

MOBILE CELLULAR AUTOMATA MODELS OF ANT BEHAVIOR:
MOVEMENT ACTIVITY OF *LEPTOTHORAX ALLARDYCEI*

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Abstract.—Mobile cellular automata (MCA) models of the activity of ant colonies were used to explore the effects of changing the parameters that govern the types of interactions that can occur between ants. Two parameters have an effect: whether interactions between active ants influence each other's activity and whether interactions between active and inactive ants influence the activity of the inactive ants. We then investigated the production of periodic activity in artificial aggregates of workers of *Leptothorax allardycei*. Using an automated data collection system to analyze the activity patterns of 126 data records of 11.5 h each, we studied the effects of three attributes on the production of periodic activity: the size of the aggregate, the time of day, and the presence of the brood. When the brood was absent, the size of the aggregate had a significant effect on the production of periodic patterns of activity; however, this effect was most pronounced during the day and nearly absent in data records obtained at night. When the brood was present, the time of day had no effect, and the effect of aggregate size was much more pronounced; the extent of periodicity increased linearly with the size of the aggregate. All of the experimental results could be reclaimed by altering the parameters of the MCA models. Mobile cellular automata models produce testable predictions that make them especially useful for models of animal behavior.

The production of a social phenotype from the characteristics of individuals is one of the major problems of social behavior. How does the behavior of a group result from the actions of the individuals that comprise the group? It is possible to identify a phenotype associated with the collective behavior of virtually any social organism (Deneuborg and Goss 1989). Some examples of social phenotypes include the design and construction of nests in social insects (Grassé 1959; Jones 1980; Franks et al. 1992), the shape and size of flocks or schools (Okubo 1986; Rose 1993), and the degree of collective vigilance in a herd (Elgar 1989; Lima 1990; Quenette 1990; Quenette and Gerard 1992). Each of these examples and others can be broken into the components of nest construction (Grassé 1959; Sudd 1970, 1975; Franks et al. 1992), the movement of individuals (Okubo 1986), or individual vigilance (Elgar 1989; Quenette and Gerard 1992). Understanding the evolution of social behavior requires understanding the mechanisms by which collective behavior is produced. It is important to understand how the components interact to produce the collective properties of social groups.

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At least two possible mechanisms may produce a social phenotype: central control or distributed control. In the first case, a central controlling mechanism or organism switches activities on and off depending on the state of the system or information that the central governor receives. An example is the production of activity in naked mole rats by queen activation (Reeve 1992). The queen acts as a central control on actions of workers. In the second case, decentralized emergence of order results from the local interactions of numerous, relatively interchangeable components (Gordon et al. 1992). The type of control will obviously influence the effect that selection has on a trait and where selection will operate effectively.

What mechanisms produce social behavior? The approach taken in this article is to construct artificial social groups that are simpler than the natural social units but that have the advantage of being manipulable. We want to be able to control the social environment of individuals and the types of interactions that are permitted in an attempt to explore the production of a social phenotype experimentally. This experimental approach gives us the power to isolate factors that are important to the production of the social phenotype.

We will look at the production of a social phenotype, movement activity, in models of ant colonies and compare them to the production of activity in experimental ant colonies. Activity in *Leptothorax allardycei* (Mann) is qualitatively different in single workers and in colonies. Colonies of *L. allardycei* have periodic bouts of activity, recurring at approximately half-hour intervals (Cole 1991b). The isolated workers of *L. allardycei* have apparently chaotic activity patterns (Cole 1991c, 1992, 1994). Individuals of *L. allardycei* from the same colony differ greatly in their activity patterns, largely as a function of worker age, while colonies do not differ from one another (Cole 1992). Similar patterns of activity in colonies of *Leptothorax acervorum* have been studied by Franks and co-workers (Franks et al. 1990; Hatcher et al. 1992; Hemerik et al. 1990; Tofts et al. 1992). Similar patterns of activity have also been observed in the colonies of other species of *Leptothorax*, *Pseudomyrmex* (*P. elongatus*, *P. cubaensis*, *P. pallidus*), *Tapinoma* (*T. littorale*, but not *T. sessile*), and *Zacryptocerus varians* and *Crematogaster ashmeadi* (B. J. Cole, unpublished data). For species other than *L. allardycei*, the activity pattern of the isolated workers is unknown.

We use spatially explicit models of behavior to understand the production of activity in an ant colony from the actions of individual workers. Models that describe these phenomena would be useful, especially if they are general enough in form that they could be moved to other behavioral contexts. The use of spatial models has changed ecology (Ermentrout and Edelstein-Keshet 1993; Molofsky 1994), and some applications to behavioral contexts have been made (Nowak and May 1992, 1993). One general class of spatially explicit models, mobile cellular automata (MCA) models, are unusually applicable to behavioral studies because they can incorporate simple behavioral rules in local interactions to produce large-scale patterns. We will use these models to produce general results concerning the relation between periodic activity and number of workers in an aggregate and discuss the empirical results in the context of these models.

MOBILE CELLULAR AUTOMATA MODELS

Mobile cellular automata models have been developed to describe ant colonies by Solé et al. (1992) and Miramontes et al. (1993). In these models, the ant nest is treated as a grid, with the ants allowed to occupy the lattice points. The ants are allowed to move between lattice points if they are active, and they remain stationary if they are not. The cell interacts locally with a set of neighbors. All lattice points in the nest need not be occupied, and usually they are not; however, they can only be occupied by one individual at a time. The distinction between an MCA model and a cellular automata model is that the “automata” are allowed to move. This feature makes MCA models more realistic in their application to behavior than the typical cellular automata models (Nowak and May 1992, 1993). These have also been termed “lattice gas” models (Ermentrout and Edelstein-Keshet 1993).

The MCA model has two components: the internal dynamics of the automaton (also called self-interaction) and the interactions that occur between them. The activity level (A_i) of an individual in the next time step is a function of its current activity, the activity of its neighbors, and the set of rules that govern the interactions that can occur between neighbors. We will first describe the internal dynamics of the automaton and then describe how the automata interact. An isolated ant becomes spontaneously active and, once active, spontaneously inactivates. The internal dynamics of an isolated worker are assumed to be random; a single unit is activated with a constant probability if it is inactive. The parameter g describes the multiplicative effect converting current activity into activity in the next time step. Provided this gain parameter is less than one, the activity level declines. The contribution of the internal dynamics of the automaton to activity at time $t + 1$ is then $S_t = gA_t$. If the active ant is alone or does not interact with another ant, its activity declines until it reaches some predefined limit. In our simulations, reaching the floating point limit of the computer sets an individual’s activity level to zero, and this state is defined as inactive. A randomly activated ant has an activity level of 0.01, which, in combination with the gain parameter of 0.1 in the simulations, means that a single ant is active for 16 time units. The values of these two parameters are chosen to give realistic durations for the spontaneous activity of isolated workers (Cole 1991*b*, 1991*c*).

Interactions between an ant and its eight nearest neighbors (there is the possibility of “kingwise” connectedness) are allowed according to an interaction matrix \mathbf{J}_{ij} (Solé et al. 1992). The terms of the interaction matrix describe whether active or inactive ants are allowed to influence the activity level of active or inactive ants, respectively. The terms of the interaction matrix define the connections that can occur between ants. When all of the terms of \mathbf{J}_{ij} are zero, ants do not interact with one another regardless of their state of activity or proximity. When all of the terms of \mathbf{J}_{ij} are one, then interactions between ants in any state are possible. If $\mathbf{J}_{11} = 1$, then the interaction matrix indicates that an active ant influences the activity of another active ant when they are in close proximity. If $\mathbf{J}_{21} = 1$ and $\mathbf{J}_{12} = 0$, it indicates that an active ant influences the activity of an inactive ant but that an inactive ant does not influence the activity of an active

ant. The effect of interactions between automata on the ant of interest is then $g \cdot \sum (\mathbf{J}_{ij} \cdot A_{kt})$, summing over the interactions of an ant with its k neighbors. Finally, the activity of an ant in the next time step is $A_{t+1} = \text{Tanh} ([g \cdot \sum \mathbf{J}_{ij} \cdot A_{kt}] + S_t)$. The hyperbolic tangent function is used because it ranges from -1 (defined as maximally inactive) to $+1$ (maximally active) regardless of the total amount of activity of an individual or its neighbors. The activity level of an ant in the next time interval is the sum of the self-interaction term and the interaction term.

An automaton is defined to be active when A_t exceeds zero. If an ant is active, it will move randomly to one of the neighboring lattice points that is not currently occupied by another ant. Since this simulation is designed to mimic behavior within experimental arenas, the boundaries are reflecting. A 10×10 grid was used for the simulations. This grid size was chosen to be appropriate for the size of the experimental arenas below. Simulations were started with individuals randomly assigned to activity levels ranging from -1 to $+1$. Since there are four terms in the interaction matrix, there are 16 possible combinations of the terms of \mathbf{J}_{ij} . The simulations tested each of these combinations using 10 replicates of each aggregate size (1, 2, 3, 5, 7, 11, and 15 ants) for each of the 16 combinations of coefficients (1,120 simulations).

One characteristic feature of MCA models is a propensity to oscillate. Solé et al. (1992) point out that MCA models oscillate under a wider range of parameters than cellular automata models because of the fact that individuals do not become trapped in interactions with particular individuals but are allowed to change connections. Variation in the terms of the interaction matrix affects the activity level in the simulated colonies (fig. 1). For each simulation, we calculated the magnitude of the largest Fourier component, to quantify the extent of periodic activity and express it as a fraction of the total variation. In this article, the focus is on the production of periodicity in these models and the circumstances that favor periodic activity. We then explore these circumstances as they occur in real ant colonies.

Figure 2 illustrates the magnitude of the largest Fourier component in the simulations as a function of the number of ants. The different lines represent the 16 different combinations of coefficients in the interaction matrix, \mathbf{J}_{ij} . For some of the sets of coefficients, there was a substantial increase in periodicity as a function of aggregate size, while for other sets of coefficients, there was no change with the size of the aggregate. To quantify the increase in periodicity, Spearman rank-correlation coefficients were calculated for each set of simulations with a given set of coefficients, using the number of ants as the independent variable and the average magnitude of the Fourier component as the dependent variable. The rank-correlation coefficients were analyzed as a function of the type of entry in the interaction matrix using ANOVA. The results of this analysis are shown in table 1. Two coefficients affect the results. The first is \mathbf{J}_{11} , which has a large and positive effect on the rank-correlation coefficient; simulations with $\mathbf{J}_{11} = 1$ showed a strong increase in the extent of periodicity as the size of the aggregate increases (see fig. 2). This coefficient represents the mutual interaction of active individuals and accords with the conclusions reached by Solé et al. (1992). Periodicity results when active ants mutually increase their activity level. The second

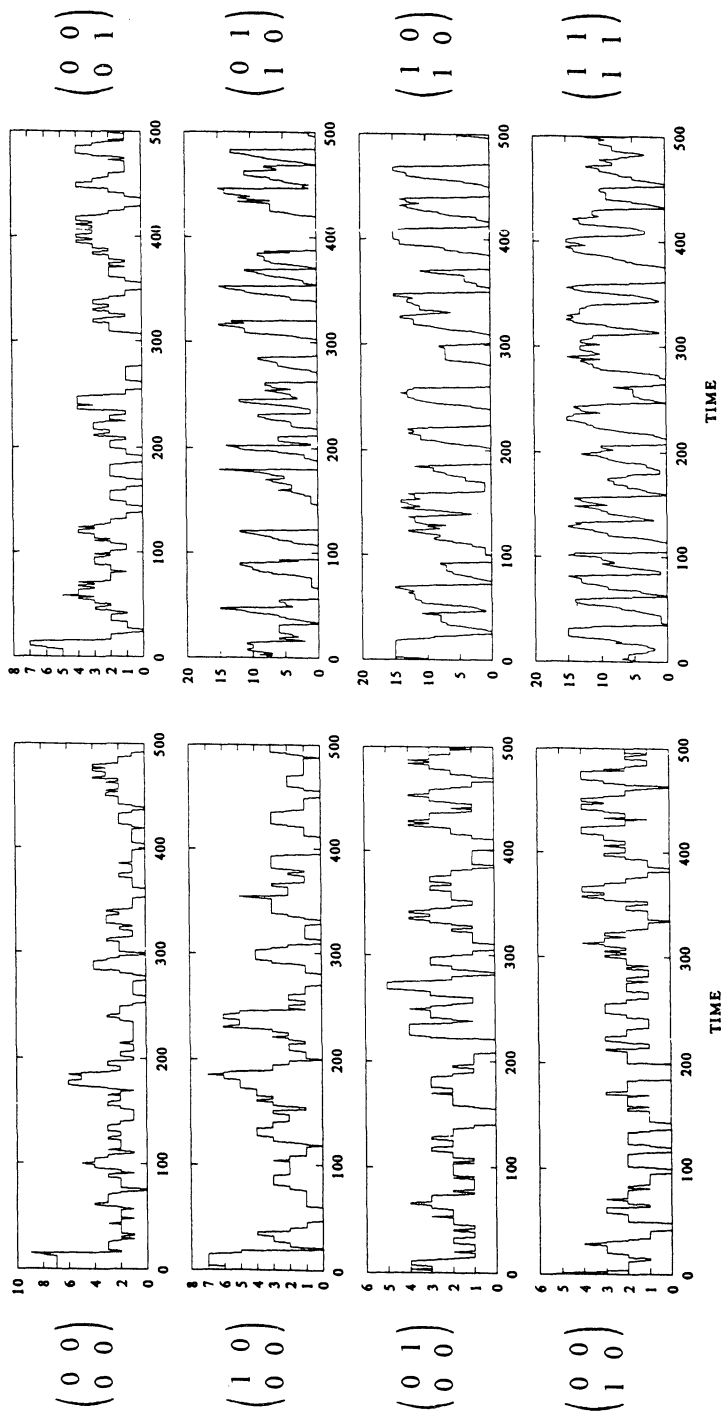


FIG. 1.—The temporal dynamics of activity in eight simulations involving different assumptions about the form of the interaction matrix. The number of ants active is out of a total of 15 for 512 time intervals. The interaction matrices are shown to the sides of the results. Of the eight simulations shown, three of them show cases in which $J_{11} = 1$ and that are therefore expected to be more periodic. The conditions of the simulations are given in the text.

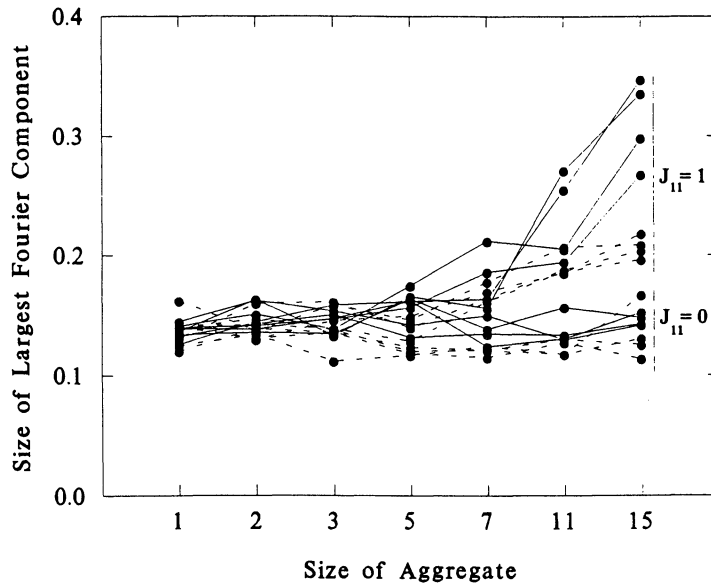


FIG. 2.—The magnitude of the largest Fourier component as a function of the size of the aggregate in mobile cellular automata models of ant colonies. The mean value is based on 10 simulations of each aggregate size and each combination of coefficients of the interaction matrix. Lines connect the results of simulations with the same set of coefficients. The line bracketing the upper eight sets of simulations show cases in which $J_{11} = 1$. Solid lines connect simulations in which the value of $J_{21} = 0$; dotted lines show simulations with $J_{21} = 1$. Note that all of the simulations for which $J_{11} = 1$ and $J_{21} = 0$ are larger than all of the simulations for which $J_{11} = 1$ and $J_{21} = 1$.

TABLE 1

ANOVA OF THE VALUE OF THE ENTRY IN THE INTERACTION MATRIX, J_{ij} , ON THE MAGNITUDE OF SPEARMAN'S RANK CORRELATION BETWEEN AGGREGATE SIZE IN A MOBILE CELLULAR AUTOMATA MODEL AND THE EXTENT OF PERIODICITY

Source of Variation	df	<i>F</i>	<i>P</i>
Element 1, J_{11}	1	96.213	<.001
Element 2, J_{12}	1	.006	.942
Element 3, J_{21}	1	11.424	.006
Element 4, J_{22}	1	.321	.582
Error	11

effect is a significant, though smaller, negative effect of J_{21} . When $J_{21} = 1$, the activity level of an inactive ant is increased by the proximity of an active ant. Simulations with $J_{21} = 1$ showed a smaller increase in the amount of periodicity with aggregate size. The dotted lines in figure 1 indicate simulations in which $J_{21} = 1$.

The dynamic outcome of activity in an aggregate is thus a function of the entries

in the interaction matrix. Activity in ant colonies can range from no periodicity as aggregate size increases when $J_{11} = 0$ to large increases in periodicity for $J_{11} = 1$ and $J_{21} = 0$. The range of activity in aggregates of real ants can be expected to reflect this theoretical range.

EXPERIMENTAL MATERIAL AND METHODS

Leptothorax allardycei were isolated in seven group sizes: 1, 2, 3, 5, 7, 11, or 15 workers to parallel the simulations. These aggregates were placed in an observation nest constructed out of two glass microscope slides held apart by a 1.5-mm balsa wood partition. The dimensions of the arena were 10×10 mm. Activity levels were obtained from video records, and activity was videotaped to produce a permanent record. After an aggregate was isolated, it was allowed to acclimate for at least 8 h and usually for 12 h. One data collection run consisted of activity measurements taken at 5-s intervals for 11.5 h (8,280 activity measurements), at the end of which isolated workers were returned to their original colony. This procedure was replicated at least 10 times for each aggregate size. The order in which the aggregates were recorded was randomized by group size. Data collection runs began at either approximately 8 A.M. or approximately 8 P.M. and were classified as day or night runs even though all data collection runs were performed under constant light conditions. This data set consisted of 85 activity records.

In a second experiment, we tested whether the presence of the brood affected the production of periodic activity. Workers in groups of 1, 3, 7, and 15 workers were isolated along with 20 immatures of various stages. These aggregates were compared to intact colonies. At least six replicates were obtained per aggregate size. The assemblages were treated and assayed as described above. A total of 31 records were obtained from the brood containing aggregates and 10 from intact colonies.

Experimental aggregates were recorded with a Dage 65C video camera. The output of the video camera was connected to an Imaging Technology, Inc., Variable-Scan-Rate Frame Grabber board. The captured image is 640×480 pixels with 256 gray levels. Custom software captures and stores video images at a selectable interval, performs video subtraction between successive images, performs a LUT (lookup table) stretch between selectable upper and lower cutoffs on the subtracted image, and writes to disk the number of pixels that have changed by a given intensity or greater. The LUT stretch is performed for two reasons. First, the lower cutoff allows insignificant, random noise to be eliminated from the image. Second, the upper cutoff allows us to increase the contrast, and thus the sensitivity, of the activity measurement. The lower and upper limits used for the LUT stretch were 32 and 100. After the subtracted images were stretched, the intensity histogram of the image was calculated, and the number of pixels that had changed by a given intensity was stored. Activity was measured as the number of pixels that changed in intensity by a value larger than a threshold that corresponds to 40 in the unstretched image. This procedure is illustrated in figure 3.

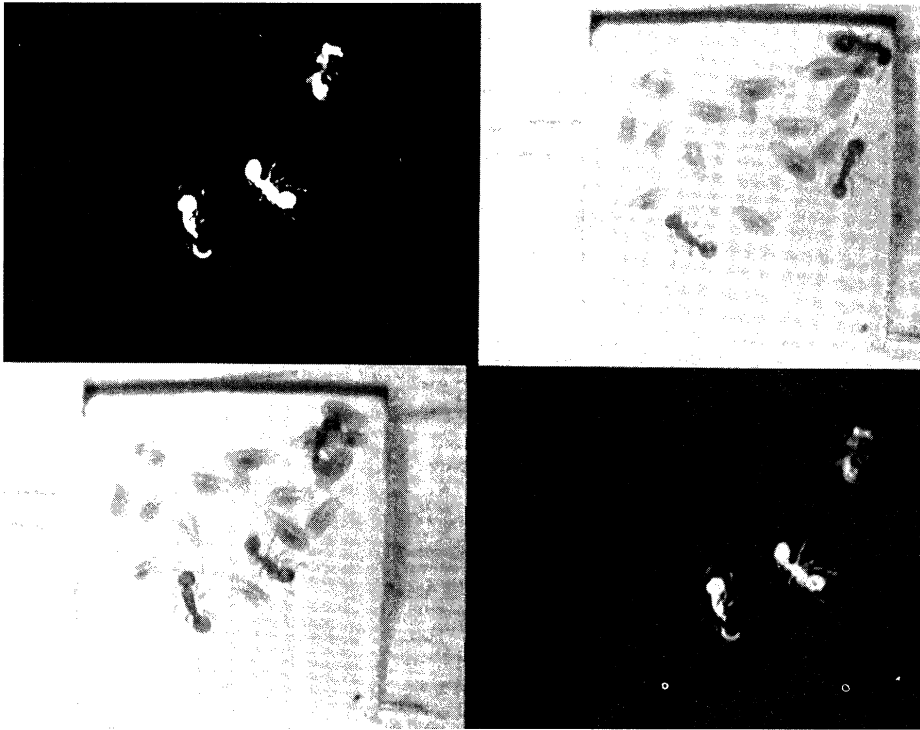


FIG. 3.—The procedure for collecting activity data. Two successive images (at 5-s intervals) are shown in the upper right and lower left portions of the image. The lower right portion of the image is the difference of the two images, with only those values larger than zero shown. The upper left image, from which the activity measurements are taken, is after processing to remove noise and improve contrast.

The 11.5-h data record for each aggregate consisted of 8,280 activity measurements taken at 5-s intervals. Each record was divided into two parts of 4,096 data entries each (leaving approximately 80 records that were not analyzed with fast Fourier transform [FFT]). An FFT was performed separately on the two segments. All results presented in this article are the average of the two separately analyzed halves. Activity records often show changes in periodic components over the course of a lengthy data run, and this procedure allows us to compensate, at least in part, for this effect. The sum of three consecutive estimates of the periodogram was used to estimate the magnitude of the Fourier component at the frequency of the midpoint of the three estimates (Press et al. 1991). The magnitude of the periodicity was standardized by expressing this sum as a proportion of the magnitudes of the first 200 Fourier components. These proportions were log transformed for normality and analyzed with ANOVA (SYSTAT; Wilkinson 1992).

To obtain an estimate of J_{11} , videotapes of two ants in the absence of the brood were analyzed. Two quantities were measured: the duration of an episode of activity and the number of times that the active ant interacted with the other

TABLE 2

ANOVA OF THE ACTIVITY OF AGGREGATES WITHOUT THE BROOD

Source of Variation	df	<i>F</i>	<i>P</i>
Time of day	1	5.879	.018
Size category	1	7.451	.008
Size × time interaction	1	142.753	.001
Error	81

NOTE.—Activity records are classified with the size of the aggregate (1, 2, 3, 5, 7, 11, or 15 workers) as a covariate and the time of day (night or day runs) as a classification variable.

active ant. Episodes of activity when an active ant interacted with an inactive ant one or more times were ignored. The effect of an active ant interacting with an inactive ant would be a measure of J_{12} , and all such encounters were excluded from the analysis. The lengths of the active periods were standardized by dividing by the average length of the active period when an ant did not interact with the other ant. If an active ant always interacted with the other ant during the period of observation, then the data could not be standardized and were not used. Because J_{ij} is a multiplicative measure, J_{11} was estimated as the log-transformed value of the ratio of observed to predicted intervals of activity.

RESULTS

Neither the colony of origin as a classification variable nor the date of testing as a covariate had any effect on the results; therefore, we combined data from various colonies and did not consider date of testing further in the analyses. The results of the ANOVA on the first Fourier component as a function of the time of day and the size of the aggregate are shown in table 2. The size of the aggregate is highly significant; smaller aggregates showed smaller periodic components, while aggregates of 15 workers were more highly periodic (Tukey's HSD test). The time of day main effect is significant (aggregates are somewhat more periodic during the day), as is the size × time interaction effect. The interaction effect is due to the difference in the magnitude of the largest Fourier component of aggregates of 15 workers during the day and night. Data records from aggregates of 15 workers, obtained at night, were no more periodic than those obtained from smaller aggregates. These effects can be seen in figure 4. Data records from aggregates of 15 workers, obtained during the day, were not significantly different from those of intact colonies ($P > .7$).

Replication of this experiment with aggregates including brood changed some of the patterns. The size of the aggregate was a highly significant covariate (see fig. 5). This effect is apparent whether colonies are included in the analysis or not (see table 3). Unlike the aggregates without a brood, the time of day did not make a difference to the size of any periodic component either as a main effect or in the interaction term.

The expected value of J_{11} , if there was no effect of an interaction with another

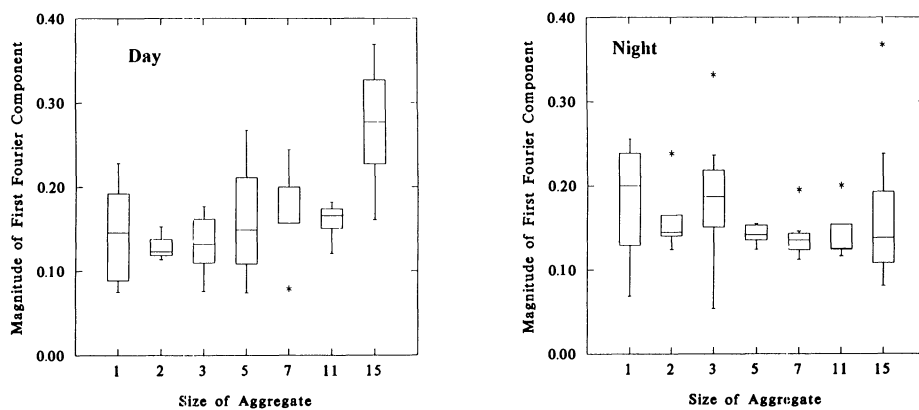


FIG. 4—Box plots showing the relation between the degree of periodicity in an activity record (fraction of the variation in the largest Fourier component) and the size of the aggregate. Note that the size of the aggregate influences the degree of periodicity more strongly during the day than at night. The central line is the median; the outer limits of the boxes represent the interquartile, or hinge, limits. The lines represent the median ± 2.5 hinge limits, and the asterisks represent single values outside a range of ± 4 hinge limits.

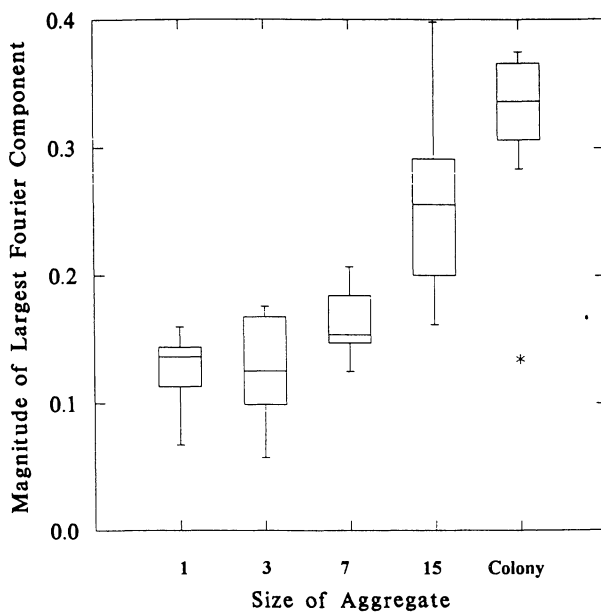


FIG. 5—Box plots showing the relation between the degree of periodicity and the size of aggregates containing brood. The conventions are the same as in figure 4.

TABLE 3

ANOVA OF THE ACTIVITY OF AGGREGATES WITH THE BROOD			
Source of Variation	df	F	P
Time of day	1	.009	.925
Size category	1	60.327	<.001
Size × time interaction	1	.301	.587
Error	37
Excluding colonies:			
Size category	1	40.853	<.001
Error	29

NOTE.—Activity records are classified using the size of the aggregate (1, 3, 7, or 15 workers and intact colonies) as a covariate and time of day (night and day runs) as a classification variable. The lower ANOVAs show the effect of size when the analysis excludes colonies.

active ant, is zero. This mean value of $J_{11} = 0.73 (\pm 0.26 \text{ SE})$ was significantly different from zero ($t = 2.79$, $df = 12$, $P < .02$). The regression of the value of J_{11} on the number of interactions with an active ant was highly significant ($J_{11} = 0.36 + 0.25[\text{int}]$; $r^2 = 0.23$, $P < .01$). The value of J_{11} predicted from this expression is 0.71. The similarity of these two estimates suggests that the effect of interactions on activity levels may be roughly additive.

DISCUSSION

Both the empirical results and the results of simulations show that under some circumstances, the amount of periodicity increases markedly with the size of the aggregate. In the experimental results, this happened in both the presence and absence of the brood, during the day. Under other circumstances (i.e., in the absence of the brood and at night) the amount of periodicity does not change dramatically with the size of the aggregate. The concordance between the simulations and the empirical results allows us to make predictions about the properties of the interaction matrix. The minimum requirement to produce the social phenotype of periodicity in *Leptothorax allardycei* workers is a sufficient aggregate size. If the aggregate is large enough (15 workers), it will be periodically active, at least during the day. The presence of the brood makes the periodicity more striking and induces periodicity to develop gradually with the addition of workers. The empirical results and the results of simulations both confirm that activity results from a distributed control mechanism (Gordon et al. 1992); no central pacemaker is required to modulate the activity of an aggregate, and there is no evidence for such a pacemaker. Although the brood has an effect of the production of periodicity, it gradually appears with the addition of larger numbers of workers rather than appearing with the addition of the brood, as might be expected if the brood were exerting some central control.

When natural selection operates on systems with distributed control, a subtle change can produce a profound effect. A critical question is how natural selection

operates on systems with distributed control. Since selection changes the characteristics of individuals, it may be operating through the components of the interaction matrix. A minor change in the terms of the interaction matrix can result in major changes in the dynamics of activity in an ant colony. It is easy to see that natural selection can produce organizational changes most efficiently in a system with distributed control when the units are sterile and genetically similar to one another. In social systems in which all individuals reproduce, the social phenotype resulting from distributed control will be disrupted by sexual reproduction each generation.

The empirical results obtained from the observations of ant activity can be imitated in the simulations by changing two parameters. When the brood is present, there is a strong, linear effect of the size of the aggregate on the amount of periodicity, which suggests that active ants affect one another (i.e., $J_{11} \sim 1$). When the brood is absent, during the night, the effect of increasing aggregate size is much reduced, which suggests that active ants have a smaller effect on one another (i.e., $J_{11} < 1$). When the brood is absent, but during the day, there is an effect of aggregate size that is not as great as the effect when the brood is present. One possibility is that both active and inactive ants affect active ants (i.e., J_{11} and $J_{21} \sim 1$).

The value of J_{11} in the absence of the brood was significantly greater than zero, a key prediction of the MCA model. Whether the value of J_{11} in the presence of the brood is greater than in the absence of the brood is not known, but given that periodicity is better developed when the brood is present, we predict that $J_{11 \text{ brood}} > J_{11 \text{ no brood}}$.

The effect that an active ant has on an inactive ant (i.e., J_{21}) has been investigated (Cole 1991a). Active ants produced a phase advance in the onset of activity of inactive ants (which is a positive J_{21}). These experiments were conducted in the absence of the brood and are consistent with both the results of the simulations and the observations presented here. This parameter has a negative effect on the production of periodicity in the simulations. When the brood is present, we predict that active ants should have less of an effect on inactive ants ($J_{21 \text{ brood}} < J_{21 \text{ no brood}}$).

What do these results tell us about ant behavior? The reduction of the effect of the interaction between active and inactive ants in the presence of the brood can be explained if active ants tend the brood rather than interact with inactive ants. This would reduce the magnitude of J_{21} . Active ants apparently monitor the maintenance requirements of the brood. D. Cassill and W. R. Tschinkel (unpublished manuscript) have studied the feeding behavior of larvae by workers of *Solenopsis invicta*. They have shown that workers feed larvae in discrete time units. Hungry larvae are fed more frequently than sated larvae, but all of them are fed for the same length of time. Franks and Sendova-Franks (1992) have shown that *Leptothorax* workers apportion the brood across the nest surface in proportion to the brood's metabolic demands. If active ants are placed in the vicinity of the brood, the brood may monopolize the activities of the active workers, greatly reducing the value of J_{21} .

The effect of interactions between active ants (J_{11}) is greater, and perhaps much

greater, in the presence of the brood than when it is absent. There are at least two possible general explanations for this result. The first is that the presence of the brood causes a qualitative change in the type of interactions that take place between active workers. It is possible that the presence of the brood acts as a switch turning on the sensitivity of active workers to the actions of nearby active workers. A second explanation is that active ants may simply be thrown together with one another more frequently, artificially increasing the rate, and thus perhaps the efficiency, of interactions between active ants.

Hemerik et al. (1992) model the production of ant activity cycles in *Leptothorax acervorum* from a somewhat different standpoint. Although the results obtained here differ from some of their results, the two sorts of models are not necessarily competing solutions to this problem. In particular, the autocatalytic models of Hemerik et al. (1992) and Tofts et al. (1992), following Goss and Deneuborg (1988), share some features, most notably the ability of specific categories of workers to interact with other categories. The MCA models presented here differ in three features. First, interactions between individuals are nonlinear; they are scaled by the gain parameter. Second, interactions between ants in all possible states are considered to determine which category of interactions should be most important for producing the observed periodicity. Third, there is an explicit spatial component in the model of activity. This spatial component was lacking from previous attempts to model this phenomenon (Cole 1992; Hatcher et al. 1992; Hemerik et al. 1992). The spatial component of the model has an effect on periodicity by inducing time lags in the spread of activity throughout the nest.

The most conspicuous difference in our results is that in the models of Goss and Deneuborg (1988), Hemerik et al. (1992), and Tofts et al. (1992), periodicity is caused by the fact that active ants increase the activity of inactive ants. In the terms of this article, they let $J_{21} = 1$. In the MCA models, the effect of letting $J_{21} = 1$ decreases the amount of periodicity in the aggregate. It is interesting to ask whether the contrasting results obtained by the two approaches are due to the explicit spatial component in the MCA models.

Hatcher et al. (1992) have postulated the periodic dynamics in colonies of *L. acervorum* result in more efficient brood care. In this interesting model, ants perform a single task at a time, and the brood cannot be simultaneously tended by two ants. Synchrony of activity in the colony is desirable because simultaneous activity of the workers reduces redundant tending of the brood and results in more even, and therefore more efficient, tending. While there is no evidence for increased or decreased efficiency in brood tending in *L. allardycei*, we can make several observations. It is possible that the terms of the interaction matrix, particularly the magnitude of interaction between active ants, J_{11} , have been molded by natural selection to increase the efficiency of colony function according to the mechanism of Hatcher et al. (1992). This would provide an adaptive explanation for the generation of activity cycles in ants. Because the production of activity cycles does not require the presence of the brood, activity cycles may increase the efficiency of brood care while not necessarily being caused by it. However, activity cycles become more prominent in the presence of the brood, which suggests a more direct causal link. A final point is that activity has a spatial

component; that is, it does not occur in all localities with equal probability. The relation between areas of high activity and the presence of the brood is not a simple one. It is certainly not the case that activity simply occurs more frequently in the neighborhood of the brood (B. J. Cole, unpublished data).

The generality of MCA models suggests that they could be applied to the social behavior of other organisms or in other situations. For example, when the activity of single *Drosophila* is compared to the activity of groups of *Drosophila*, there is no modulation of activity into cycles (Cole 1994). The mechanistic explanation for this observation is that $J_{11} = 0$. Conversely, the activity of social aggregates of the willow leaf beetle (Breden and Wade 1989) shows a strong periodic component (B. J. Cole, unpublished data), which suggests that $J_{11} > 0$.

The two parameters of the MCA models that affect the production of aggregate activity, the gain parameter, and the terms of J_{ij} can be measured experimentally. Clear, qualitative predictions can be made about the relative magnitude of certain interaction coefficients under particular experimental conditions that can be used in further tests of the validity of this approach. Mobile cellular automata models have a clear applicability to the study of processes in animal behavior that make them a promising approach for further work.

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