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SHORT COMMUNICATIONS

Temporal polyethism in social insects is a developmental process

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Interdisciplinary studies in animal behaviour are on the rise because of a growing awareness that behaviour is best understood by integrating analyses at multiple levels of biological organization (e.g. Stamps 1991; Crews 1992; Ketterson & Nolan 1992). For example, new insights into social insect behaviour, especially short-term changes in worker behaviour associated with the division of labour, have been gained by considering insect societies as self-organized complex systems (e.g. Deneubourg & Goss 1989; Page & Mitchell 1991; Gordon et al. 1992). Division of labour in many insect societies is also based on long-term, age-related, changes in task specialization by workers, i.e. 'temporal polyethism'. A recent model of temporal polyethism (Tofts 1993; summarized in Tofts & Franks 1992) is intriguing because it is consistent with an emerging view of an insect society as a self-organized complex system. The following critique of this model, however, illustrates that complex systems, such as insect colonies, need to be studied with an approach that integrates descriptions of higher-level patterns with a more comprehensive treatment of underlying mechanisms.

Tofts & Franks (1992) suggest that temporal polyethism in ants emerges simply as a consequence of competition among workers for employment. In their 'foraging-for-work' model, new adult workers compete with older workers for a job in the broodnest. This results in centripetal migration of the older workers from the broodnest to the periphery, from which they eventually begin to forage outside the nest. Tofts & Franks (1992) argue that temporal polyethism in ant and honey bee societies is an epiphenomenon and not an organizational principle that is based on a causal link between worker age and task performance. However, their model is rooted in an incomplete portrayal of temporal polyethism and is not consistent with studies of some ants and bees, and especially with recent behavioural, physiological and genetic analyses of the honey bee, *Apis mellifera.*

Tofts & Franks (1992) assert that temporal polyethism is a 'highly static' system and then question how a division of labour determined by worker age can function because physiological ageing is slow relative to changing colony needs. However, ants and bees have been shown to accelerate, delay, or reverse their behavioural development in response to changing colony conditions (reviewed by Lenoir 1987; Robinson 1992), sometimes in as little as 24 h (Robinson et al. 1992). These responses are often accompanied by changes in exocrine gland secretion (see Oster & Wilson 1978). Delayed changes in behaviour, due to time-dependent physiological changes, may stabilize colony behaviour by reducing inappropriate mass action responses to transient environmental stimuli.

Individuals do perform different tasks in different regions of the nest, as specified in the foraging-for-work model, but this model fails to appreciate the 'urban' nature of some large insect societies. In these societies, a dense population of workers often is confronted simultaneously with stimuli that elicit the performance of a variety of different tasks, some performed at different ages. Tofts & Franks (1992) apparently dismiss the possibility that age-related response thresholds play a causal role in task choice in favour of the simpler foraging-for-work algorithm. However, social insect workers often respond much differently to the same stimuli as they age (see Lenoir 1987; Jaisson et al. 1988; Robinson 1992), suggesting that an underlying developmental process is at work. For example, disturbing a honey bee colony

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by dropping a brick on it provokes a defensive response only by older colony members (Breed et al. 1990). Laboratory studies have shown that sensitivity to alarm pheromones increases with increasing worker age (Collins & Rothenbuhler 1978; Robinson 1987) and age-related increases in juvenile hormone contribute to these developmental changes in response thresholds (Robinson 1987). Age-related increases in juvenile hormone also are associated with the onset of foraging behaviour (Robinson et al. 1989), presumably because of changes in response thresholds to foraging-related stimuli. A causal role for juvenile hormone in the ontogeny of foraging behaviour has been demonstrated for honey bees (see Robinson 1992) and *Polybia occidentalis* wasps (O'Donnell & Jeanne 1993): young workers given hormone treatments become precocious foragers.

Tofts & Franks (1992) admit that their model generates weak temporal polyethism, similar to what is observed in some ant species. The model lacks generality, however, because other ants, termites, and bees can exhibit very strong temporal polyethism (see Lenoir 1987; Jaisson et al. 1988; Robinson 1992). Dramatic effects of temporal polyethism have been observed in honey bee colonies (Page et al. 1992). In experimental colonies composed of 8- to 13-day-old workers, the addition of a cohort of younger bees caused many of the older bees to become foragers (consistent with the foraging-for-work model), but age differences among these older bees, some as little as one day, produced significant differences in the probability of becoming a forager, with older bees more likely to forage than younger bees. After removing the younger cohort, bees with the least amount of foraging experience were the most likely to 'revert' and perform within-nest activities. This study, and others (e.g. Calderone & Page 1988, 1991) also demonstrated genotypic differences in rates of behavioural development that affect temporal polyethism. These results demonstrate strong effects of worker behavioural development on division of labour, effects that are not predicted by the foraging-for-work model. Another result not predicted by this model is the dramatic and persistent increase in unloading time experienced by returning nectar foragers in a honey bee colony after experimental removal of all the 'receiver bees' over a 2-day period (Seeley 1989); this finding suggests that there was a developmental lag in the replacement of receiver bees.

Tofts & Franks (1992) propose that nest structure results in the ordering of tasks in an insect colony, but anecdotal evidence argues against a strictly causal relationship between the two variables. Studies of temporal polyethism in honey bees often begin when a cohort of young workers is placed into a hive, for convenience often at the top where honey is stored. This region is usually occupied by older bees performing food storage tasks prior to initiating foraging activities (Seeley 1982). These young bees end up in the central region of the nest within hours of introduction, performing brood-rearing activities like other individuals their age. If these young bees forage for work, they are foraging for brood-rearing work!

We agree with Tofts & Franks (1992) that a worker's chronological age per se is not an important determinant of task performance. However, a worker's physiological age, or state of behavioural development, is. Behavioural development in honey bees is regulated by levels of juvenile hormone, which in turn are influenced by worker genotype (see Page & Robinson 1991; Robinson 1992) and the environment (Robinson et al. 1989), especially colony age structure (Huang & Robinson 1992). In other words, while we agree that a worker's occupation is dependent, in part, upon environmental conditions, evidence from honey bees indicates that environmental effects on behaviour occur via changes in a (hormonally mediated) programme of behavioural development. Learning and other forms of experience, such as the effects of unemployment hypothesized by Tofts & Franks (1992), also may play a role.

In summary, the foraging-for-work model provides a simple explanation of temporal polyethism that is consistent with the behaviour of some, but not all, social insects. It cannot serve as a general model because it cannot account for the strong, but flexible, temporal polyethism exhibited by other species. It also is not consistent with the current understanding of the mechanistic basis of temporal polyethism in one species, the honey bee. We believe that division of labour in social insects can best be understood by an approach that combines theories of self-organization with an appreciation of temporal polyethism as a developmental process that has physiological and genetic determinants. This approach is the basis of a new model of temporal polyethism (Huang & Robinson 1992).

In the study of complex systems there is a synergism between studying higher-level patterns and lower-level processes that should not be ignored. Or, as Churchland & Sejnowski (1992) wrote in reference to studies of another complex system, the brain, 'Research at one level provides correction, constraints, and inspiration for research at (other) levels.'

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