Short-term activity cycles in ants: age-related changes in tempo and colony synchrony

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Summary. This paper examines the characteristics of the spontaneous acivity levels of individual worker ants of *Leptothorax allardycei* and explores the influence of spontaneous worker activity on colony activity patterns. While there are substantial differences among workers in the characteristics of their spontaneous activity, all of the variation occurs within the colony. There are virtually no differences in the levels of spontaneous activity between colonies. Variation among workers is due to age; workers decline exponentially in their probability of becoming active, p_a, at a rate of -0.02 per day. I built computer models under four different sets of assumptions about the spontaneous activity patterns of workers, and performed simulations to test the ability of colonies of simulated workers to synchronize their movement activity. The most realistic results are obtained with models in which workers already have an underlying propensity to oscillate and which interact with one another to produce Type 1 phase resetting. The simulations generate predictions concerning the ability of colonies to synchronize, the most significant of which is that the average age of workers in a colony is very important in determining the extent of colony synchrony, while the distribution of ages is not.

Introduction

Changes in the behavioral repertoire of worker ants, or age-related castes, are a virtually universal feature of ant colonies. With the exception of *Amblyopone pallipes* (Traniello 1978), all species of ants are known to show age-graded polyethism. The extent and structure of polyethism varies considerably among species, but typical behavioral roles can be broadly divided into two categories: activity taking place within the nest (*Innendienst*) and activity taking place outside of the nest (*Außendienst*). Invariably, the younger age category of workers is the *Innendienst* caste. Categories of labor may vary concordantly with one another, as in *Pheidole den-*

tata (Wilson 1976), or they may change independently of one another as in *Pheidole hortensis* (Calabi et al. 1983). Regardless of the details in any species, developmental or maturational changes in behavior are clearly an important feature of ant caste structure.

A characteristic feature of social insect behavior is the tempo of activity, the overall pace at which activity occurs (Oster and Wilson 1978). The tempo of activity is often one of the identifiable traits of a species or group. For example, dacetine ants are characteristically slow moving, while dolichoderine ants, such as *Tapinoma*, move rapidly and appear very "nervous". The tempo of activity of a species of ant will be a function of both the ecology and the phylogenic relationships of the species.

In this paper I will examine the tempo of activity of individual workers of the ant *Leptothorax allardycei*. I shall show that the tempo of activity of single workers is quite variable within a colony and that this variation is associated with the age of the worker. In addition, I will present computer models of the activity of colonies of *Leptothorax* ants that are based on the measured properties of individual workers. The models begin to provide insight into the relative importance of the characteristics of individual workers in producing the group phenotype.

Colonies of *L. allardycei* display periodicity in activity levels. The period of activity is about 25 min in intact colonies (Cole 1991 a). The cycles of activity in *L. allardycei* are similar to those seen in *L. acervorum* (Franks et al. 1990) and *L. muscorum* (pers. obs.). Although the colonies are invariably periodic, not all workers are active during all colony activity periods. While the activity of intact colonies of *L. allardycei* is evidently periodic, the activity of individual workers is not. Single, isolated, workers become active and inactive spontaneously in a chaotic pattern (Cole 1991 a, b, c). Interactions among individuals causes predictable changes in the phase relationships in the activity of pairs of ants resulting in synchrony (Cole 1991 b). Individuals appear to vary considerably in a number of features of their spontaneous ac-

tivity patterns such as the probability of becoming active when inactive and the length of time that they are active.

The mechanism by which periodicity in colony activity is produced from the chaotic activity of individuals is not understood. In order to develop a predictive model for the production of colony activity patterns, it will be essential to examine the behavior of individual workers. If we observe individual variation in the attributes of spontaneous activity this could be due to variation among colonies, variation among individuals within a colony, to ontogenetic changes that occur over the lifespan of an individual or simply due to chance variation (Cole 1988). The purpose of this study is to determine how variation in activity patterns among the workers of different colonies is apportioned among workers and colonies and to begin to study the correlates of variation in the activity patterns of individual workers in order to develop predictive models of colony organization.

Materials and methods

Spontaneity was assessed by measuring two independent quantities: the probability of becoming active given that the ant is currently inactive, p_a, and the probability of becoming inactive, given that the ant is currently active, p_i (see Fig. 1a). The independence of these quantities can be seen by noting that one could assign any values (between 0 and 1) to p_i and p_a. We cannot adequately describe the activity phenotype of a worker by simply measuring the fraction of time that it is active. It is possible to have the same average level of activity with differing probabilities of becoming active and inactive. These two quantities were measured from activity records generated using a MicronEye camera and software to compare images (Cole 1991a). A digitized image is stored in a computer and compared to another image that is collected 30 s later. The data are the number of pixels that have changed from the previous image. Large amounts of movement change large numbers of pixels, smaller amounts of movement change smaller numbers of pixels. I define activity to have begun when the number of changed pixels exceeds a threshold value. The threshold is determined by examining a probability plot (Sokal and Rohlf 1981) of the activity levels. The MicronEye has associated with it Gaussian noise which appears as a straight line on the probability plot. A sharp break in the linearity of the probability plot indicates data which exceed the noise level. The length of time that the ant is active or inactive can also be determined from the activity record.
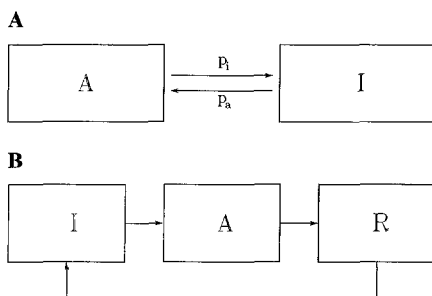
A

B

Fig. 1A, B. Schematic diagrams to illustrate the organization of activity patterns and definition of parameters. **A** The definition of p_i and p_a is given as the probability of becoming inactive or active given that the ant is currently either active (A) or inactive (I), respectively. **B** A schematic diagram of the activity of a single ant that passes from active (A), to refractive (R) to inactive (I)

Five ants were randomly chosen from each of ten colonies for measurement of spontaneity. Each ant was placed in a observation arena and allowed to acclimate for at least 1 h before testing. The ants were tested in a randomized complete block design in which one member of each colony was tested in each block before the next set of workers was tested. The order in which colonies were tested was randomized. Only one to two ants could be measured on any given day, therefore data were analyzed by block to test for any long-term change in activity over the course of the experiment. The colony effect was determined in order to test for differences among colonies in the measures of spontaneity. The response variables, the two probabilities, p_a and p_i, were analyzed as a multivariate anova (MANOVA) to control for possible correlated responses.

A second experiment was performed to determine the effect of age on spontaneous activity. After approximately 6 weeks 15 workers were selected to be retested for spontaneity. The workers were ranked by the ratio of the two spontaneity measures (p_a/p_i), and placed in either a high or a low category based on whether they were above or below the median. The worker which had the median ratio was not used in the analysis. The quantity p_a/p_i is directly related to the proportion of time that an individual was active. The workers were retested and the spontaneity measures were recalculated. The two response variables used in the MANOVA were the change in the probability of becoming active (change in p_a) and the change in the probability of becoming inactive (change in p_i).

Results

The measures of spontaneity are shown in Fig. 2. For these randomly chosen workers, the mean probability of becoming active, p_a, was 0.13 and the mean probabili-
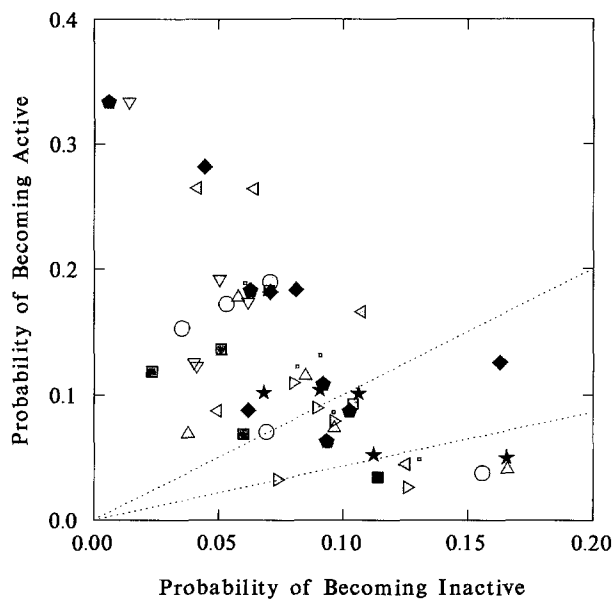

Fig. 2. The probability of becoming active, p_a, as a function of the probability of becoming inactive, p_i, measured for five worker ants from each of ten colonies. The identity of a colony is given by different *symbol shapes and shadings*. A *straight line through the origin*, on this plot, connects those individuals that are active for the same fraction of time. The *dotted lines* indicate where an individual that is active 0.5 of the time (*top line*) or 0.3 of the time (*bottom line*) would lie. Colonies are active over this range, although individual workers are not constrained to lie within this region
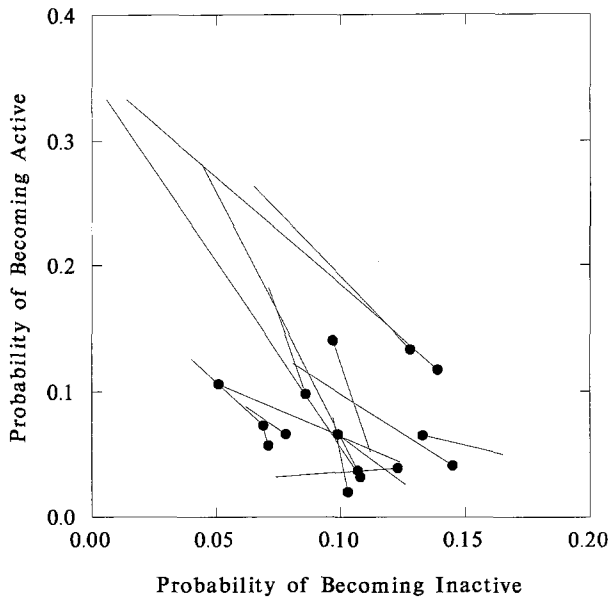
Fig. 3. The probability of becoming active and inactive for workers that were tested twice. The second measurements of p_i and p_a, (the *solid dots*) were made approximately 6 weeks after the initial measurements (represented as the *origin of the line segments*). There is a significant tendency for the probability of becoming active to be lower in the second trial

Fig. 4. The difference in the probability of becoming active as a function of the initial probability of becoming active. The linear relation between the amount of change and the initial value suggests an exponential relation between the probability of becoming active and age or time

ty of becoming inactive, p_i, was 0.08. The two probabilities were highly negatively correlated with one another ($r = -0.64$, $df = 49$, $P < 0.001$). The MANOVA results (Hotelling-Lawley trace $= 0.88$, $df = 26$, 68, $F = 1.15$, $P > 0.3$) showed that neither block nor the colony affected the measures of spontaneity. This conclusion is also reached when the data are analyzed with or without the blocks. The negative correlation between the two measures of spontaneity occurs in each of the colonies, as can be seen from the various symbols and shadings representing the colonies in Fig. 2. There is also no effect of either colony or block if the data for either measure of spontaneity is analyzed separately as a univariate AN-OVA.

When workers are classified simultaneously by the two measures of spontaneity and retested, there is a strong directional change (Fig. 3). The magnitude of the change in p_a and p_i is highly dependent on whether they were originally classified into the high or low group in their original level of spontaneity (MANOVA, Hotelling-Lawley trace $= 1.78$, $df = 2$, 11, $F = 9.81$, $P < 0.005$). Thus it appears that, although workers vary in their levels of spontaneity, the data are consistent with the interpretation that it is the age of the worker, not the colony of origin, which determines their level of spontaneous activity. If we consider p_a and p_i separately, there is a difference; the values of p_a decline, while the values of p_i do not change significantly (paired t-tests, $t = 2.25$ and 1.89 respectively, $P = 0.04$, 0.08, $df = 14$).

We can go at least one step further to show that there is a linear relation between the amount change in the probability of becoming active and the initial probability of becoming active (Fig. 4). This linear rela-
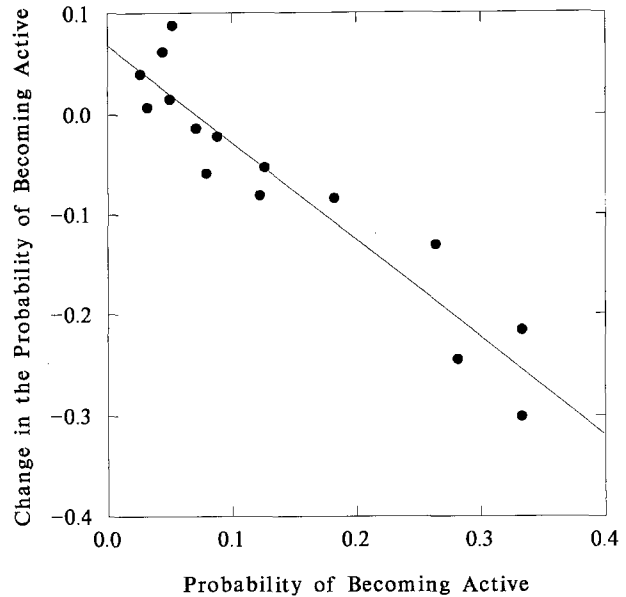
tion implies a negative exponential change in the value of p_a for a worker ant through time. The relation: $p_a(t) = p_a(0) \cdot e^{rt}$ should then describe the ontogenetic change in the probability of activity. A first estimate of the parameter r can be obtained from the slope of the relationship in Fig. 4, but since the time interval between the two tests for any worker is not a constant, I used the exact interval between measurements for each worker to obtain a more accurate measure of $r = -0.022$ per day.

Computer simulations

I constructed four different type of simulated ant colonies to explore the effect of the measured levels of spontaneity, variation in spontaneous activity and the effects of interactions on the production of periodic colony behavior and the level of colony synchrony. The basic features of these models are summarized in Table 1. In two of the models (A-I and A-R-I), the individual workers move between states (Active to Inactive or Active to Refractive to Inactive), but there is no a built-in tendency for the workers to become active periodically. In the second category of models (Type 0 and Type 1) the workers are assumed to have an inherent propensity to oscillate in activity. This second class of models incorporates periodicity in the activity of workers along with either Type 0 or Type 1 phase resetting (see below). In all models I assume that active workers encounter inactive workers randomly, a probability defined as p_{AB} per unit time. As the number of individuals which are active within the colony, N_a, changes, the probability that at

Table 1. The major characteristics and summary of the outcome of model colonies

Type of model colony	Pattern of isolated worker activity	Effect of interaction on inactive ant	Effect on colony dynamics
A-I	Random	Activity	Rapid approach to equilibrium
A-R-I	Random	Activity	Damped oscillations
Type 0	Periodic	Activity	Oscillations or continuous activity
Type 1	Periodic	Phase change depending on timing of interaction	Sustained oscillations with high colony synchrony

The pattern of isolated worker activity refers to the temporal pattern of activity of one of the model workers in the absence of interactions with other nestmates. The effect of interaction refers to whether an interaction with a model ant produces immediate activity in the modelled ants (in the A-I or A-R-I models), phase resetting which results in immediate activity in the Type 0 colony or a phase change that can reset the inherent periodicity to any other phase (Type 1). The effect on colony dynamics refers to the typical effect of a colony of such workers interacting in the given fashion given the experimentally determined range of parameters
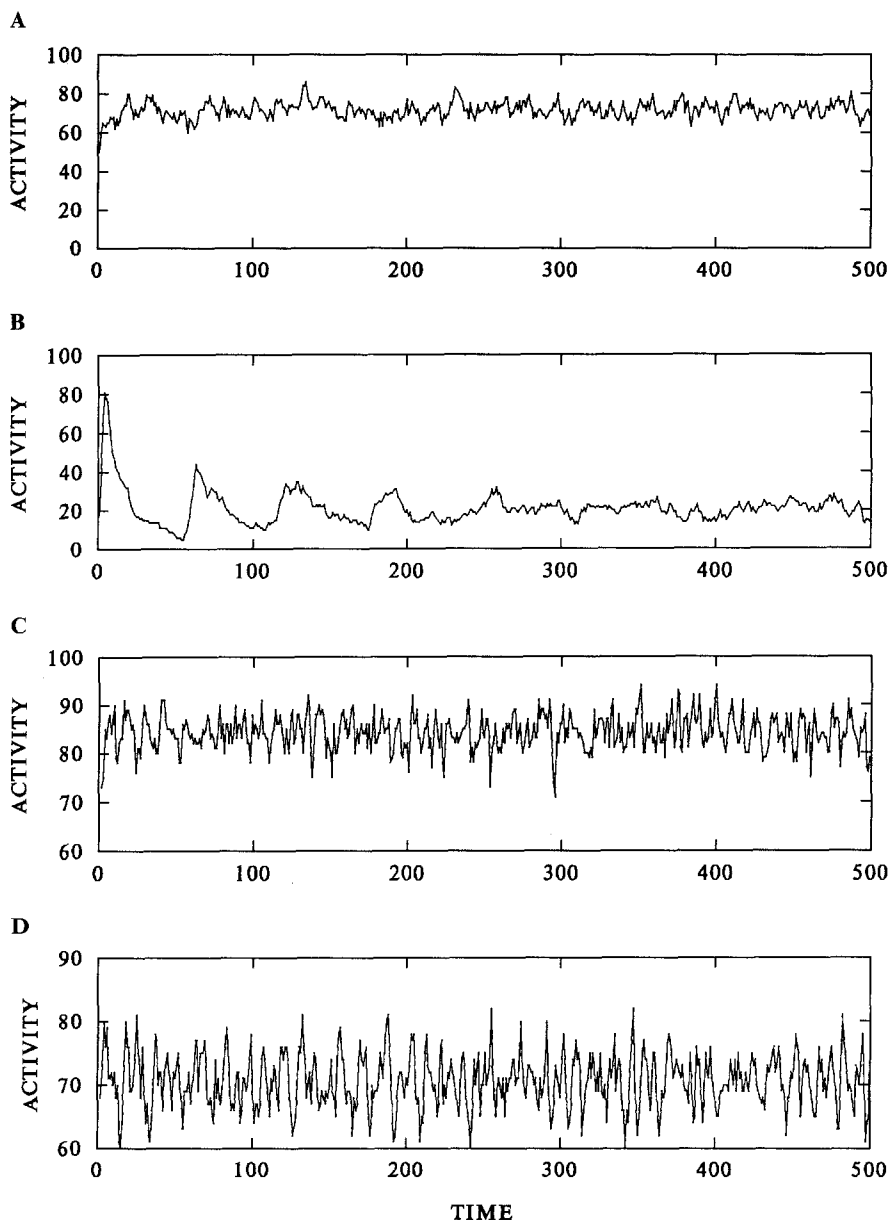

A

B

C

D

TIME

Fig. 5. A–D Simulated colony activity patterns. A A rapid approach to equilibrium in an AI model colony with 100 workers. The probability of interaction in 0.001. B Damped oscillations in an ARI model colony with 100 workers. C A colony composed of 100 workers with Type 0 resetting interactions. The probability of interaction is 0.005. D A colony of 100 workers with Type 1 resetting interactions. The probability of interaction is 0.005

least one active ant interacts with an inactive ant changes as:

$$p(\text{int}) = 1 - (1 - p_{AB})^{Na}.$$

If we assume a model colony composed of workers that behave as illustrated in the diagram of Fig. 1 a, then there are only two states, 'active' or 'inactive'. The worker can either become spontaneously active at some rate, p_a, or become active by interacting with another individual. An aggregate of such individuals will rapidly reach a equilibrium proportion active that depends on p_i, p_a, and the probability of an interaction, p_{AB} (Fig. 5 a).

The colony level of activity will oscillate only if there is a refractive period during which interactions with other individuals do not produce activity (see e.g. Fig. 1 b). An example of this is given in Fig. 5 b for a simulated colony of 100 workers which is followed for 500 time units. Ordinarily this sort of A-R-I model will exhibit damped oscillations to an equilibrium. As Goss and Deneuborg (1988) point out, one can obtain oscillations for a substantial interval but it requires a refractive period that is quite long. All of the individuals which are currently active must revert to the refractive state before any of the refractive ants become sensitive to interactions (Fig. 1 b). Sustained oscillations are maintained only when the refractive time is much longer (e.g. 5–10 times longer) than the amount of time spent active. Since, in this model, the probability of becoming inactive, p_i, given that an ant is active, is a constant, the distribution of intervals of activity will be a negative exponential. The expected time active is then $1/p_i$. The minimum measured values of p_i are in the range 0.01–0.02, indicating that the length of the refractive period would have to be much larger than 50–100 time units (at least 250–1000 time units). This corresponds to a required refractive period of perhaps an order of magnitude greater than the 15–40 min which is observed (Cole 1991 b); this value is not consistent with the observation that ants become active more frequently.

If we assume that the workers have some underlying tendency to oscillate, as I do in the Type 0 and Type 1 models, then the colony dynamics are fundamentally different. In both cases, if there is variation among workers, such that some individuals are active for a greater fraction of the time, then we will automatically produce a negative relation between p_i and p_a. I have simulated workers that have either a Type 0 resetting function or a Type 1 resetting function. The distinction between the Type 0 and Type 1 models refers to the effect of one worker on the activity of another worker. In both models workers are presumed to be able to influence one another's activity through interactions. In Type 1 resetting, an interaction between an active and an inactive worker can potentially reset the phase of the activity cycle of the inactive ant to any value depending on when, during the activity cycle of the inactive ant, the interaction occurs. In a Type 0 interaction the active worker can reset the phase of the inactive worker only to a limited range of possible values rather than to all possible ones. Winfree (1980, 1987 a, 1987 b) gives a more

complete description of the differences between Type 0 and Type 1 phase resetting. I have determined that interactions between _L. allardycei_ workers produce Type 1 resetting (Cole 1991 a). I used the function that I have experimentally determined in the simulations. For the Type 0 function, I caused the workers to become active immediately after an interaction. When the simulations are performed on colonies composed of workers with a Type 0 resetting function, there is a very poor synchronization of the activity of all the workers (Fig. 5 c). Synchrony cannot be achived because, although the workers cause one another to become immediately active upon interaction, the workers are all active for differing durations. When the Type 1 resetting function is used, far greater synchrony is observed and the simulated colony activity records are periodic (Fig. 5 d). When the colony is composed of independently cycling workers which have Type 1 interactions, I observe periodicity in colony activity as well as the negative relation between p_i and p_a.

In order to study the effects of the age of workers on colony activity pattern I performed simulations in which I varied the spontaneous activity levels of workers. Since the Type 1 model is the most realistic model of colony activity and generates the most realistic activity patterns, I used this model. Synchrony within the simulated colony is a function of both the probability of pairwise interaction between workers and the fraction of time, during the activity cycle of a single worker, that it is active. In general, the degree of synchrony in the colony (as measured by the ratio of the variance in the number of workers active to the mean number active) increases both with a decreasing probability of
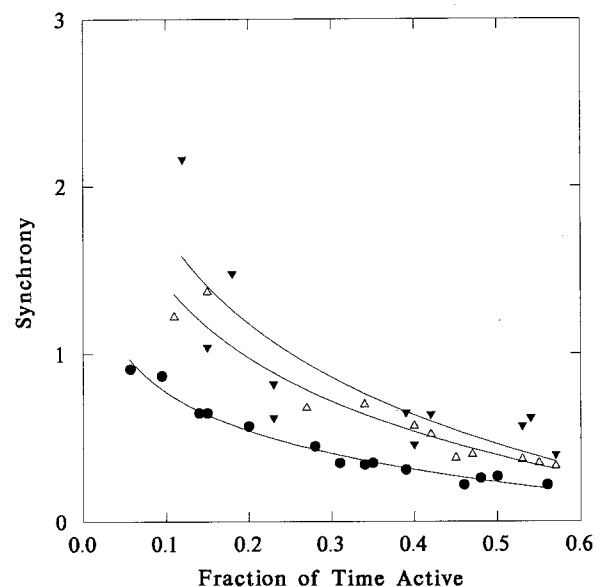

Fig. 6. The relation between the degree of colony synchrony and the fraction of time that a worker is active for simulated colonies. The degree of colony synchrony is defined by the variance of number of workers active divided by the mean number active. The symbols indicate simulations of differing probabilities of interaction: _solid circles_ = 0.01; _upright shaded triangles_ = 0.005; _inverted solid triangles_ = 0.001. The _lines_ are a regression of synchrony on log (fraction of time active)

interaction and a declining proportion of time that workers are active. Figure 6 shows the results of simulations involving workers which vary in these two parameters. Since the fraction of time that the workers are active is a function of worker age, simulation model results suggest that those colonies which are relatively older will be more synchronized.

In these simulations I not only vary the mean fraction of time that the simulated workers are active, but also the variance in the time active. After accounting for the difference among the simulations due to changes in the mean time active, the variance among workers in the time active contributes nothing to the residual variation in synchrony. The implications of the simulation results is that the age structure of the colony has little effect on colony synchrony. The average age of the workers is very important but the distribution of ages is not.

These simulations are not completely realistic and further work could improve the realism by the addition of at least three characteristics. (1) Not all workers have the same period of cycling. If workers are themselves close to periodic there is certainly variation in the period length of individuals. The impact of such a modification is likely to make the relation between colony synchrony and the mean time active somewhat less exact. (2) The activity variation of workers is probably not simple periodicity but rather chaotic (Cole 1991c). This is probably not a serious flaw in the models, because for long intervals a chaotic process can seem rather periodic. Ideally, however, it would be appropriate to develop a model that can start with the chaotic activity of workers and reproduce the periodic activity of colonies. There is evidence that in epidemic processes, a similar transition between chaotic and periodic processes occurs as one moves from smaller to larger cities (e.g. in measles, Sugihara et al. 1990). (3) All pairs of workers are presumed to have equal probabilities of interacting with one another. Clearly, the probability that two near neighbors will interact with another is greater; I have neglected any spatial component in these models although it may be important.

Discussion

The results of this study have implications for the organization of colony activity and for our ability to determine the tempo of activity of colonies from the actions and interactions of workers. The results of this study suggest that virtually all of the variation in the levels of spontaneous activity is due to variation among the individuals of a colony. The among-colony fraction of variation is estimated to be 13%, an amount not distinguishable from zero. The variation among individuals arises from age differences among the workers; the probability of spontaneous activity declines exponentially with age.

In order to understand the importance of the activity of individual workers for the functioning of colonies, it is important to relate the properties of individual workers to the properties of the intact colony. The proportion of time that an individual worker ant is active

F_A, can be measured directly from the activity records. Furthermore, it is easy to show that $F_A = p_a/p_a + p_i$, under the assumption that activity turns on and off a large number of times. Therefore, a set of individuals that is active for some particular fraction of time will be distributed along a straight line through the origin in a plot of p_a versus p_i (e.g. Fig. 2). Along this line, at a greater distance from the origin, individual workers are turning their activity on and off more frequently, but the overall fraction of time that they are active remains a constant along the line.

The average fraction time that a colony is active is roughly 0.3–0.5 (Cole 1991 b). I have indicated with dotted lines in Fig. 2 the boundaries of the region that is indicated by this range. The activity of individual workers is not constrained either to lie within this region or even to show a positive slope. If there was a strong selective advantage for the members of a colony to have some overall constancy in their level of activity, in order to produce a similar constancy in colony activity, this should result in a positive relation betwen p_a and p_i. By striking contrast, there is a highly significant negative correlation between the two quantities. Clearly, the absence of a positive relationship shows that workers will not spontaneously maintain the approximate level of activity in the colony.

Goss and Deneuborg (1988) have developed a model of the synchronization of activity in social insect behavior which shows that under certain circumstances periodic activity of aggregates of individuals can be obtained. This model is similar to those that have been developed for studying the dynamics of infectious diseases (e.g. May 1985; Olsen and Schaffer 1990); all we have to do is substitute infected for active, susceptible for inactive and immune for refractive. The dynamics of this system show damped oscillations toward an equilibrium value. Several stochastic elements prevent a perfectly stable equilibrium from being reached. First, interactions between individuals occur randomly so that the probability that an inactive ant is stimulated by at least one active ant is: $1 - (1 - p)^N$, where there are N active ants and p is the probability that an active ant interacts with any randomly chosen ant. The second form of randomness built into the model is in a random choice of the values p_i and p_a. For the simulations illustrated in Fig. 5b, c there is negative correlation between the values of p_i and p_a which are chosen randomly to lie within the measured range of values.

The consequences of characteristics of the spontaneous activity of workers for the activity pattern of colonies is illuminated by computer simulation. The first and major conclusion is that sustained oscillations are a characteristic outcome of a colony that is composed of workers that are themselves periodic and which have Type 1 phase resetting interactions. The second major conclusion from the simulations is that the average age of the workers within the colony is an important determinant of the degree of colony synchrony, but the distribution of ages is not important.

The relation between ability of a colony to synchronize their activity, the probability of interaction and the

probability of spontaneous activity allows several predictions to be made: (A) Artificial aggregates of exclusively older workers should be more synchronous than aggregates of exclusively younger workers. Older workers have much lower probabilities of becoming active than young workers and this should increase the ability of the aggregate to synchronize. (B) Aggregates of exclusively young workers should not be as synchronous as aggregates of workers of mixed aged. Increasing the fraction of individuals with smaller probabilities of becoming active should increase the synchrony in comparison to groups of individuals that only high levels of activity. (C) Increasing the probability of interactions, perhaps by crowding the colony should decrease the synchrony. Each of the predictions is capable of empirical test.

An isolated worker ant does not become active randomly, but tends to become active after a specific interval (Cole 1991a). This suggests that there is an underlying time scale to the activity of single workers. Type 1 phase resetting facilitates the development of colony periodicity. If the production of colony periodicity is essential to colony function, then the existence of Type 1 phase resetting would predispose a species to produce such periodicity. On the other hand, colony periodicity may be an incidental consequence of the fact of Type 1 phase resetting in worker interactions. It is interesting to speculate that the reason that certain species, such as *Tapinoma sessile*, do not exhibit colony cycles of activity is that interactions between workers result in Type 0 resetting.

The change in the probability of becoming active as a function of age should increase the synchrony of colony periodicity, but this is not sufficient to make it an adaptation. First of all, there has been no demonstration that synchrony of colony activity is functionally more efficient. There can be reasons to suppose that synchrony of activity may allow workers to coordinate their activities more exactly. However, it seems equally reasonable to suppose that synchronous activity causes workers to interfere with one another's actions more frequently. Even if synchronous colony activity were shown to be beneficial to the colony any trait, such as an age-related change in behavior that promotes colony synchrony, is not necessarily an adaptation. The origin of age-related changes in activity is not known and could be an unavoidable physiological byproduct of aging. Age related changes in behavior may promote colony periodicity, but they would exist apart from any effect on colony activity. If colony periodicity can be shown to be inefficient for colony function, a trait that promotes periodicity may still occur if it represents a physiological constraint.

Even if the generation of age-related changes in spontaneity cannot be ascribed to some adaptive category, the effect of changes in spontaneity can be conceived. Age-related changes in specific types of behavior such as brood care, trophallaxis, foraging and allogrooming have been documented, in detail, in a number of ants (Calabi et al. 1983; Wilson 1976; Calabi and Rosengaus 1988; Carlin and Hölldobler 1983; Mirenda and Vinson 1981). The frequency with which an individual worker performs any behavior clearly depends on the frequency with which the worker becomes active. A gradual decline in the probability of activity will probably induce a gradual decline the frequency with which any activity is performed and the frequency with which stimuli that release behavior are perceived. A thorough exploration of the activity of individuals is important if we are to obtain an adequate picture of the functioning of temporal castes.

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