SHORT-TERM ACTIVITY CYCLES IN ANTS: GENERATION OF PERIODICITY BY WORKER INTERACTION

BLAINE J. COLE

Department of Biology, University of Houston, Houston, Texas 77204-5513

Abstract.—Activity levels within ant colonies are monitored by using a solid-state automatically digitizing camera. The movement-activity levels of whole colonies and of isolated groups of workers are studied. Whole colonies of *Leptothorax allardycei* show rhythmic changes in movement-activity level. Fourier and autocorrelation analyses indicate that the activity levels of colonies are periodic, with an average period of 26 min. Single, isolated workers do not show the pattern of periodic changes in activity level. Single workers become active spontaneously, but at no particular interval. Pairs of workers, confined together, also do not show periodicity in activity level. One worker can stimulate another worker to become active, thus coupling their movement-activity patterns. As ants are placed in larger groups, the variation in the interval between activity peaks declines in a manner predicted by coupled-oscillator theory. It is argued that the colony can be regarded as a population of excitable subunits, and it is shown that the results of this paper can be explained in this light. The formal similarity between movement-activity patterns in ant colonies and the dynamics of epidemics is noted. It is further argued that periodicity in the movement-activity levels of the colony is probably an epiphenomenon rather than an adaptation. Selection at the colonial level probably acts on the spontaneity of activity and coupling strength to produce changes in the overall activity level of the colony. One of the patterns that can result is periodicity in the colony's activity level, but it is not the only possible outcome.

Comprehending how the complexity of social behavior arises from the interaction of individuals is fundamental to understanding the evolution of social behavior. If a particular behavior of the social unit is simply the summation of the behavior of its individual members, then the whole is the resultant of the component parts. If, however, individuals interact to produce the behavior of the social unit, then social behavior has an emergent property that can itself be subject to natural selection and investigation.

The study of social behavior is fundamentally the study of levels of organization and thus impinges directly on questions of the levels of selection. If a social behavior can be predicted solely from the sum of the behavior of individuals, then any explanation for its existence rests only at the individual level. If there are emergent properties of a social behavior, natural selection can act on the emergent properties independent of the individual characteristics.

In this study, I examine the relation between the behavior of individuals and the behavior of the social unit in colonies of *Leptothorax* ants. I chose to study movement activity because it is a prerequisite for other kinds of behavior. I do

not subdivide activity into various kinds of behavior. Although activities may vary tremendously, here I distinguish only between movement activity and inactivity.

I describe a new method of automatically monitoring the movement-activity levels of whole ant colonies, single ants, and intermediate-sized groups. I show that the movement-activity levels of whole colonies of *Leptothorax allardycei* vary cyclically, with a period of approximately 25 min. The movement-activity levels of individual ants, however, are not periodic. I discuss the emergence of cyclic movement activity within colonies from the interactions among individual ants.

MATERIALS AND METHODS

I studied movement activity in the ant *Leptothorax allardycei* (Mann). A description of the basic biology of this species is found elsewhere (Cole 1981, 1984, 1986, 1988*a,* 1988*b*). The species occurs in the Florida Keys, where it inhabits the hollow stems of sawgrass (*Cladium jamaicense*), with colonies of a single queen and 20–120 workers living in a single internode. Workers are characteristically aggressive toward one another and are arranged in a dominance hierarchy. The high-ranking ants have highly developed ovaries and lay eggs that produce males (Cole 1981, 1986).

Colonies were collected from Sugarloaf and Cudjoe Keys and housed in observation nests consisting of two glass slides held apart by a cardboard or balsa-wood partition. The nests were housed in plastic boxes with a food and water source. Colonies can be maintained in this way for several years in the laboratory.

Activity is monitored with a MicronEye solid-state camera. The MicronEye has a light-sensitive semiconductor chip. The image of a colony is focused on the chip, producing an image of 128 × 640 pixels (81,920 total pixels) on a computer screen. The result is an image of the colony, an example of which is shown in figure 1. A single ant in a whole-colony preparation covers approximately 100–150 pixels.

Additional software was developed to enable the camera to compare images after a selected time interval. For the purposes of this study, 30-s intervals give adequate temporal resolution. Each image, which is already digitized, is stored and compared with the preceding image. The total number of pixels that have changed from black to white, or vice versa, is recorded. If there is no activity in the colony, there is no movement and successive images are similar. An unchanging image changes slightly when viewed through the MicronEye; the irreducible noise level is approximately 0.1% of the total number of pixels. If there is a great deal of movement activity and movement in the colony, successive images differ markedly; the total number of pixels that change is large and is stored for later analysis. The number of pixel differences between successive images is determined individually for each of the 16 sectors (a 4 × 4 grid) into which the image is divided. The results of this paper are presented as the sum of all 16 sectors of the image.

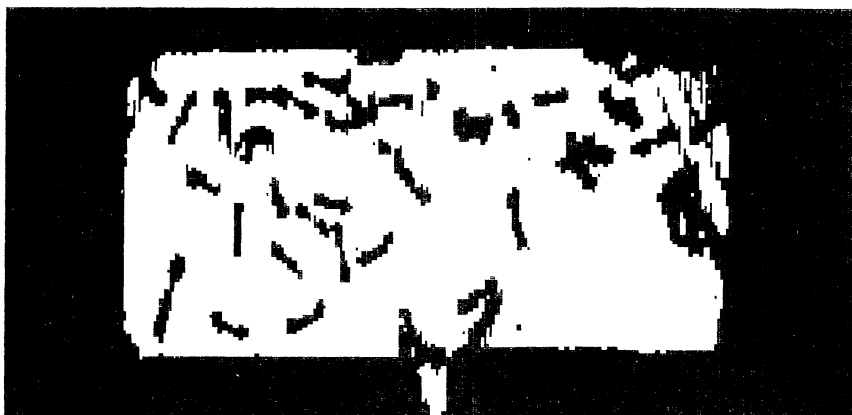Colonies are placed under the MicronEye and allowed to acclimatize for ap-

FIG. 1.—A MicronEye image of a nest of *Leptothorax allardycei*. Note that the queen is the larger image in the lower left corner (extending almost vertically about one-third of the height of the nest).

proximately 30 min before activity monitoring begins. Whole colonies are moni-tored at a distance of 30 cm from the nest to the MicronEye. I recorded the number of individuals in the colony to determine the effect of the colony's size on movement-activity pattern.

I obtained activity records of single ants by isolating workers in a chamber with three walls of cardboard and a fourth, removable, wall of cotton. The protocol for recording activity was identical to that for colonies except that the chamber was observed from a distance of 15 cm. I obtained activity records for two, five, and seven ants by arbitrarily removing the appropriate number of workers from a single colony, confining the workers together, and observing them from a distance of 15 cm.

A typical activity record is approximately 512 observation intervals of 30 s each, or about 4.25 h. Analysis of the time series was facilitated by having the number of data points be a power of two. These data were analyzed for periodicity by several methods of time-series analysis. These techniques are straightforward and are described in any introductory textbook on the analysis of time series (e.g., Chatfield 1984). Computer data analysis was carried out using BMDP-PC and Statgraphics (1987).

RESULTS

The data consist of 44 activity records, 18 from intact colonies and 26 from isolated groups of workers. I first present results from the movement activity of complete colonies and then those from the movement activity of isolated groups of workers.

Whole Colonies

The movement-activity records of three representative colonies are shown in figure 2. The results from 18 complete colonies are available, but their general
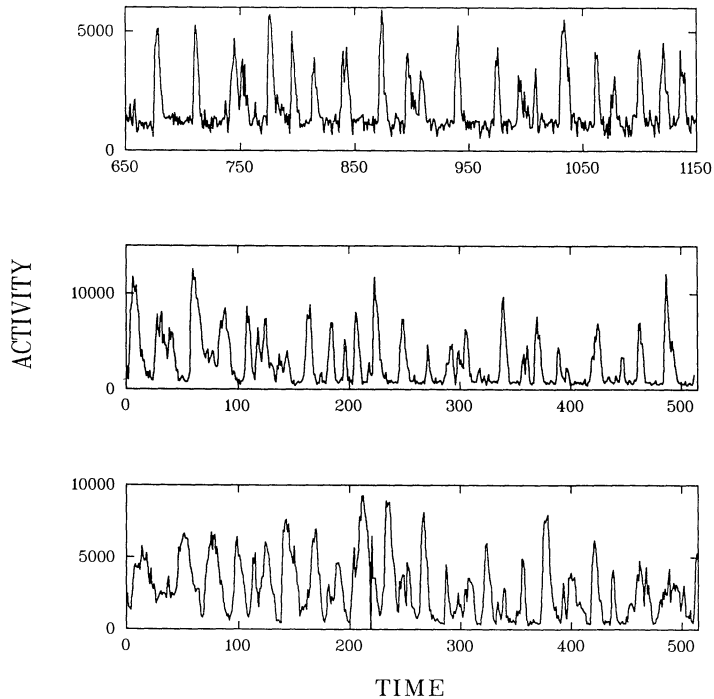
FIG. 2.—Activity records for three colonies of *Leptothorax allardycei*. The activity records shown in the three panels of this figure are those used in figs. 3 and 4. *Horizontal axis*, time, measured in 30-s intervals. *Vertical axis*, activity, as measured by the number of pixel differences between two successive MicronEye images taken 30 s apart.

form does not differ from these examples. The movement-activity levels of the colonies change markedly over relatively short periods of time.

I analyzed movement-activity records by spectral analysis and autocorrelation analysis for evidence of periodicity. The periodogram of each of the activity records shown in figure 2 is given in figure 3. I plotted the squared amplitude of the Fourier components against the logarithm of the frequency in figure 3. The activity patterns have a strong periodic component as shown by the large peak at certain frequencies. The dominant period of the frequencies obtained from spectral analysis ranges from 15 to 37 min per cycle (mean, 26.8 ± 6.9 SD).

The autocorrelation function of a time series gives the correlation between the points delimiting a given interval in the time series, as a function of that interval. The autocorrelation functions of the three activity records of figure 2 are shown in figure 4. The sinusoidal nature of the autocorrelation function indicates that the time series is periodic and probably based on an autoregressive process. The first peak of the autocorrelation function indicates the lag that produces the highest correlation and is an estimate of the period of the time series. The estimates of the period of the time series vary from 12 to 35 min (mean, 25.5 ± 5.9 SD).

The partial-autocorrelation function of a time series gives the residual correlation between values with a lag k after the effect of all $k - 1$ preceding partial
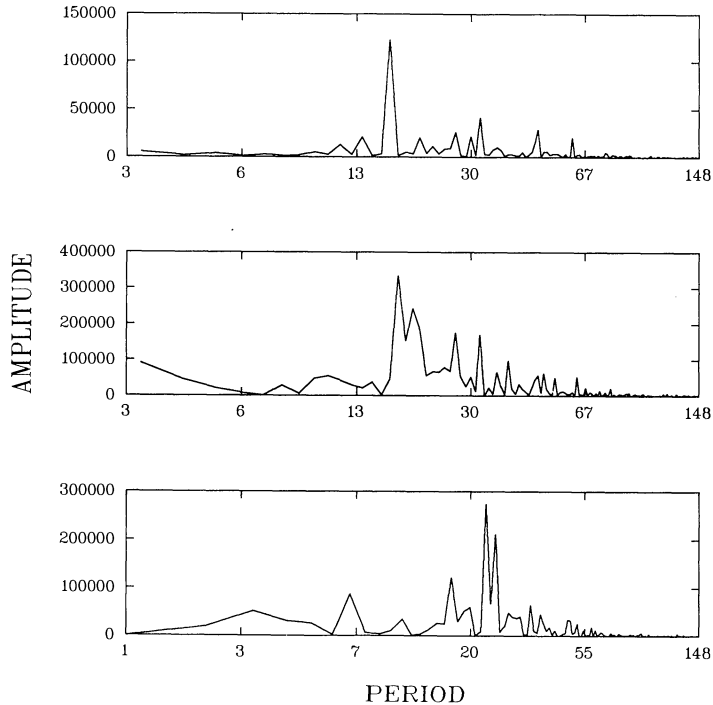
FIG. 3.—Periodograms of the colony's activity records given in fig. 2. *Horizontal axis,* the natural logarithm of the frequency. *Vertical axis,* the squared amplitude of the Fourier component at that frequency. The squared amplitude is directly proportional to the variance accounted for by oscillations at that frequency.

autocorrelations have been removed. Each partial-autocorrelation function of the activity records shown in figure 2 has a significant, positive, first partial-autocorrelation coefficient and a significant, negative, second partial-autocorrelation coefficient. A negative, self-damping term is necessary for a time series to show oscillatory behavior.

Although the movement-activity records of all colonies of *Leptothorax allardycei* have exhibited periodicity, they do not have exactly the same period. In figure 5, I plot the relation between the size of the colony and the period of the movement-activity rhythm. There is no relation between the size of the colony and the length of the colony's movement-activity cycle (slope = 0.04, t = 0.8, n = 18, P > .4).

Single Ants

In order to discover whether periodicity in the movement activity of whole colonies results from the periodic activity of single worker ants, I measured the activity of 10 singly confined individuals. The presentation of these results is analogous to that for the whole-colony results. Figure 6 shows the activity record of three individual ants. The movement-activity level of an individual ant varies;
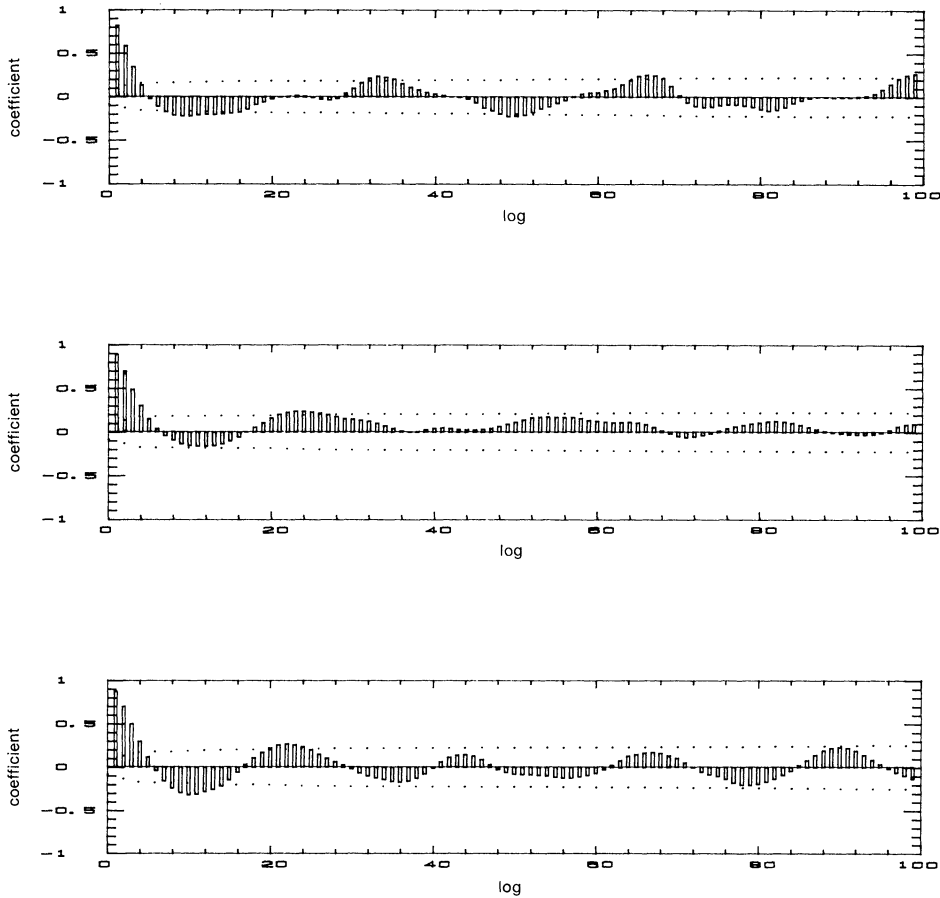
FIG. 4.—The autocorrelation functions for the activity records given in fig. 2. The autocorrelation function gives the correlation between activity levels after a time interval, as a function of that interval. The interval length is 30 s. *Dotted lines*, 2 SEs around zero.

individuals become active spontaneously and do not remain active for long periods of time. Activity records for each ant are similar.

Unlike whole colonies, single ants do not show a periodic pattern of movement activity. The power spectra of the single-ant movement-activity records (fig. 7) lack the obvious peak in power that one sees in intact colonies. This pattern is repeated when one looks at the autocorrelation function for the single-ant activity records. There is no periodicity, and seemingly no pattern, to the autocorrelation function. Finally, the partial-autocorrelation function indicates a significant, first partial-autocorrelation coefficient but no other significant partial-autocorrelation coefficients.

A histogram of the movement-activity peaks for single ants is shown in figure 8. The height of the movement-activity peak is the maximum number of pixels
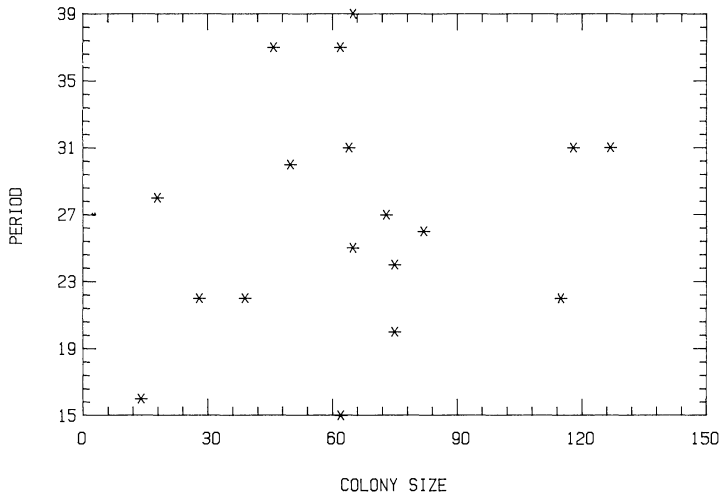
FIG. 5.—The relation between the period of a colony's activity cycle (from spectral analysis) and the number of individuals in the colony. There is no pattern.
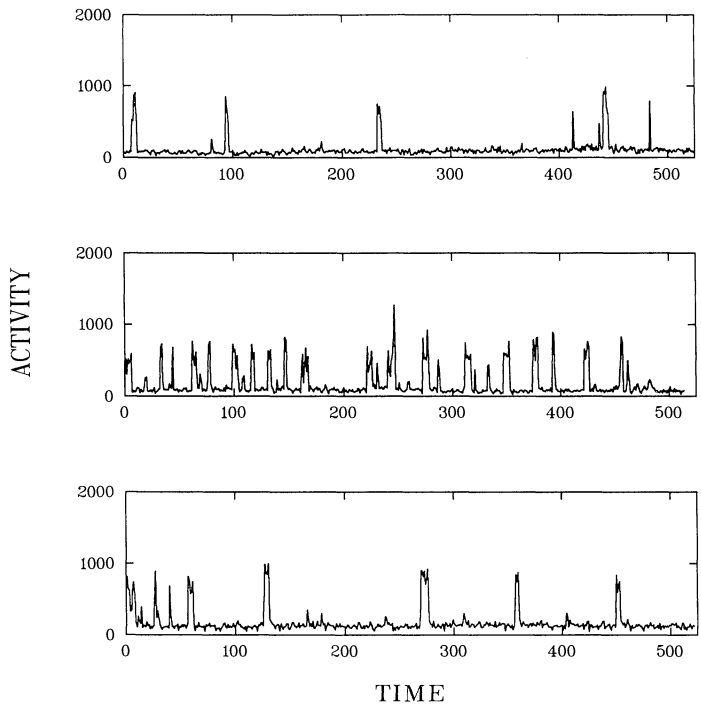

FIG. 6.—Three activity records for single worker ants. These activity records are the basis for the power spectrum in fig. 7. Axes as in fig. 2.
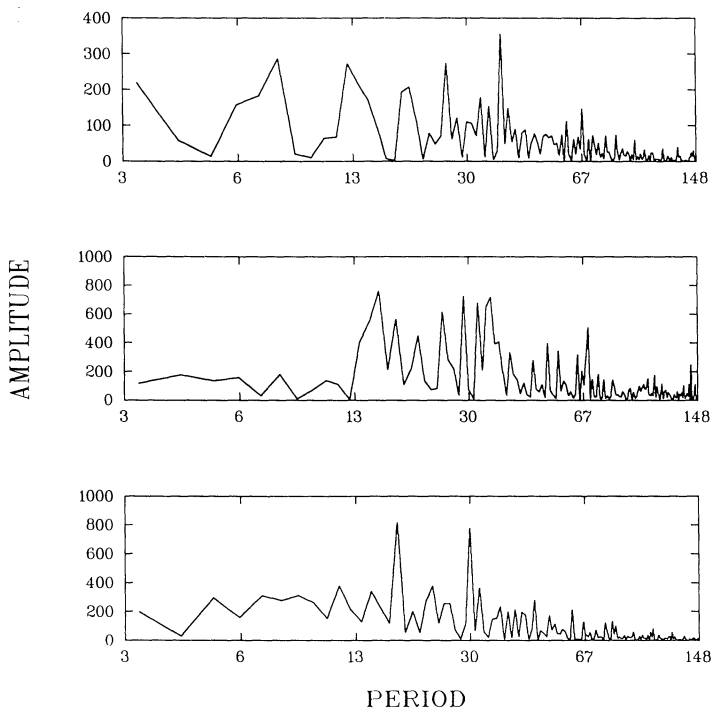
250

FIG. 7.—Periodograms for the activity records of single ants given in fig. 6. See the legend for fig. 3. Note the lack of any dominant frequency of oscillation.
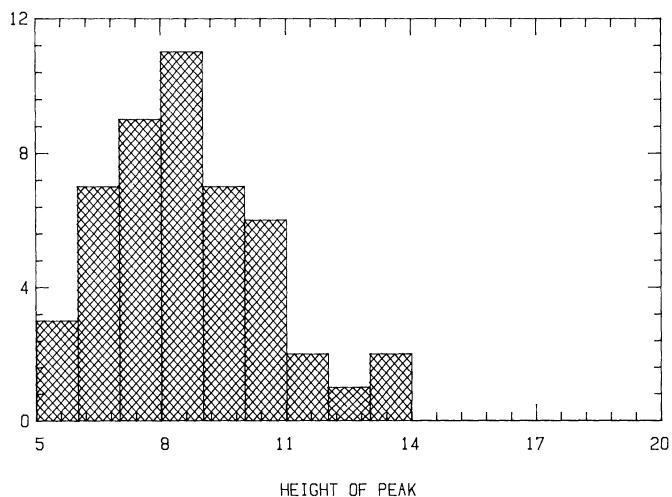

FIG. 8.—A frequency histogram of the height of activity peaks for single ants. The height of each peak times 100 is measured in pixel differences (the same as the vertical axis of fig. 6) and has a mean of approximately 800.
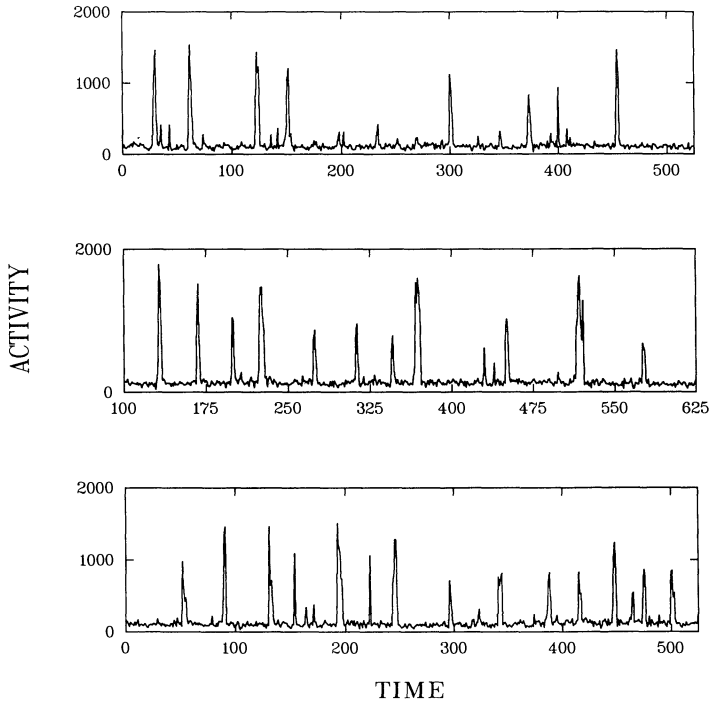
251

FIG. 9.—Three activity records for pairs of worker ants confined together. Axes as in fig. 2. Notice that certain peaks are about twice as high as other peaks.

that change during one activity bout. The mean height of an activity peak for a single ant is about 800 pixels. This represents the approximate number of pixels changed by the movement of a single ant.

Two Ants

Activity recording was repeated with six pairs of ants confined together. Three such records are shown in figure 9. Once again the power spectrum and the autocorrelation functions of the movement-activity records of pairs of ants do not indicate any sort of periodicity.

The frequency distribution of the height of the movement-activity peaks for pairs of ants is bimodal (fig. 10). The lower mode of the frequency distribution is at approximately 900 pixel changes, indicating the movement activity of a single ant. The upper mode of the frequency distribution is at approximately 1,500 pixel differences. That the upper mode is nearly twice the lower mode indicates that both ants are active. The relative number of peaks within the single-ant and two-ant activity modes indicates the degree to which the two ants interact.

To show that the upper mode represents two ants interacting with one another, one must rule out the possibility that the movement-activity peaks of two ants represent the chance superposition of independently acting individuals. From the duration of the movement-activity peak of a single ant, one can calculate the
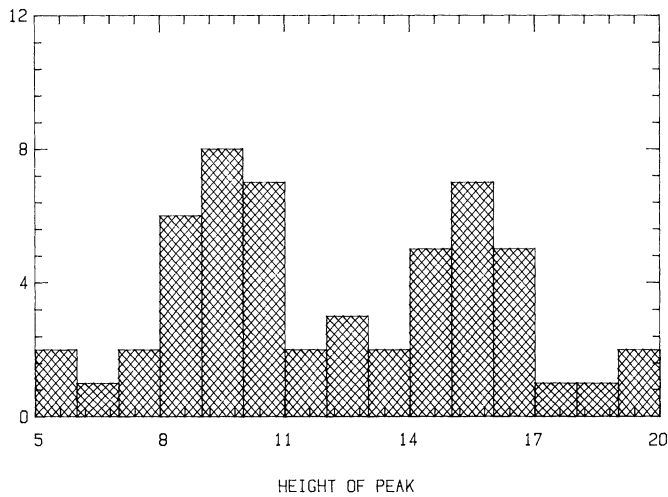
FIG. 10.—The frequency distribution of peak heights for two ants. Axes as in fig. 8. Note the bimodal character of the frequency distribution, showing that some activity peaks result from the actions of one ant and other activity peaks result from the simultaneous activity of both ants.

probability that two peaks will be superposed by chance. From the total number of movement-activity peaks, one can then estimate the expected number of superposed activity peaks. The number of observed activity peaks representing two ants is 25, in contrast to the expected number of 1. It is highly unlikely that this is a chance phenomenon. I performed Monte Carlo simulations of two peaks overlapping and estimated that the upper 99% confidence limit is four superposed peaks. Thus, the upper mode in the frequency distribution does represent pairs of ants that are interacting.

One can estimate the extent of the interaction in several ways. The most straightforward is to express the number of two-ant peaks as a fraction of the total. By this measure, the interaction strength is 0.45. It is perhaps more informative, however, to express the strength of the interaction as the fraction of the movement activity of a single ant that occurs in concert with another. For two ants, this measure is $I = 2F/(1 + F)$, where F is the fraction of peaks involving two ants. By this measure, $I = 0.62$. Although it would be appropriate to correct this measure by an estimate of the number of peaks that should be superposed by chance, in this case it would make a negligible difference.

Larger Groups of Ants and the Predictability of Activity

I monitored five groups of five ants and five groups of seven ants and present a movement-activity record for a group of five and a group of seven worker ants in figure 11. These groups of ants do not produce movement-activity cycles that are sustained and regular; however, they can be at the borderline of periodicity.

I measured the time interval between peaks of movement activity for groups of one, two, five, and seven ants. The standard deviation of the time interval
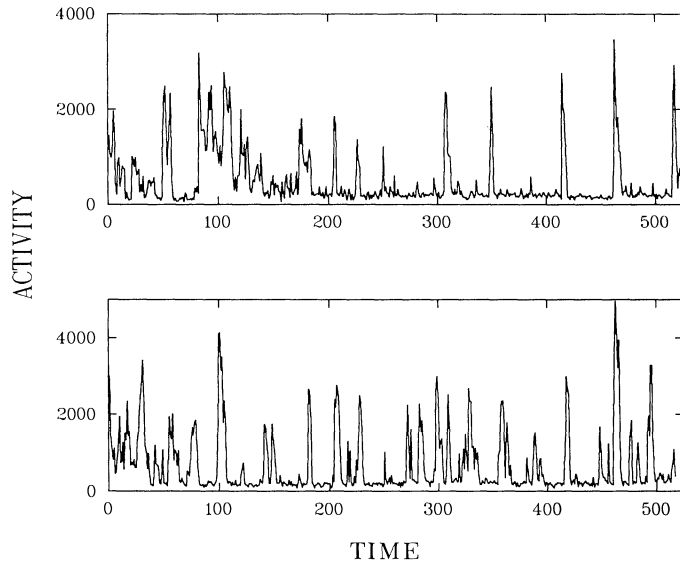
FIG. 11.—Activity records for a group of five ants (*top*) and seven ants (*bottom*). See the legend for fig. 2.

between activity peaks is taken as a measure of the predictability of the next bout of movement activity. The relation between the logarithm of the standard deviation of the interval between peaks and the logarithm of the number of workers is shown in figure 12. There is a significant negative relation ($P < .01$) between the variability in peak interval and the number of worker ants present. As the number of workers increases, the predictability of the movement activity in the aggregate also increases. This result is important in discussing the predictions of coupled-oscillator theory below.

DISCUSSION

In this discussion I summarize the results, discuss the result of varying movement-activity levels in the light of coupled-oscillator and epidemic theory, and consider the adaptive aspects of colony-activity cycles. The basic results of this paper are that (1) movement-activity levels in intact colonies of *Leptothorax allardycei* are periodic; (2) movement-activity levels of single ants show that they become active spontaneously and that the interval between successive peaks of movement activity is unpredictable; and (3), although the movement-activity patterns of groups of two, five, and seven ants are also typically aperiodic, the variation in the interval between movement-activity peaks declines with larger numbers of ants.

Coupled Oscillators

It can be useful and appropriate to regard an ant colony as a population of weakly coupled oscillators. If the action of one oscillator can stimulate the action
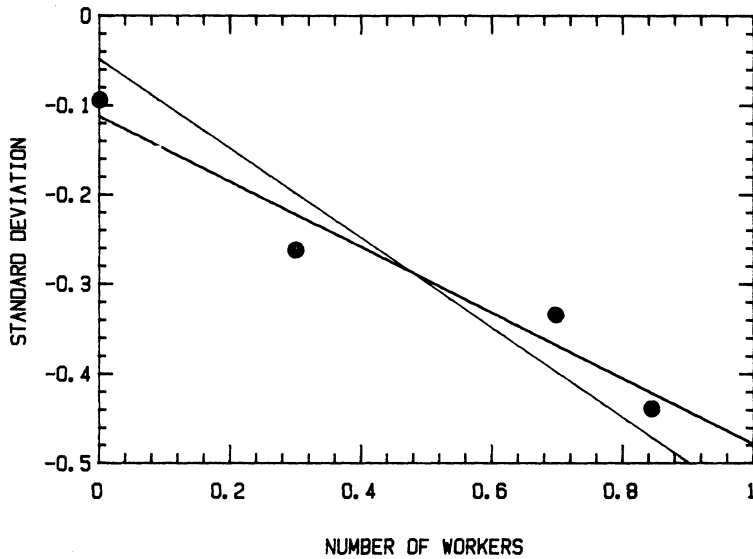
Fig. 12.—The relation between the standard deviation of the interval between successive activity peaks for groups of one, two, five, and seven workers. The scale of each axis is the logarithm of the standard deviation between peaks. The line with the shallower slope is the regression (slope = -0.37; different from zero with $P < .01$). The steeper line has a slope of -0.50. The data do not differ significantly from this slope (see the text).

of the other, the two oscillators are said to be coupled. The applicability to ant colonies seems straightforward. A single, isolated ant does not have a precise activity period but becomes active spontaneously, producing peaks of movement activity. The activity of single individuals can be compared with the action of a single excitable subunit or a single member of a population of imprecise oscillators. When this excitable subunit is triggered (either spontaneously or by stimulation from another ant), the ant becomes active. When a single ant is considered in isolation, the outcome is unpredictable.

The movement activity of pairs of ants suggests how periodicity in the colony's movement activity results from individual activity. Pairs of ants interact with one another. Their activity patterns are coupled with one another, but since the movement activity of one ant does not guarantee movement activity in another ant, they are weakly coupled. The height of the activity peaks indicate that both ants are active approximately 45% of the time.

The decline in the standard deviation of the interval between successive activity peaks suggests that the predictability of the movement-activity pattern increases with the number of interacting individuals. Populations of coupled oscillators can show a similar pattern (Enright 1980a, 1980b). The way in which the oscillators are coupled to one another can influence the outcome. Consider one possible coupling scheme discussed by Enright (1980a, 1980b). Suppose that all the oscillators fire when a certain fixed proportion of the oscillators are triggered. In terms of an ant colony, when a certain fraction of the total workers become active (a relative threshold), the entire colony becomes active. Then, after the movement

activity dies out, a fixed proportion of the colony must again become active for the entire colony to become active.

Such a coupling scheme has two consequences. First, one can obtain a periodic phenomenon from completely aperiodic components. Second, one can make a quantitative prediction concerning the relation between the number of oscillators and the predictability of the interval between successive activity peaks. Enright showed that the standard deviation of the interval between activity peaks is proportional to the reciprocal of the square root of the number of oscillators. In a log-log plot, the slope should be -0.5. Figure 12 shows this relation. The observed slope, although significantly different from zero, is not significantly different from -0.5. This, of course, is not a direct demonstration that the movement activity of the workers in a colony is coupled in this way, since other coupling schemes can produce the same prediction, but it does satisfy a key prediction of the model. This result parallels a hypothesis for the accuracy of circadian rhythms. The period of a large population of oscillators that are capable of mutually entraining one another may be far more precise than that of single oscillators (Winfree 1967, 1980).

In order for an ant colony to behave as a population of loosely coupled oscillators, it is necessary that a product of the oscillation be capable of coupling the oscillators. In *L. allardycei,* it appears that physical encounters, a necessary by-product of movement activity, can stimulate activity (Cole, in press).

Aggregates of coupled oscillators occur in a wide variety of behavioral and other contexts. The synchronized flashing of fireflies (Hanson et al. 1971; Hanson 1978), chorusing of crickets (Walker 1969), and aggregation of slime mold amoebas (Novak and Seelig 1976; Malchow et al. 1978) have been interpreted as mutually entraining populations of oscillators. Oscillations in predator-prey populations that are coupled to one another by diffusion have been analyzed theoretically (Murray 1975, 1976; Jorne 1977). Other possibilities abound, for example, synchrony in frog choruses, activity in bird nesting aggregations, and episodic vocalization in bird leks.

Epidemics and Activity

A strong formal similarity exists between patterns of movement activity in ant nests and one type of coupled interaction, the dynamics of the spread of an epidemic. The trait of movement activity is infectious in that it can be transmitted from one individual to another. Individuals remain "infectious" for some period of time and then recover. The colony shows a pattern of increasing activity, which builds to some maximum and then subsides, as in an epidemic. The dynamics of epidemics are the subject of many theoretical and empirical studies (e.g., Anderson and May 1979, 1985; May 1985).

A characteristic of many models of disease transmission is the tendency to oscillate. However, the precise dynamic outcome of the epidemic depends on the value of certain parameters, such as the transmissibility of the disease, the duration of the infection, and the extent of immunity. By varying the parameters in a model of the epidemic, it is possible to produce sustained oscillations, damped oscillations, or even chaotic outbreaks. This same variety of dynamics in activity

level is to be expected for ant species. Certain species would likely have sustained, periodic oscillations in movement activity, as does *L. allardycei*. Other species may show damped oscillations between disturbances or erratic outbursts of activity that may be chaotic.

Adaptive Significance of Short-Term Activity Cycles

Short-term movement-activity cycles within colonies of ants may have adaptive significance if some activities must be performed on a cyclic schedule or if periodic cycles of activity contribute to the colony's efficiency. It is difficult to rule out either of these possibilities. However, no activity is known to be performed without fail during a bout of colonial activity. Brood care (including larval feeding, grooming, and brood movement), mutual food exchange between adult workers, allogrooming, care of the queen, and dominance behavior take place exclusively during periods of colonial activity, by definition, but colonial activities do not occur on any evident schedule or in any evident order (personal observation; Calabi and Rosengaus 1988).

It is unlikely that periodic movement activity in the colony contributes to efficiency of the colony. Rather, simultaneous actions of individuals may cause colonial inefficiency because of a "rush hour" phenomenon. This may be especially true in the case of *L. allardycei*, in which encounters with other ants cause workers to alter their movement patterns according to their relative hierarchy rank (Cole 1988*a*). In the absence of data, it is unwise to attribute short-term movement-activity cycles in the colony to the ergonomic advantage of simultaneous activity.

I argue that short-term activity cycles in ant colonies are not themselves adaptive but are the inevitable outcome of interactions within social groups. Activity by one ant stimulates activity by another ant. One possible outcome of mutual entrainment of the actions of worker ants is periodicity. It need not be the only outcome. Depending on the details of the interaction between ants, the result may be sustained oscillations in activity, damped oscillations, or chaotic bursts of activity. For different species, with different size, social organization, or caste structure of the colony, colonial activity may have any one of these patterns.

If periodic movement activity per se is not adaptive, what is? I propose that at least two features of the activity patterns of individuals—the spontaneity of activity and the coupling strength of one activity pattern to another—can be subject to selection. Whether a single ant becomes active depends on these two parameters. If the spontaneity is high relative to the coupling strength, then movement activity of an individual is likely to be self-generated. If the coupling strength is higher, then the movement activity of an ant is more likely to result from interactions with nest mates. Both of these traits contribute to the colony's activity pattern and may, therefore, be subject to selection at the colonial level. Changes in spontaneity and coupling strength will produce various colonial-level activity patterns, including periodic fluctuation in movement-activity levels.

There may be a number of possible solutions to the problem of changing activity levels in the colony. It is conceivable that the same colony phenotype could be generated by various levels of spontaneity and coupling strength. Selection at the

level of the colony can produce changes in the characteristics of the activity patterns of individuals.

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