Caste and division of labour have formed the core of the study of the organization of insect societies for the past four decades. Indeed, the description and analysis of task allocation between colony members are fundamental to understanding the organization of a complex biological system whose functioning depends upon the behavioural integration of a potentially large number of individuals. Recent research has emphasized the dynamic nature and fluidity of task allocation (Gordon 1989, 1995), the role of self-organization (Page & Mitchell 1991) and the physiology and genetics of task partitioning (Page & Robinson 1991; Robinson 1992). The study of caste and division of labour, however, has historically been established in the evolution and ecology of social insects (Oster & Wilson 1978; Calabi & Traniello 1989; Hölldobler & Wilson 1990; Schmid-Hempel 1992; Tschinkel 1993; Beshers & Traniello 1994). Although the basic tenets of caste theory were first formulated to explain the origin and significance of physical castes, caste theory has also provided a conceptual framework to examine the adaptiveness of age-based division of labour, although this aspect of caste theory has rarely been tested and is thus poorly understood (Schmid-Hempel 1992). The theory predicts that the behavioural characteristics of individuals, including worker behavioural development, have been shaped as part of the overall evolutionary design of a colony of a given species. As Hölldobler & Wilson (1990, page 312) have stated, ‘Each species has its own distinctive pattern of temporal polyethism’. (In this commentary we consider the terms ‘age-based division of labour’ and ‘temporal polyethism’ to be interchangeable, and follow the definitions and usage of Oster & Wilson (1978) and Hölldobler & Wilson (1990). We also believe that these terms and the social phenomena they describe adequately cover aspects of worker behavioural development and task performance flexibility, and therefore we prefer not to adopt Franks’ (1994) definition of temporal polyethism.)

The recent dialogue between Robinson et al. (1994) and Franks & Tofts (1994) provides a critical discussion of theoretical, genetic and physiological analyses of age-based division of labour; their debate on temporal polyethism relies on socially advanced hymenopteran species as model systems. The genetic and physiological approaches described by Robinson et al. (1994) focus on the mechanisms of polyethism and are relevant to the evolution and ecology of division of labour, because they detail the proximate basis of what appear to be adaptive patterns of behavioural development. Franks & Tofts (1994), in contrast, suggested that the behavioural schedules commonly identified as age polyethism emerge as a consequence of the rules workers follow in their search for tasks to perform in a colony. Specifically, they attempted to identify a simple regulatory process involving nest design and the spatial array of tasks to be carried out to explain polyethism (Tofts & Franks 1992; Sendova-Franks & Franks 1993; Franks & Tofts 1994; reviewed in Bourke & Franks 1995). Provocatively asserting that age polyethism ‘is a myth’ and that the relationship between age and task performance is not causal, Franks (1994) advocated a paradigm shift in the study of polyethism.

We argue, as have other researchers, that patterns of division of labour in the social insects appear to be highly variable and species-specific. And, as has long been recognized, we acknowledge that division of labour may be related to the
spatial array of tasks faced by a colony (Wilson 1976). The pattern of division of labour might depend upon worker development and reproductive potential, nest architecture, colony size, foraging ecology and other characteristics, and depending on the species, may or may not involve age-related behaviour and/or flexible aspects of task performance by workers (Oster & Wilson 1978; Wilson 1985). Interspecific variation in colony organization thus may be more accurately accounted for by historical and ecological factors than by a simple rule such as the ‘foraging for work’ algorithm. Franks & Tofts (1994) and Tofts & Franks (1992) failed to acknowledge the diversity and significance of the individual and colony-level behavioural profiles that characterize different social insect species, and thus neglected the role of phylogeny as a constraint and the importance of ecology as a selective force in the organization of temporal division of labour. Given the diversity of social systems in insects, it would indeed be difficult for one organizational principle to have widespread phylogenetic application. In their rush to champion their model and herald what they claim as its broad significance, Tofts & Franks (1992) proceeded straight from the eusocial Hymenoptera to naked mole-rats without as much as a token evolutionary nod to the termites (Order Isoptera), a group phylogenetically unrelated to the Hymenoptera but strongly convergent in many aspects of sociality, including their systems of physical polymorphism and temporal polyethism. For example, the caste systems of the African fungus-growing termite Macrotermes parallel those of the Neotropical fungus-growing ant Atta (Wilson 1980; Bardertscher et al. 1983; Gerber et al. 1988). The socio-ecological similarity between ants and termites raises questions concerning the organization of division of labour and the applicability of the foraging for work to isop teran species.

The foraging-for-work model assumes that the ordering of tasks by workers ‘arises naturally from the structure of nests, and simplistically is just the distance at which the task can be performed from the centre of the brood pile’ (Tofts & Franks 1992, page 342; see also Tofts 1993). Termite species vary in nest structure and the degree of spatial segregation of tasks. Some termite species (the lower termites) have a ‘one-piece nest’, forming their colonies within their wood food source, but other species build elaborate mounds or carton structures and have a distinct food/nest separation (Abe 1987). One-piece-nest species, such as the dampwood termite, Zootermopsis angusticollis, provide an opportunity to examine division of labour in a species in which it is extremely easy to measure the spatial structure of some important colony activities. In this species, there appears to be no segregation of brood care and foraging, which in ants and higher termites occur inside and outside of the nest, respectively, because in Z. angusticollis the nest itself is the colony’s food source. Yet there is a nest ‘centre’ where the primary reproductives and eggs are found, and there appears to be a potential for task displacement because maturing larvae may eventually leave the labour force as they differentiate into alates and disperse. Developing larvae could move centrifugally from the nest centre to perform non-brood care tasks such as excavation, repair and feeding at the periphery of the nest and show some form of division of labour, but these termites seem to show no temporal polyethism (Rosengaus & Traniello 1993). First- and second-instar larvae are virtually inactive, and individuals from the third to seventh instars perform all colony labour with no apparent bias towards age or size. This study of termite polyethism was not designed as a specific test of the foraging for work algorithm, but results do offer a reasonable first approximation of the form of division of labour in a lower termite. The nutritional ecology of Z. angusticollis, among other factors, may provide insight into the social organization of this species (Rosengaus & Traniello 1993).

Another concern in the evolution of polyethism in termites is that Z. angusticollis and other lower termites do not have a truly non-reproductive worker caste; larvae may eventually attain reproductive status in the parent nest (Noirot & Pasteels 1987). This reproductive plasticity could cause individuals to remain near the egg pile (where they might deposit their own eggs) and perform brood-related tasks as they age, rather than provide labour at other sites in the nest. West-Eberhard (1979, 1981) offered a similar argument concerning temporal polyethism in the social Hymenoptera, but suggested that in this group worker reproduction should result in a bias towards brood care in young adults that have functional ovaries. Because reproductive competency in termites increases with age, older larvae
may be predisposed to brood care in some isopteran species.

Although insufficient information exists to permit conclusions about the effect of reproductive plasticity on task performance in the Isoptera, a comparison of the lower and higher termites suggests that worker sterility and temporal polyethism may be linked. As discussed above, termites in the lower sub-families construct one-piece nests; an individual termite retains the ability to reproduce through its life. In at least one of these species, labour does not appear to be organized through temporal castes (Rosengaus & Traniello 1993). Termite species in the higher subfamilies have separate nesting and feeding habits, a true sterile worker caste and well-developed age-related division of labour (Jones 1980; Abe 1987; Noirot & Pasteels 1987; Gerber et al. 1988; Higashi et al. 1991). The loss of reproductive options among workers and/or the separation of nest from food source therefore appear to have been prerequisites for the evolution of termite polyethism. Perhaps the separation of nest and food source created a spatial predisposition for the centrifugal movement of workers through task space as predicted by Tofts & Franks’ model. However, age-related behaviour in termites may have depended on nest stability and the evolution of worker sterility, rather than emerging as an inevitable by-product of workers ‘foraging for work’. A comprehensive explanatory framework for the evolution of temporal division of labour in termites thus appears to require an understanding of termite reproductive biology and nesting ecology.

In addition, the so-called ‘primitive’ ant species appear to have biological characteristics that offer important insights into their patterns of labour organization. Moreover, some species have attributes that appear to satisfy the assumptions of the foraging-for-work model but do not seem to provide support for it. The ponerine ant *Amblyopone pallipes* is a case in point. This species lacks age-based division of labour (Traniello 1978), yet has a nest structure that is sufficiently complex to generate the pattern of polyethism predicted by Tofts & Franks’ algorithm. In contrast to most ants, workers begin to forage after eclosion. In *A. pallipes*, foraging is part of brood-care behaviour because larvae are directly provisioned with prey, and the same worker performs both tasks. The Tofts & Franks’ task displacement model does not explain this atypical pattern of task performance in *A. pallipes* and other ‘primitive’ ants as effectively as arguments that concern demographic constraints, foraging specialization and the retention of ancestral behavioural traits (Traniello 1978; Traniello & Jayasuriya 1985; Jaisson et al. 1992). Also, the degree of sociality itself may play a role in generating division of labour in *A. pallipes* and other ancestral ant species. For example, *Nothomyrmecia macrops* is considered to be the closest among living ant species to the ancestral ants; individuals infrequently interact in *N. macrops* colonies, and no age-based division of labour exists, although colonies have a nest centre with brood, and workers forage outside the nest (Jaisson et al. 1992). At what level of social complexity should we expect tasks to allocate workers? We do not draw attention to the biology of the above-named species simply to illustrate curious variation and an apparent lack of congruence with the foraging-for-work model, but to accentuate the need for a comparative socio-ecological approach in the study of division of labour.

Robinson et al. (1994) noted that behaviour is best understood by integrating analyses at multiple levels of biological organization. In the case of division of labour, the results obtained at different levels should be synthesized and reconciled in light of the evolution and ecology of each species to form an understanding of the how and why of polyethism. There is strong evidence in favour of a causal relationship between worker age and task performance (Calabro 1996) and there is ample documentation of the genetic and hormonal correlates of behavioural development in some social insect species (Page & Robinson 1991; Robinson 1992; Robinson et al. 1994). There is also evidence to show that behavioural development is flexible and task allocation is socially regulated (Hölldobler & Wilson 1990; Gordon 1995). Empirical research on the ecology of division of labour indicates that worker age distributions are not necessarily associated with task schedules, and that the demographic and flexible behavioural components that contribute to colony-level patterns of division of labour may be selected over evolutionary and ecological time scales (Calabi & Traniello 1989). Realistic models and simulations and developmental studies of task allocation can
complement physiological and etho-ecological approaches and perhaps offer alternative hypotheses to explain temporal polyethism. To fully achieve the integrative approach that is of current interest in the study of biological complexity, however, the role of ecology and historical constraints must be recognized. We believe that such a biological approach will continue to lead the search for general principles of the organization of division of labour.

Describing the autonomy of biology in relation to the physical sciences, Mayr (1982, page 36) suggested that biologists should view the application of physical models to biological systems with great caution. He noted that when in the past naturalists and other biologists have stressed the importance of uniqueness and history in biology, their efforts were erroneously ‘brushed aside as bad science’ by physical scientists and that ‘the biological approach was considered inferior because it lacked mathematical form’. We do not doubt that simple models can be valuable in understanding the dynamics of a complex system such as an insect society, if one is aware that the system itself is biological and is likely to be more complex and varied than a model.

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