Social resilience in individual worker ants and its role in division of labour

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SUMMARY

This paper extends the notion of spatial efficiency in the organization of social insect colonies. We demonstrate for the first time that ants (individually marked workers in three colonies of *Leptothorax unifasciatus* (Latr.)) are not only faithful to particular positions within the nest, but they also quickly readopt these positions, relative to one another, when the colony emigrates to an entirely new nest site. This phenomenon, which we term social resilience, has implications for the role of learning in the maintenance of an efficient division of labour to which, in part, the great ecological success of social insects has been attributed. As we demonstrate with observations of another three colonies over a period of six months, workers change their positions asynchronously and different age cohorts are intermingled. Thus the reconstruction of colony spatial order cannot be accounted for by age-based task allocation (i.e. age polyethism), as at any one time the colony meshwork represents a heterogeneous mixture of different generations. These findings also show that ant colonies have a much more precise spatial structure and greater cohesion than previously assumed, and demonstrates the importance of detailed quantitative examination of the sociogenesis or developmental biology of these societies.

1. INTRODUCTION

Social insects are successful in most terrestrial ecosystems, and part of this success can be attributed to the efficiency that accrues from the division of labour within their colonies (Holldobler & Wilson 1990; Wilson 1990). Specialization into different tasks, however, is only likely to be effective if there is also spatial efficiency, i.e. if the tasks themselves are localized, hence travel time and other costs are minimized (Seeley 1983, pp. 31–36; Wilson 1985a). Even though *Leptothorax* workers often spend 70% of their time in inactivity, this does not imply that they should be less efficient when they are actively working (see Franks et al. 1990; Cole 1991; Hatcher et al. 1992). In addition, during a period of activity each individual could easily move many times from one end of the nest to the other, but they do not (Sendova-Franks & Franks 1993). From the specialization of workers into tasks, and the localization of tasks, it follows that spatial efficiency also includes the localization of the ants themselves. The idea of spatial efficiency is implicit in recent models suggesting that task allocation in social insects could be organized very flexibly on the basis of production lines (Tofts & Franks 1992; Tofts 1993). Here we test the hypothesis that following colony emigration workers will readopt their relative positions, because performance will be enhanced even further if the spatial pattern of tasks can be rebuilt and the relative positions of workers reconstructed after colony reassembly, so that learnt skills, for example, are not wasted.

Colonies of the ant *L. unifasciatus* have a sophisticated spatial organization. The brood tasks are localized as the brood is sorted in concentric circles with the smallest items in the middle and the largest larvae on the periphery, so that the brood with greatest need is fed or groomed first (Franks & Sendova-Franks 1992). Also, the movement of individual ants is restricted to particular parts of the nest (Sendova-Franks & Franks 1993). We have demonstrated that the brood is quickly resorted after emigration to a new nest (Franks & Sendova-Franks 1992). We now show that following an emigration the spatial order of the individual ants is re-established, and that this is not based on an association between age and task.

2. METHODS

We tested the hypothesis of social resilience by provoking emigrations in three colonies of the ant *L. unifasciatus* in which workers were individually marked with minute coloured paint dots on their gasters (see Sendova-Franks & Franks 1993). The colonies were housed in nests made from two microscope slides separated by a thin cardboard perimeter (see Sendova-Franks & Franks 1993). The emigrations were provoked simply by removing the roof of the current nest site whilst presenting another complete nest site nearby for the ants to colonize (see Franks et al. 1992). The positions and behavioural acts of workers were recorded from colour photographs taken at half-hour intervals 20 times per day for 5 days before and after the emigration. Each colony was allowed 24–48 h to recover from the disturbance of changing its nest. The position of each individual ant over each of the

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Figure 1. Correlations of the ranked spatial positions of all ants before and after the emigration. (a) Colony 1 ($r_s = 0.86$, $p < 0.01$ at 55 d.f.); (b) colony 2 ($r_s = 0.80$, $p < 0.01$ at 69 d.f.); (c) colony 3 ($r_s = 0.92$, $p < 0.01$ at 91 d.f.). $r_s$ is the Spearman's rank correlation coefficient, tested as an ordinary product-moment correlation coefficient because the sample sizes were greater than 10 in all cases (Sokal & Rohlf 1981, p. 607).

two observational periods was established as the median of the distribution of distances between the ant's positions and the centre of the egg pile.

To challenge the received wisdom that age polyethism might underlie this social resilience, we observed another three colonies with individually marked workers. This second set of observations was over a period of 6 months, without any disturbance of the colonies. Photographs were taken at most three times per day (avoiding fixed hours) so that there were at least 50 photographs of each colony over a period of one month. Again the position of each individual ant over

Figure 2. Correlations of the ranked brood care frequencies of all ants before and after the emigration. (a) Colony 1 ($r_s = 0.86$, $p < 0.01$ at 55 d.f.); (b) colony 2 ($r_s = 0.67$, $p < 0.01$ at 69 d.f.); (c) colony 3 ($r_s = 0.78$, $p < 0.01$ at 91 d.f.). The identities of all ants performing brood care were recorded from each photograph. Subsequent ranking of individuals was based on the total count of brood care events per observation period (i.e. set of photographs) before and after the emigration. The number of symbols in each plot is smaller than the number of workers (equal to the number of degrees of freedom plus 2) in the colony, because some workers share the same rank and are represented by the same symbol.
Figure 3. Correlations of ranked outside-the-nest frequencies for all ants before and after the emigration. (a) Colony 1 ($r_s = 0.80$, $p < 0.01$ at 55 d.f.); (b) colony 2 ($r_s = 0.60$, $p < 0.01$ at 69 d.f.); (c) colony 3 ($r_s = 0.77$, $p < 0.01$ at 91 d.f.). The identities of all ants outside the nest were recorded at the time each photograph was taken. Subsequent ranking of individuals was based on the total count of outside-the-nest events per observational period before and after the emigration.

3. RESULTS AND DISCUSSION

The results demonstrate that the positional and behavioural ranks of individuals before the emigration correlate significantly with their positional and behavi-
oural ranks after the emigration (figures 1–3). It is clear that the spatial and social order of the ants is rebuilt with great fidelity.

How can this be achieved? A traditional explanation, which we can demonstrate to be false, might involve: (i) age polyethism (in species composed of monomorphic workers it is a widely held view that division of labour is based on the principle of age, so that the youngest workers look after the youngest brood while the oldest workers do the most dangerous task of foraging) (Wilson 1985b); and (ii) the known brood spatial structure in these Leptothorax colonies (Franks & Sendova-Franks 1992). According to this scenario, the youngest workers will be nearest to the centre of the colony and the oldest furthest away. In this scheme the spatial structure of the adult workers before emigration could be rebuilt after emigration on the basis of the age structure to which it is directly related.

However, empirical results suggest that age structure is unlikely to be sufficient for the workers to re-establish their positions relative to one another following an emigration. Observations of another three colonies over a period of 6 months show that the spatial structure of the workers does not correspond to their age structure (figure 4; see also Lenoir (1979) for findings with the same implications in the ant Lasius niger). The positional ranks of the workers do not remain the same over the 6 month period, i.e. their relative positions are not maintained and different age cohorts would eventually intermingle even if they were segregated at the beginning of the experiment. As a result, the age structure of workers is dissociated from their spatial structure and each task is addressed by ants of different age groups. Thus neither the mechanism of task allocation nor the mechanism for rebuilding the colony social structure after emigration can be based on the principle of age.

The production line model of task allocation (Tofts & Franks 1992; Tofts 1993), however, can redistribute the appropriate number of ants to each task after colony reassemblage and can also accommodate differences among individual workers. For example, in honey bees, developmentally based variations in juvenile hormone titres (Huang & Robinson 1992; Robinson 1992) and related physiological changes, genetic heterogeneity (Frumhoff & Baker 1988; Robinson & Page 1988; and in ants, Stuart & Page 1991) and learning (Seeley 1985) may all play a role in individual task susceptibility. Deneubourg et al. (1987) have suggested that learning may also play a role in task allocation in ants. In the case of the rebuilding of the spatial organization of L. unifasciatus colonies, it is possible that workers use information they have learnt on one or more of the following: (i) the identity of their neighbours; (ii) particular types of brood odours (Champalbert 1986; Jaisson & Fresneau 1988; (iii) their own distances from the queen; and (iv) the task they were performing. Alternatively, they may sort themselves according to activity levels, the least active workers at the centre and the most active ones on the periphery. Perhaps such behaviour is crucial for re-establishing quickly the appropriate distribution of individuals into a production line with efficient task allocation in a new nest site.

Franks & Scovell (1983) have reported dominance hierarchies in leptoethracine ants in which there was a correlation between an individual’s rank in the dominance order and its spatial position. High-ranking workers were closest to the queen at the centre of the nest, and lowest ranking workers were more peripheral. We do not believe that dominance is the basis of the positions taken by workers in the L. unifasciatus colonies we have studied because in all the colonies queens were present and there was no overt aggression among the workers.

Colonies of the ant L. unifasciatus clearly possess social resilience and cohesion beyond the simple aggregation of individuals. Each worker ant has its own place in the social meshwork and in the colony’s production lines. Spatial efficiency is such that after perturbation individual workers return to their places and little time should be wasted acquiring new skills.

Our findings open up the possibility of studying sociogenesis (Wilson 1985a) in much more detail, in particular the topology of task allocation in social insect colonies and its relation to learning by individual workers.

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