

The Influence of Brood Type on Activity Cycles in *Leptothorax allardycei* (Hymenoptera: Formicidae)

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*We investigated the effect that different categories of brood had on the production of periodic activity within artificial aggregates of the ant, *Leptothorax allardycei*. Colonies of this species exhibit periodic patterns of movement activity with a period of approximately 20–30 min. Artificial aggregates of this species show that periodic activity appears gradually as the number of workers in the aggregate increases to 15 workers. In addition, it has been noted that the presence of brood with the workers makes the periodic activity more pronounced. In this paper we investigate the effect that four categories of brood had on the periodic activity of worker ants. Eggs, small larvae, large larvae, and pupae were tested with four different-sized aggregates of workers. We hypothesized that brood care is responsible for the increase in periodic activity and therefore that larvae (which require more tending) would be more effective at increasing periodic activity than eggs or pupae. Contrary to our expectations, eggs and both size categories of larvae were equally effective in enhancing periodicity in our experimental aggregates. Pupae, in contrast, were completely ineffective at enhancing periodic activity. We discuss some possible reasons for the differential effects of eggs, larvae, and pupae on the behavior of worker ants.*

KEY WORDS: periodic activity; cycles; ultradian rhythms.

INTRODUCTION

One of the central questions in social behavior concerns the mechanisms by which the actions of individuals within a social group produce a complex social

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variable we used was the log-transformed fraction of variability in the largest fourier component.

Because the results of previous work (Cole and Cheshire, 1996) showed that brood affected the amount of periodicity in an aggregate, we hypothesized that the effects of the brood on worker periodicity may result from brood care. We expected that the activity of an aggregate should reflect varying amounts of care that each type of brood required and that this might be reflected in the degree of periodicity. We planned three *a priori* contrasts: larvae would have a greater effect than eggs or pupae and large larvae would have a greater effect than small larvae.

RESULTS

Both the size of an aggregate, as a covariate, and the type of brood, as a classification variable, had significant effects on the production of periodic activity (Table I). Across all brood types the activity became more periodic with increasing aggregate size (Fig. 1). Within an aggregate size the type of brood influenced the extent of periodicity. Aggregates with eggs or larvae were more periodic than aggregates with pupae. In Fig. 2 we show the mean effect of brood type after aggregate size has been removed.

We tested our three *a priori* contrasts: larvae > eggs ($F = 1.76$, $df = 1,75$, $P > 0.18$), larvae > pupae ($F = 11.68$, $df = 1,75$, $P < 0.001$), large larvae > small larvae ($F = 0.007$, $df = 1,75$, $P > 0.90$). In contrast to our expectations, only pupae differed significantly in the amount of periodicity; aggregates with pupae reduced the magnitude of the largest Fourier component by over 40% compared to aggregates with eggs or larvae.

There was no interaction effect between the type of brood and the size of the aggregate. Although aggregates with pupae were far less periodic than aggregates containing other types of brood, there was still a significant effect of aggregate size on the magnitude of the largest Fourier component for pupae ($r^2 = 0.26$, $N = 21$, $P < 0.02$).

Table I. Analysis of Variance of the Type of Brood and the Size of the Aggregate on the Amount of Periodicity in the Aggregate

Source	Sum of squares	df	Mean square	F	P
Brood type	1.965	3	0.655	6.01	0.0010
Size	1.658	1	1.658	15.21	0.0002
Type * Size	0.260	3	0.087	0.80	0.50
Error	8.176	75	0.109		

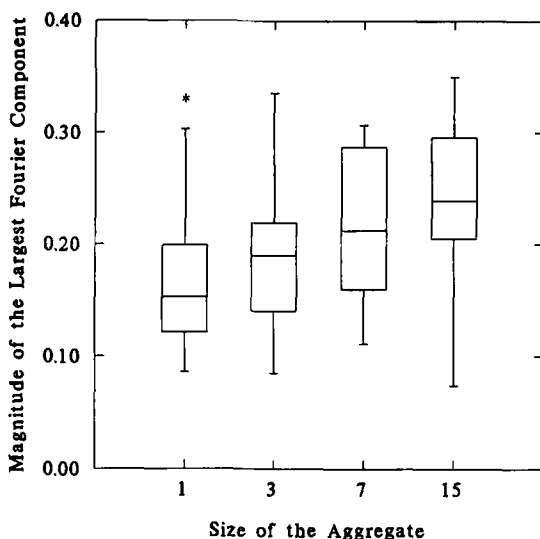


Fig. 1. Box plots showing the relation between the degree of periodicity in an activity record (fraction of the variation in the largest Fourier component) and the size of the aggregate. The central line is the median; the outer limits of the boxes represent the interquartile, or hinge, limits. The lines represent the median \pm 2.5 hinge limits and the asterisks represent single values outside a range of \pm 4 hinge limits.

DISCUSSION

The results obtained in this study corroborate the earlier results of Cole and Cheshire (1996), who found that the presence of brood caused periodic activity in aggregates to emerge gradually with increasing aggregate size. Although the effects of different types of brood on the magnitude of periodic activity differ substantially, the interaction term between the type of brood and the size of the aggregate is not significant. The effect of brood observed by Cole and Cheshire, who used mixtures of brood of different ages, is almost certainly due to the effects of the eggs and larvae. The mixed brood treatment is indistinguishable from that obtained with eggs or large larvae; the small larvae are marginally significantly more periodic than mixed brood. However, the effect that pupae have is not different from that observed when brood are absent.

These results suggest a distributed control mechanism (Gordon *et al.*, 1992). Although the larvae and eggs influence the amount of periodicity, aggregates of seven workers are not as periodic as aggregates of 15 workers. Increased periodicity emerges from the interactions of larger numbers of workers. If larvae

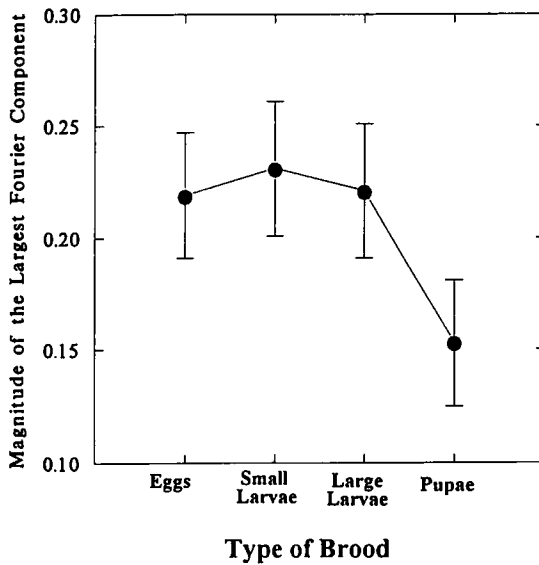


Fig. 2. The relation between the degree of periodicity in an activity record and the type of brood that are placed with the aggregate. We have plotted the least-square means \pm 2 SE.

were a central pacemaker, they should drive periodic activity at least as effectively in a group of 7 workers as in a group of 15.

We did not alter the ratio of the number of brood to workers in this experiment. We manipulated only the number of workers, which alters the brood-to-worker ratio. If this ratio influences the level of periodicity, then decreasing the brood-to-worker ratio increases periodicity among aggregates of the workers. The results of this study are unaffected, however, since (1) different types of brood influence periodicity in different ways, and (2) the effect changes gradually with gradual changes in the brood-to-worker ratio. The brood-to-worker ratio reaches a minimum in aggregates of 15 workers (1:1.33). In natural colonies of *L. allardycei* the brood-to-worker ratio is very nearly 1:1 for the brood apart from the eggs (Cole, personal observation). The number of eggs varies considerably among colonies.

Eggs and larvae obviously modulate the activity of workers, but they are not responsible for the production of periodicity *per se*. Why do eggs and larvae cause periodicity to develop differently from when brood and absent or pupae are present? If the amount of brood care is important in modulating the interactions among workers, larvae should have the largest effect. Although larvae require more tending than do pupae, it is not clear that eggs require more care

than pupae. However, this prediction was not upheld by the data. We do not know how both the eggs and the larvae are able to have such an effect.

Franks and Sendova-Franks (1992) and Stickland and Franks (1994) have examined patterns of activity within nests of other species of *Leptothorax* ants, with results that are particularly relevant. Franks and Sendova-Franks show that the brood are distributed across the nest in a manner that corresponds to the metabolic rate and thus the amount of labor that is required to tend a piece of brood. In other words, large larvae are more widely spaced than small larvae. Ants moving among the brood encounter the brood at roughly the rates that are required for efficient care. Stickland and Franks find that larger brood are located in areas within the nest that have higher levels of activity. The combination of the two phenomena provides a simple mechanism for the allocation of brood care effort. In *L. allardycei* the effect of small larvae and eggs is indistinguishable from that of large larvae on the generation of activity cycles. The allocation of effort is evidently a different problem from the generation of cyclic activity and it is not clear whether activity cycles are related to colony efficiency.

Although the mechanism by which the eggs and larvae influence the workers is not known, we can make some general predictions about this phenomenon. Mobile Cellular Automata models for the production of periodic activity in ant colonies have been developed by Solé *et al.* (1992), Miramontes *et al.* (1993), and Cole and Cheshire (1996). The models predict that the critical parameter for the production of periodicity is the effect that active ants have on one another. If an interaction between two active ants causes them to remain in the active state longer than without an interaction, that is sufficient to generate periodicity. In the terms of the model, we predict that the magnitude of the interaction term between two active ants is larger in the presence of the eggs and larvae than in the presence of the pupae or the absence of brood. That is, the effect of an interaction between two active ants is greater in the presence of larvae and eggs than in the presence of pupae. It is also possible that the presence of brood alters the frequency of interactions between workers. If the frequency of interactions between workers is altered in the presence of particular types of brood, there must be either fewer interactions among the workers when only the pupae are present or more interactions when other brood are present. We have no evidence that the presence of the pupae depresses the level of interaction among the workers. An increase in the rate of interaction among workers seems plausible for the larvae and was the basis of one of the *a priori* predictions. If the larvae are frequently tended, then workers who are doing the tending are frequently in the vicinity of the larvae. However, this explanation does not seem as plausible for the eggs. Eggs appear to require little care; in fact they can be hatched without care from the workers (Cole, personal observation). But the behavior of workers is different in the presence of eggs; aggressive interactions are more likely to be escalated in the presence of the eggs (Cole, 1988b). Aggressive

interactions are next most likely to be escalated in the presence of the pupae, reducing the plausibility of this explanation. Movement patterns, especially those of high-ranking workers, are altered in the presence of the eggs and the patterns of space use within nests are directly related to the position of the eggs (Cole, 1988a). Since space use and movement patterns are altered in the presence of the eggs in such a way as to keep workers in closer contact with the eggs, then it may result in an increase in the frequency of contact of workers when the eggs are present.

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