to give a sense of the important characteristics of social organization that may be responsible for one species showing periodic activity and other species not.

result in the emergence of collective behavior? At one end of the continuum of possibilities a centralized control mechanism directs the production of an outcome. At the other extreme collective patterns emerge from a decentralized control mechanism by dynamic interactions among individuals. In this chapter we will discuss the production of activity patterns in ant colonies. We will argue that decentralized control causes the self-organization of activity cycles.

Colony activity, defined here as movement of any type within the colony, is the subject of this review. We regard activity patterns as important for study for two basic reasons. First, activity itself is a fundamental property of behavior. It is difficult to conceive of behavior without movement. If activity has temporal pattern, then other behaviors such as foraging, brood care, nest construction and so on must also be affected. We also see the study of colony activity levels as a model system for the general question of how colony level phenomena are produced by the actions of individuals. Activity has the useful property that it can be objectively and automatically quantified. This gives considerable flexibility to data collection.

This chapter consists of three parts. In the first we discuss the empirical evidence concerning colony activity cycles, the activity of individuals and the interactions among them. In the second section we discuss models that have been developed to describe this phenomenon, the data that pertain to each model and the relationship among the models. In the third section we discuss the significance of activity cycles in ant colonies.

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## The phenomenon of activity cycles

Although observers of ant behavior have long been aware that activity in ant colonies was not constant, this phenomenon has only been quantified relatively recently [1, 2]. For long periods of time, all of the workers under observation may be completely immobile. One ant initially becomes active, and then activity appears to spread to neighboring workers. Eventually, all of the workers under observation may be actively moving about. This activity reaches a peak and gradually dies out, and every worker may be quiescent again (Fig. 1a). These episodes of activity last approximately 30 min. We shall first describe the cycles of activity in intact colonies of ants, emphasizing work using *Leptothorax allardycei* and *L. acervorum*, about which the most is known. Next, we shall summarize exper-