TASK ALLOCATION IN ANT COLONIES WITHIN VARIABLE ENVIRONMENTS (A STUDY OF TEMPORAL POLYETHISM: EXPERIMENTAL)

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We briefly review the literature on the division of labour in ant colonies with monomorphic worker populations, and show that there are anomalies in current theories and in the interpretation of existing data sets. Most ant colonies are likely to be in unstable situations and therefore we doubt if an age-based division of labour can be sufficiently flexible. We present data for a type of small ant colony in a highly seasonal environment, concentrating on individually marked older workers. We show that contrary to expectation such workers undertake a wide variety of tasks and can even retain their ability to reproduce, even whilst younger workers are actively foraging. Our analysis shows that old workers occupy four distinct spatial stations within the nest and that these are related to the tasks they perform. We suggest that correlations between age and task in many ant colonies might simply be based on ants foraging for work, i.e. actively seeking tasks to perform and remaining faithful to these as long as they are profitably employed. For this reason, employed older workers effectively displace unemployed younger workers into other tasks. In a companion paper, Tofts 1993, Bull. math. Biol. develops an algorithm that shows how foraging for work can be an efficient and flexible mechanism for the division of labour in social insects. The algorithm creates a correlation between age and task purely as a by-product of its modus operandi.

**Introduction.** One reason for the success of social insects is that social life permits a division of labour which can greatly enhance efficiency (Hölldobler and Wilson, 1990; Wilson 1990). Tasks are divided among the members of the society so that individuals specialize for considerable periods in certain roles. Such specialization might mean that individuals can gain particular skills through practice or simply seek work in certain spatial locations so that time and energy consuming movement between widely distributed tasks is minimized. But specialization carries with it the possible cost of a lack of flexibility, which might be important especially in unstable environments.

An age-based division of labour would appear to be inherently inflexible. Nevertheless, the concept of an age-based division of labour dominates current interpretations of how tasks are allocated among ants of one and the same physical caste (i.e. in monomorphic work forces). This concept is central both to West-Eberhard’s hypothesis (1979, 1981) for the origin of a centrifugal system of task allocation and to Wilson’s (1985; see also Oster and Wilson,
1978) theory of adaptive demography. In a centrifugal system young workers
stay in the safe confines of the nest and as they age they do tasks that are further
and further from the centre of the nest. In this way the oldest workers, who are
closest to the end of their physiological lives specialize in the dangerous task of
foraging, where life expectancy is short due to encounters with predators and a
hazardous environment. Wilson’s (1985) hypothesis of adaptive demography
states that since the demographic structure of worker population determines a
colony’s division of labour and hence the inclusive fitness of its members, it is
likely to be directly influenced by selection. By contrast, in populations that are
not highly social, demographic structure is more likely to be an epiphenome-
non of selection acting on individuals (Wilson, 1985). West-Eberhard (1979,
1981) has suggested that the origins of the centrifugal system of temporal castes
are associated with selection at the level of the individual. Younger workers,
who may be able to lay their own viable eggs and have greater reproductive
value than their older sisters, stay near the brood in the safety of the nest. In
Hymenoptera, males develop from unfertilized, haploid eggs—so certain
uninseminated workers can produce sons (see Bourke, 1988). Only when
worker fertility declines, as they age, do they switch to serving their kin by
undertaking dangerous foraging tasks.

These hypotheses of West-Eberhard and Wilson, both based on the notion
that there is a tight association between age and task, may have some
explanatory value for colonies in relatively stable social and ecological
environments. However a tight association between age and task is more likely
to be a problem than a solution in unstable situations, such as might occur in
highly seasonal or unpredictable environments or within small colonies.

Consider a small colony producing one generation per year. The brood
profile will change throughout the active season and so will the tasks. In the
case of a crisis, losses of 10 workers might be 10% or more of the total worker
population. In addition, worker reproduction is common in small colonies
(Bourke, 1988; Franks et al., 1990a), but as we show here it is not always tightly
coupled to age. For all these reasons, it would seem a necessity that ants
respond flexibly to the changing situation and needs of their society.

Much recent evidence shows that the division of labour in a variety of social
insects has some flexibility. Certain individuals can change their tasks in
response to the changing needs of the society (Calabi, 1988; Gordon, 1989).
However, this flexibility is still mostly interpreted as a mechanism for fine
tuning an age-based division of labour. The fundamental problem is that
observed relationships between age and task are correlations and do not
establish cause and effect.

Here we begin to address the question: are the observed (and often weak)
associations between age and task simply the result of systems for task
allocation that are fundamentally flexible and not based on aging? Such systems