Individual *versus* social complexity, with particular reference to ant colonies

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ABSTRACT

Insect societies – colonies of ants, bees, wasps and termites – vary enormously in their social complexity. Social complexity is a broadly used term that encompasses many individual and colony-level traits and characteristics such as colony size, polymorphism and foraging strategy. A number of earlier studies have considered the relationships among various correlates of social complexity in insect societies; in this review, we build upon those studies by proposing additional correlates and show how all correlates can be integrated in a common explanatory framework. The various correlates are divided among four broad categories (sections). Under 'polyphenism' we consider the differences among individuals, in particular focusing upon 'caste' and specialization of individuals. This is followed by a section on 'totipotency' in which we consider the autonomy and subjugation of individuals. Under this heading we consider various aspects such as intracolony conflict, worker reproductive potential and physiological or morphological restrictions which limit individuals' capacities to perform a range of tasks or functions. A section entitled 'organization of work' considers a variety of aspects, e.g. the ability to tackle group, team or partitioned tasks, foraging strategies and colony reliability and efficiency. A final section, 'communication and functional integration', considers how individual activity is coordinated to produce an integrated and adaptive colony. Within each section we use illustrative examples drawn from the social insect literature (mostly from ants, for which there is the best data) to illustrate concepts or trends and make a number of predictions concerning how a particular trait is expected to correlate with other aspects of social complexity. Within each section we also expand the scope of the arguments to consider these relationships in a much broader sense of 'sociality' by drawing parallels with other 'social' entities such as multicellular individuals, which can be understood as 'societies' of cells. The aim is to draw out any parallels and common causal relationships among the correlates. Two themes run through the study. The first is the role of colony size as an important factor affecting social complexity. The second is the complexity of individual workers in relation to the complexity of the colony. Consequently, this is an ideal opportunity to test a previously proposed hypothesis that 'individuals of highly social ant species are less complex than individuals from simple ant species' in light of numerous social correlates. Our findings support this hypothesis. In summary, we conclude that, in general, complex societies are characterized by large colony size, worker polymorphism, strong behavioural specialization and loss of totipotency in its workers, low individual complexity, decentralized colony control and high system redundancy, low individual competence, a high degree of worker cooperation when tackling tasks, group foraging strategies, high tempo, multi-chambered tailor-made nests, high functional integration, relatively greater use of cues and modulatory signals to coordinate individuals and heterogeneous patterns of worker-worker interaction.

Key words: Ants, insect societies, individual complexity, social complexity, polyphenism, totitpotency, work organization, functional integration, sociality.

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I. INTRODUCTION

In insect societies – colonies of ants, bees, wasps and termites – significant correlations exist among certain properties of the colony and of the individuals that comprise it. For example, the degree of behavioural specialization and intracolony colony conflict among the workers both correlate with colony size and colonies in which the nest is simple in structure also tend to have simple communication systems. In the most recent review of the subject, Bourke (1999) used the term 'simple' to describe colonies with 'few or no morphological differences between reproductive individuals and workers, no physical caste polymorphism among the workers and relatively simple nests and communication systems'. (The converse characteristics apply for 'complex' colonies.) Here, we initially adopt his view of complexity as a small cluster of correlates. However, as we proceed through the various sections we extend the investigation and consequently expand Bourke's (1999) cluster to include aspects of colony life not previously considered.

The above usage of complexity is generally consistent with that elsewhere in the social insect literature, where the term been used to refer to a number of variables, such as mean size of behavioural repertoire (Cole, 1985), body size and *per capita* productivity (Karsai & Wenzel, 1998), number of castes (Oster & Wilson, 1978), negentropy of nestmate recognition signals (Jaffe, 1987; Jaffe & Perez, 1989), degree of cooperation and coordination among workers (Beckers *et al.*, 1989; C. Anderson, N. R. Franks & D. W. McShea, in preparation), reproductive dimorphism (Peeters, 1997; Bourke, 1999) and colony size (Wilson, 1971; Peeters, 1997; Karsai & Wenzel, 1998; Bourke, 1999). This study expands the scope of certain related treatments of social insects (e.g. the above references and Michener, 1974; Bonner, 1988; Alexander, Noonan & Crespi, 1991; Seeley, 1995) and our usage of the term 'social complexity' is more inclusive; indeed, our hope is to develop a common scheme that shows how many of these variables, along with others, are related to each other.

Our usage also suggests a connection with the broader literature on hierarchy in biology, where there has been considerable interest in the factors affecting degree of emergence, or individuation, of entities at various hierarchical levels, such as the

Table 1. *Social correlates of individual and social complexity in insect societies. The correlates are intended to illustrate general trends only and not to encompass the behaviour of every social insect species. All of these trends are discussed in the text. Numbers in parentheses refer to the subsections of the sections (in bold) where the particular trait or correlate is primarily discussed. (0) refers to the introduction of a section*

	Simple societies	→	Complex societies
I. Introduction			
(0) Colony size	Low		High
II. Polyphenism			
(1) Worker polymorphism	Low		High
(2) Individual specialization	None → behavioural → physiological → morphological		
(2) Type of specialization	Temporary		Permanent
III. Totipotency			
(1) Functionality of ovaries	High		Low
(1) Morphological skew	Low		High
(1) Worker policing	Absent		Present
(1) Intracolony conflict	High		Low
(2) Physiological constraint	Low		High
(3) Individual complexity	High		Low
IV. Organization of work			
(0) Colony control	Centralised		Decentralised
(0) System redundancy	Low		High
(0) Homeostasis	Low		High
(1) Groups and teams	Absent		Present
(2) Task partitioning	Absent		Present
(3) Nest complexity	Low		High
(3) Colony-constructed nest	No		Yes
(3) Number of chambers	One		Many
(4) Foraging strategy	Individual → tandem running → mass → trunk trail → group hunting		
(5) Defence	Generalist non-sacrificial workers		Specialist sacrificial defenders
(6) Tempo	Low ('cool')		High ('hot')
(6) Individual competence	High		Low
(6) Most complex task type	Individual → group → team & partitioned		
(6) Efficiency	High		Low
V. Communication and functional integration			
(1) Average system connectedness	High		Low
(2) Use of cues	Low		High
(3) Use of modulatory signals	Low		High
(4) Heterogeneity of interaction	Low		High

eukaryotic cell and multicellular organisms as well as entities at the colony level [e.g. Spencer, 1904; Beklemishev, 1969; Pattee, 1970; Boardman & Cheetham, 1973; Leigh, 1983; Salthe, 1985, 1993; Buss, 1987; Bonner, 1988, 1998; Wimsatt, 1994; Maynard Smith & Szathmáry, 1995; Simon, 1962; Keller, 1999; Michod, 1999; Wilson, 1999; McShea, in press *b*; see also supplement issue to *American Naturalist* (1997) 150(1)]. In present terms, a eukaryotic cell can be understood as a 'complex society' of prokaryotic cells and a highly individuated multicellular organism as a complex society of eukaryotic cells. Here, we explore this connection further, raising the possibility that at least some of the same principles governing colony complexity in the social insects apply and that a similar cluster of correlates will be found across the hierarchical spectrum.

We divide the whole suite of correlates considered in this study among four major sections. Section II, 'polyphenism', considers the differences among individuals and in particular considers the concept of caste. Section III, 'totipotency', considers complexity of individuals within a colony (as opposed to the complexity of the colony itself), especially their totipotency with respect to behavioural and reproductive capacities. Section IV, 'organization of work', considers how the nature of

work itself may change with increasing colony complexity and the important changes observed in the way that individuals cooperate in order to tackle colony tasks. Lastly, Section V, 'communication', considers how individuals communicate with each other and coordinate their activities. These categories are by no means exclusive and the fact that many of the different characters and traits are correlated means that there is some overlap across the sections. Within each section, we identify a number of new correlates of interest and, with examples, expand Bourke's (1999) cluster. Wherever possible we attempt to identify any causal relationships and put these correlations or causal mechanisms in a broad context of 'sociality' with comparisons to other 'social systems' such as multicellular organisms. The principal concepts, trends and predictions are summarized in Table 1.

Two major themes are found linking all these sections. The first is the influence of colony size, one of the most important correlates when considering social complexity (e.g. Wilson, 1971; Peeters, 1997; Karsai & Wenzel, 1998; Bourke, 1999). The second is the relationship between the complexity of the individual and that of the colony. This presents an ideal opportunity to test Jaffe & Hebling-Beraldo's (1990) hypothesis that 'individuals of highly social ant species are less complex than individuals from simple ant societies', in a much broader context, i.e. set of correlates, than was previously possible. We suggest that, generally speaking, as social complexity increases, there is indeed a correlated decrease in individual complexity. In other words, there is a decline in independence or autonomy of the individual and in its ability to function on its own.

Some explanatory notes are required before proceeding. First, describing the many pair-wise relationships within even a moderate-sized group of correlates in an orderly way is difficult. We have taken an approach in which we begin with a small number of basic correlates in the first section (e.g. colony size and differentiation) and build up incrementally, in each section adding a small suite of additional variables and discussing their relationships to those in previous (sub)sections. Importantly, the order in which variables are discussed does not reflect causal primacy.

Second, ideally we would like to be able to map some of the social correlates onto a phylogeny. This would enable us for instance to evaluate whether 'simple' maps onto 'primitive' insect societies and 'complex' maps onto more derived and 'advanced' societies. A phylogeny could also be used to assess whether complexity has any tendency to increase in evolution, a tendency that is widely acknowledged but for which little empirical evidence exists (McShea, 1996 and references therein). Unfortunately, at the present time a suitable phylogeny does not exist and as such thus we shall avoid the two value-laden, yet often-used, terms 'primitive' and 'advanced' (see Sherman *et al.*, 1995). Third, our treatment of complexity in social insects is restricted mainly to ant societies, where the best data seem to be available.

Fourth, implicit in our understanding is our view of social complexity as a continuum running from simple to complex. However, occasionally, it will be convenient to frame the discussion solely as a contrast of these two extremes without discussing the whole suite of intermediates.

II. POLYPHENISM

The following section considers differentiation among individuals, i.e. temporary and permanent differences in morphology (polymorphism), physiology and behaviour among individuals.

(1) Polymorphism

Simple societies are composed of monomorphic individuals whereas complex societies contain a polymorphic workforce (Michener, 1974; Wheeler, 1986; Hölldobler & Wilson, 1990; Peeters, 1997; Bourke, 1999). Polymorphism has evolved independently at least eight times (Hölldobler & Wilson, 1990) but only 15% (44/297) of all ant genera exhibit some degree of worker polymorphism (Oster & Wilson, 1978: p. 4). Importantly, polymorphism tends only to be associated with species that have large colonies (Bourke, 1999: Table 1). Analyzing Jaffe's (1987: Table 1) data (although not taking into account phylogenetic relationships) we found a highly significant relationship between $\log_{10}$(colony size) and $\log_2$(variation of worker size), specifically: $\log_{10}$(colony size) $= 1.11 \times \log_2$(variation of worker size) $- 1.85$ ($F = 19.78$, $P < 0.0002$; solid line in Fig. 1A). Jaffe (1987) did not specify how he quantified this worker size variation. Non-linear regressions give better fits to the data and the linear fit is still significant when the two obvious outliers are removed ($F = 8.15$, d.f. $= 22$, $P < 0.01$; dashed line in Fig. 1A).

It is unfortunate that the analysis cannot easily be extended to quantify the degree of polymorphism
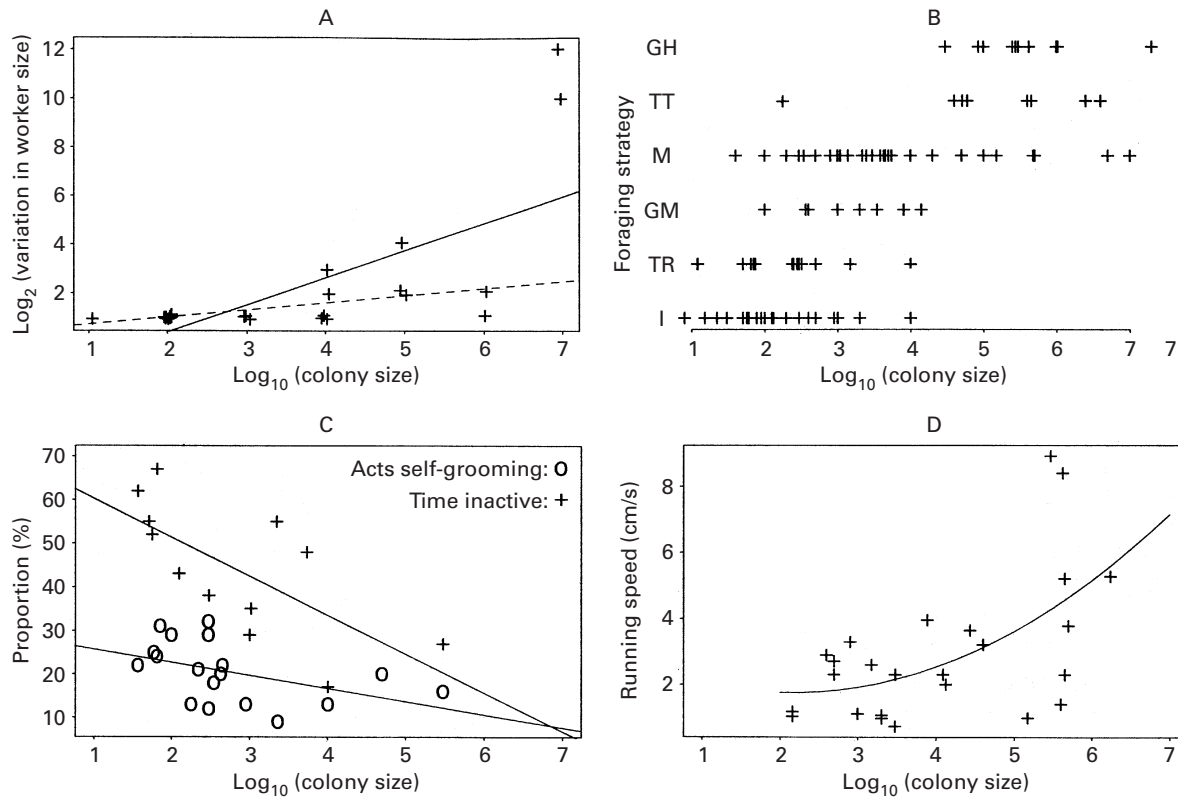
Fig. 1. (A) Log_2(variation in worker size) *versus* log_{10}(colony size) (data from Jaffe, 1987: Table 1). A small amount of scatter has been added to the data to separate points. The solid line is the least-squares fit to the data while the dashed line is the least-squares fit when the two obvious outliers have been removed. (B) Foraging strategy changes from individual foraging (I) to group hunting (GH) as colony size increases (data from Beckers *et al.*, 1989). Other foraging strategies: TR, tandem running; GM, group/mass foraging; M, mass foraging; TT, trunk trail. (C) Proportion of time spent inactive and proportion of acts spent self-grooming both decrease with increasing colony size (data from Schmid-Hempel, 1990). Reprinted by permission @ University of Chicago Press. (D) Running speed increases with log_{10}(colony size). Running speed data are listed in the Appendix.

more precisely. In ants, morphological castes are produced developmentally by altering the relative growth rates of different body parts (see Bourke & Franks, 1995 and references therein). The relationship between just two body parts may be isometric, di- or tri-phasic allometric, or even completely dimorphic (Wilson, 1953; Wheeler, 1991) and it is not even always possible to distinguish different castes in a supposedly multi-modal species (e.g. *Daceton armigerum*, Moffett & Tobin, 1991). In addition, within a species different relationships may exist between many pairs of body parts (including internal organs such as brains: see Jaffe & Perez, 1989) may exist between many pairs of body parts making any overall measure of 'degree of polymorphism' a challenging, but not necessarily intractable, multidimensional concept.

Only very recently have researchers begun to appreciate that polymorphism does not necessarily mean a difference in size among individuals: size may be similar but shape may differ. This is clearly the case when considering winged queens *versus* wingless workers of similar size (A. F. G. Bourke, personal communication). However, shape may also vary among individuals in which both queens and workers are winged. This was recently shown to be the case in *Apoica pallens*, a polistine wasp in which the overall size of queens and workers does not differ, but queens are smaller than workers anteriorly yet significantly larger posteriorly (Jeanne, Graf & Yandell, 1995). Importantly, this research suggests that morphological castes may evolve without a divergence in body size. Such studies may show that morphological differences and 'caste' in insect societies may be greater and more widespread than previously thought. We predict that the greatest differences among individuals – not just in size (including isometric allometry) but also in shape –

will be found in the species with the largest colony size and suggest that polymorphism is a significant facet of social complexity (contra Wilson, 1953: p. 153).

(2) A continuum of specialization

An additional facet of polyphenism is worker specialization. We suggest that simple societies are composed of generalist workers whereas complex societies contain workers that are specialized in a variety of ways, i.e. behaviourally, physiologically, or morphologically (Oster & Wilson, 1978; Anderson, 1998), to allow a certain amount of division of labour. Consequently, the ant *Amblyopone pallipes*, which completely lacks division of labour (Traniello, 1978), excepting reproductive division of labour, must class as one of the simplest societies from this aspect. We suggest that the various forms of specialization form a continuum (Table 1). At the lower extreme are true generalists, species such as *Amblyopone pallipes*, in which the probability of performing a task is independent of age. In other species, however, individuals concentrate their activities on a subset of the colony's repertoire and thus exhibit temporal specialization and division of labour. This temporal specialization may only be temporary – age or temporal polyethism may occur in which individuals tend to pass through an 'average' sequence of tasks over time, or individuals may switch tasks through recruitment when the need arises – but we still consider them specialists.

We suggest that a greater degree of specialization occurs when physiology imposes temporary behavioural specialization by making individuals particularly well adapted to certain tasks. For instance, between the 6th and 14th day of their lives, honey bee workers produce royal jelly (Manning, 1975) which effectively forces them to specialize in feeding queen larvae. As the workers age, special cells in their abdomens start to secrete wax and thus these individuals become naturally suited to a comb-building role. Finally, the extreme of this continuum is associated with morphological castes. In this situation, individuals are not subject to temporary changes in their abilities to perform certain tasks but to permanent differences in skills and abilities. For instance, a morphologically specialized soldier is likely to be inherently better at defence than other activities (e.g. brood care) throughout its life. In *Crematogaster smithi* ants there are two worker castes: 'large' and 'small'. Large workers appear to be specialized in the production of trophic eggs, i.e.

unfertilized worker-laid eggs used as food. Effectively, these workers specialize in turning protein from perishable food such as insect prey into internally stored eggs that they may store for several weeks (Heinze, Cover & Hölldobler, 1995; Heinze, Foitzig & Oberstadt, 1999).

(3) Differentiation

Three main arguments support the notion that differentiation should be correlated with colony size. As will be seen, they are quite general applying in principle to complex societies of prokaryotic cells (i.e. eukaryotic cells) and of eukaryotic cells (i.e. multicellular organisms) as well as to colonies of multicellular individuals. First, in a large aggregate of generalist individuals, performance can often be improved if individuals differentiate in order to specialize on particular tasks. In particular, differentiation is expected when individual specialists are able to perform functions more efficiently than non-specialists (Smith, 1776; Bonner, 1988) or when synergistic interactions among specialists improve performance (Corning, 1983). A requirement is that it must be possible for individuals to share resources (Harvell, 1994) and for tasks to be coordinated (Oster & Wilson, 1978; Corning, 1983; Bell, 1985). What factors control the degree of differentiation or number of specialist types? One possible constraint follows from a model developed by Oster & Wilson (1978) relating numbers of castes and tasks in social insects. Generalizing their result, selection is expected to favour differentiation of types until the number of types equals the number of tasks to be performed; it follows that the number of types could be limited by the number of tasks. However, the number of tasks doubtless reflects the number of selection pressures, including the number of selective opportunities and we have no reason think that these are sufficiently limited so as to impose a significant constraint, especially considering that tasks can often be readily subdivided into subtasks (see below).

Another possibility is that the number of types is limited by the number of individuals available to differentiate, so that each individual is specialized for a unique function. In this case, the number of types would be expected to increase directly with the number of individuals and therefore with colony size. However, other constraints tend to reduce the rate of increase. For example, in large aggregates, a specialized type is rarely a single individual, possibly because single individuals are often too small to

make a significant contribution to the whole (Bell & Mooers, 1997). Also, in small aggregates, fluctuations in demand for specialized tasks on the aggregate as a whole are often severe, in relative terms and as a result, specialized individuals will sometimes be left idle. Thus, differentiation is not expected even to begin until colonies reach at least a moderate size (Bell & Mooers, 1997). Consistent with this, in volvocacean algae (e.g. *Volvox*), differentiation of cells (into somatic and germ cells) is evident only in species with colony sizes of 64 or greater (e.g. *Eudorina*, Bell, 1985). Differentiation may also be limited by constraints imposed by development (Oster & Wilson, 1978), environment (Schopf, 1973), life history, etc.

A second argument is that differentiation may actually be required at large group sizes. Bonner (1988) proposed that increased size reduces surface-area-to-volume ratios, which changes the performance requirements of certain tasks, which in turn favours the evolution of specialized devices composed of differentiated lower-level individuals. For example, single-celled organisms can obtain food and oxygen by diffusion alone but larger multicelled organisms have cells differentiated to function in specialized devices, circulatory systems, for food and oxygen delivery.

Also, a connection between differentiation and group size is a prediction of Spencer's (1904) metaphysic, in particular of what he calls 'the instability of the homogeneous'. Spencer argues that in an aggregate, the component elements are subject to different forces by virtue of their differing locations within the aggregate – internal *versus* external, for example – and these differences in forces produce differences in structure. The greater the size of the aggregate, the greater the range of variation of environments within it and therefore also of the forces producing differentiation. Thus, even in the absence of selection, larger systems are expected to become more differentiated.

The relationship between aggregate size and differentiation has been studied in multicellular organisms and the results are consistent with expectations. In particular, Bell & Mooers (1997) have demonstrated a significant correlation between body size and number of cell types (see also Bonner, 1988). They further found that the number of cell types increased very slowly with body size; assuming a log-linear relationship, they estimated an exponent of 0.056, much less than 1.

So far we have discussed the complexity of the colony in the sense of degree of differentiation among individuals within it. We now turn to the question of the complexity of the individuals themselves.

III. TOTIPOTENCY

Workers in complex societies tend to be less totipotent (Crespi & Yanega, 1995; Bourke, 1999). Crespi & Yanega (1995: p. 110) define totipotency as 'the potential, throughout life, to express the full behavioural repertoire of the population (even if never actually expressed) and the ability to produce offspring like oneself, exhibiting the full behavioural repertoire of the population without help'. Thus, reduction in totipotency includes not only loss of reproductive potential but also of behavioural repertoire. A distinction must be made between two types of reduction in repertoire. First, individuals may be subject to socially mediated and temporary behavioural specialization in which they retain their behavioural flexibility and can potentially switch to other tasks (see Section II). Second, an individual's repertoire may be reduced due to physiological and morphological constraint. That is, differentiation, in terms of morphology or physiology, causes a difference in abilities to perform certain tasks. Here, only the latter is part of totipotency.

(1) Totipotency, morphological skew and intracolony conflict

One of the most significant losses of totipotency is the loss of functional ovaries – and in some cases, complete loss – in workers of some complex societies. Oster & Wilson (1978: p. 101; see also Noll, 1999) demonstrated a positive relationship between monomorphism of the colony and possession of ovaries by workers concluding that 'to develop into an extreme caste is to surrender reproductive potential'. Thus, it appears there is a correlation between differentiation, specifically polymorphism (Section II) and totipotency, in the sense of worker reproductive potential.

Bourke (1999) studied morphological skew in insect societies. Morphological skew is the degree of morphological dimorphism, usually external, between reproductives and workers. It is a consequence of specialization of queen and worker roles and reduced worker reproductive potential. For instance, workers lacking ovaries, a form of extreme skew, have been reported in the genera *Solenopsis*, *Pheidole*, *Monomorium*, *Tetramorium* and *Eciton* and in the

subfamilies Myrmicinae and Ecitoninae (see Villet, Crewe & Duncan, 1991). Bourke (1999) showed that species with large colonies had a high degree of morphological skew. Alexander *et al.* (1991) proposed a causal relationship between colony size, worker reproductive potential and morphological skew. Briefly, in large colonies, due to competition from the many other workers, any particular individual has a small chance of replacing the queen and thus selection maintaining reproductive potential will be weak. Bourke (1999) extended these ideas to consider the relationship between colony size and one aspect of intra-colony conflict: worker policing. Worker policing is the set of behaviours in which workers search for and eat eggs laid by other workers (Ratnieks, 1988; Ratnieks & Reeve, 1992; Keller & Reeve, 1999). Worker policing is a component of totipotency because it prevents workers from reproducing. Bourke (1999) argued that independent of mating frequency (which affects average worker-worker relatedness), it is easier for worker policing to invade large colonies. That is, in small colonies it is easier for an individual to monopolise reproduction and so there is greater conflict among individuals fighting for reproduction (Ratnieks & Reeve, 1992). However, in large colonies, in which each individual has a small chance of personal reproduction, individuals are more likely to favour worker-policing and fitness gains through inclusive fitness from the queen(s) than personal reproduction. Bourke & Ratnieks (1999) consider additional conflict in insect societies: worker suppression of new queen production, which is predicted to increase with a reduction in reproductive skew.

(2) Physiological and morphological constraint

Other forms of physiological differentiation, in addition to loss of ovaries, can impose behavioural specialization. So, honey bees producing royal jelly should specialize upon feeding queen larvae and honey bee workers producing wax should specialize on comb building. It is conceivable that non wax-producing workers could remove the wax from the wax-producing bees and use it themselves to build the comb. [This is the situation with propolis, a sticky tree resin, used by honey bees. Propolis foragers cannot unload themselves and require other bees to unload them. These unloaders and not the foragers, use the material to mend cracks in the nest (Ratnieks & Anderson, 1999*a*).] However, it is likely to be far more efficient if the wax-producing bees –

who can remove the wax themselves – remove and build with the material themselves. In effect, as an individual becomes physiologically specialized, it becomes more 'subjugated' and thus less of an independent individual. This is more so with morphological differentiation. In this situation, individuals are subject to permanent restrictions in their abilities. One of the more extreme examples of reduction of individuality of workers occurs when soldiers physically cannot feed themselves and must rely on trophallaxis for survival (e.g. *Daceton armigerum* majors; Wilson, 1962).

The greatest loss of individuality must surely be that associated with suicidal and sacrificial defenders. These traits are only expected to occur in complex societies. Sting autotomy – self-amputation of a sting (usually barbed) – is found in various social insect taxa among the ants, bees and wasps (Hermann, 1971, 1981). 'One predicts that barbed stings will be used in defence only in species that form new colonies in swarms such as honey bees and some tropical wasps [i.e. complex societies]. In very small colonies [simple societies] workers are too valuable for suicidal attacks to be beneficial' (Alexander *et al.*, 1991: p. 31). However, alternative sacrificial and suicidal behaviour does occur in ants such as in the 'walking bombs' (Oster & Wilson, 1978: p. 226) of *Globitermes sulfureus* and *Camponotus saundersi* ants who literally explode in front of their attackers. These ants use hydrostatic pressure to burst their gaster and mandibular glands releasing stick fluids, a process termed 'autothysis' by Maschwitz & Maschwitz (1974). Although these adaptations, such as barbed stings and specially adapted mandibular glands, may be morphological and physiological adaptations, they are present in the whole workforce and therefore are not part of differentiation (Section II). Our point is that the possession and use of these adaptations constitutes a reduction in individual autonomy and that these adaptations are expected only in complex societies.

(3) Individual complexity

Reduction of totipotency has a number of possible correlates, which we predict will be manifest at all hierarchical levels. First, there is a direct correlation with colony size. In small colonies, each individual in the colony is a scarce and valuable resource and therefore remains totipotent. Second and more generally, we expect a correlation between loss of behavioural and reproductive capacities on the one hand and loss of morphological structures and

physiological capacities on the other. Further, all of these should be correlated with colony size. As size increases and individuals specialize, they become dependent on others, or more precisely on the colony as a whole, for the performance of various survival-related functions. An individual that is specialized for defence, for example, relies on other specialists for foraging, colony-homeostatic activities and so on. As a result, the number of different functional demands on specialist individuals is reduced, along with the selection pressures maintaining the morphological structures, behaviours and physiological mechanisms associated with these activities. [An underlying assumption is that functions tend to be localized in such structures and mechanisms (McShea, 2000).] Indeed, selection is expected to favour the loss of these structures, behaviours and mechanisms in the interest of economy (McShea, in press *a*).

Third, the emergence of function at the level of the colony requires the loss of some degrees of freedom at the level of individuals (Guttman, 1969; Pattee, 1973; Bar-Yam, 1997). Buss (1987; see also Maynard Smith & Szathmáry, 1995) has pointed out that selection on the colony favours loss of reproductive capacities in some individuals, as discussed above in ants. But more generally, selection should act to reduce individuals' degrees of freedom in order to limit their interference with the co-ordinated function of the whole. Thus, individuals specialized for metabolism must not reproduce; likewise, reproductive specialists should not have metabolic capability, as their metabolic processes are unlikely to be coordinated with and indeed are likely to interfere with, those of the specialists. The loss of degrees of freedom may be achieved either by policing (Michod, 1999) – self-policing or totalitarian control – or, more effectively, by the loss of morphological structures, behaviours and physiological mechanisms associated with superfluous capacities.

In addition to the findings in social insects discussed above, a number of observations in colonial marine invertebrates are consistent with these expectations. For example, Wood, Zhuravlev & Debrenne (1992) noted that individuals in colonies are often smaller and less complex than related solitary individuals and Beklemishev (1969) noted that zooids in colonial forms are simpler compared those in related free-living species. At the cellular level, metazoan and land plant cells contain fewer macroscopic morphological structures than free-living eukaryotic cells (McShea, in press *a*). Extreme examples include mature human haemocytes, which contain almost no macroscopic structures and free-living *Euglena*, which have a variety of structures (e.g. nucleus, mitochondria, plastids, a flagellum, contractile vacuoles and so on). These extreme cases aside, even the more typical metazoan cells are, at least impressionistically, less complex in this sense, on average, than typical free-living cells (Gerhart & Kirschner, 1997: p. 242).

These observations are based on comparisons between extreme cases of social complexity, between free-living forms in which social complexity is essentially zero and individuals in colonies, in which it is present to some degree. There has been no demonstration yet that losses of structure accompany incremental increases in social complexity. In other words, it has not been established that the two are correlated as continuous variables, or that such losses are connected with any of the various correlates of social complexity, such as degree of differentiation. Also, most of the evidence for losses is based on morphology (e.g. ovaries in ants, parts in cells, etc.), but the expectation of loss at the level of the individual extends to behaviours and physiological mechanisms as well. Individual zooids in marine invertebrate colonies and cells in metazoans and land plants show little motor behaviour, but possible losses of physiological mechanisms could be investigated. Finally, in social insects, we predict that individuals in complex colonies should have fewer behaviours, on average, than those in simple colonies. Methods for counting behaviours have been developed (e.g. Wilson & Fagen, 1974; Fagen & Goldman, 1977) and thus testing could be straightforward.

IV. ORGANIZATION OF WORK

The complexity of the colony also has consequences for the organization of work within the colony. In addition to worker policing (see Section III), reduced intracolony conflict in complex societies has another important consequence: the type of social control. In small simple societies, as in the ponerine ant *Dinoponera quadriceps* (Monnin & Peeters, 1999), there is much aggression and direct control of colony activity by the queen or 'gamergate'. [Gamergates are mated reproductive workers in queenless ants (Peeters, 1997).] In effect, the reproductives centrally control simple conflict-ridden societies. However, in the relatively harmonious larger societies, colony control and decision-making tends to be decentralized. That is, workers react to local in-

formation and configurations and so are 'self-organized' (e.g. Théraulaz & Bonabeau, 1995; Bonabeau *et al.*, 1997; Bonabeau, Dorigo & Théraulaz, 1999; Camazine *et al.*, in press). Centralized control would be difficult or impossible in large colonies. However, decentralized control can be very adaptive at the colony level, even with very large colony sizes and importantly does not necessarily require complexity at the individual level (e.g. Bonabeau, 1998; Bonabeau *et al.*, 1999; Anderson & Bartholdi, 2000).

Interestingly, there are theoretical reasons to suppose that a large decentralized colony can be both efficient and reliable (high probability that tasks are completed) even when the individuals tackling the tasks are simple and not especially competent. Specifically, when activity is concurrent and individual competence is low, efficiency and reliability can be achieved by having redundancy – replication of parts – at the subunit level rather than the system level (Barlow & Proschan, 1975; Oster & Wilson, 1978; Herbers, 1981; see below). Thus, we expect many (spare) individuals in the vicinity of a task who are able to tackle that task. Even though all the individuals may not be fruitfully employed, at least the task will be completed.

It has been noted that complex societies tend to have a perennial cycle and in wasps and bees are swarm-founded rather than independent-founded (Bourke, 1999) and so do not go through a bottleneck of small colony size. Not only is colony size less variable through the year in more complex societies but larger systems are inherently more homeostatic (Wilson, 1971). For instance, there are automatic benefits to group foraging such as reduced variation in food influx rate (Wenzel & Pickering, 1991) and a greater potential for food storage to supply the colony during forage dearths (Jeanne, 1991). In summary, complex societies have a more constant colony size and structure, have less intracolony conflict, are inherently more homeostatic and rely more on decentralized control. This has huge implications in the organization of work as shown below.

(1) Groups and teams

One very apparent aspect of work organization in complex societies is the degree of cooperation among individuals when tackling some tasks. We suggest that in complex societies tasks may be completed by groups and teams rather than by individuals. Anderson & Franks (2001) suggest that there are four types of task in insect societies: individual,

group, team and partitioned tasks. The first three types are defined and reviewed in Anderson & Franks (2001). The fourth task type, partitioned tasks, are considered in the next subsection. All four task types are summarized in Table 2 and are further explored in C. Anderson, N. R. Franks & D. W. McShea (in preparation).

Briefly, individual tasks are tasks that can satisfactorily be performed by an individual, e.g. feeding a larva within a cell. Group tasks require many individuals working together for successful task completion. In a group task, there is no division of labour and the behaviour of the individual is the same as that of the group. For instance, group ambush and bivouac construction in army ants (Schneirla, 1971; Gotwald, 1995), intimidation of competitors in *Myrmecocystus mimicus* ants (Hölldobler, 1976, 1979), and 'stigmergic' nest construction in termites (Deneubourg, 1977; Bonabeau *et al.*, 1998*b*; see also Karsai, 1999) are all examples of group tasks. By contrast, Anderson & Franks (2001) propose that a team task requires different subtasks to be performed concurrently, i.e. there is division of labour. They propose that a task is 'an item of work that potentially makes a positive contribution, however small, to inclusive fitness (i.e. direct and indirect fitness)'. However, sometimes a subset of the behaviours required to complete a task may appear as a unit in themselves but cannot contribute to inclusive fitness when performed in isolation. This unit is a subtask.

Under the above definition of a team task, one such example is nest construction in *Oecophylla* spp. (weaver) ants. To construct the nest, leaves must be glued with silk while pulled together (subtask 1). The silk is produced by larvae (subtask 2) who are held above the seam by other workers (subtask 3) (Anderson & Franks, 2001). Anderson & Franks (2001) are careful to point out that team tasks do not require that individuals in a team must be members of different castes (*contra* Oster & Wilson, 1978: p. 151). However, they do highlight that polymorphism and thus presumed inherent differences in abilities among individuals to perform different activities, may favour specialization of castes upon certain subtasks thus enhancing team task performance.

A team task requires more cooperation than a group task. This is because in a team workers must coordinate their different work contributions. In turn, a group task requires more cooperation and coordination than an individual task because a group task requires the concurrent activity of multiple individuals (Table 2). These concepts are

Table 2. *Characteristics of various task types. This table defines the various task types. For instance, a team task requires a number of different individuals (column 2) performing multiple subtasks (column 3) concurrently (column 4).* [*From Anderson & Franks (2001).*]

Task	Number of individuals	Divided into subtasks?	Organization of subtasks
Individual task	Single	No	—
Group task	Multiple	No*	—
Partitioned task	Multiple	Yes	Sequential
Team task	Multiple	Yes	Concurrent

* But concurrency is required.

explored in depth in C. Anderson, N. R. Franks & D. W. McShea (in preparation). We hypothesize that in simple societies, the most coordinated tasks observed will generally be individual tasks. High intracolony conflict, monomorphism and small colony size will disfavour more coordinated activity in such colonies. In more complex societies we also expect to observe individual tasks but additionally we expect the most coordinated activity to be group tasks. For instance, we may observe group foraging or group nest construction activity. These group tasks will be favoured by large colony size in that many individuals may be available in the immediate vicinity for recruitment to the task. In even more complex societies we expect to observe team tasks. These too will be favoured by large colony size. However, they are more likely to be favoured by differences in performance efficiency among individuals arising from polymorphism (e.g. N. R. Franks, A. Sendova-Franks & C. Anderson, in preparation) and also from the increased potential for behavioural specialization due to increased colony homeostasis.

(2) Task partitioning

Task partitioning (Jeanne, 1986; reviewed in Ratnieks & Anderson, 1999*a*), in addition to groups and teams, is another task type that is only tenable in relatively complex societies. A task is said to be partitioned when it is split into a number of sequential stages and material is passed from one worker to another. In short, the task is split into a number of sequential subtasks (Table 2) which are explicitly linked by the act of material transfer. For instance, in the obligate termite-hunting ant *Megaponera foetans* minor workers enter the termite nest, hunt for termites and deposit them in a pile outside the termite nest. Major workers then transport the termite prey back to the ants' nest (Longhurst & Howse, 1979). Like group and team tasks, partitioned tasks require the coordination of a number of individuals for successful task completion (Table 2).

Partitioning a task may involve a number of advantages and disadvantages, which are reviewed in Ratnieks & Anderson (1999*a*). The most relevant to social complexity are as follows. First, task partitioning usually occurs when there is a difference in abilities of individuals to perform different parts of the task. For instance, small *Oecophylla longinoda* workers are better at milking scale insects than are larger workers. Small workers collect the honeydew and pass it onto larger workers who are better able to transport it back to the nest (Hölldobler, 1984*b*). Thus, division of labour enhances task partitioning and is most likely to occur when the worker population is polymorphic, i.e. in complex societies. Second, when direct transfer occurs searching for a transfer partner takes time (a cost) and average search duration decreases exponentially as the number of individuals in the working group increases. Consequently, when the group is large, these queueing and search delays are negligible (Anderson & Ratnieks, 1999*a, b*). Third, when group size is large, workers are significantly better able to assess the status of the system and make correct recruitment decisions to optimize worker allocation and efficiency (Ratnieks & Anderson, 1999*b*). However, because work demands are inherently more stable in a complex society anyway, there is less need for individuals to switch tasks and this increases efficiency (e.g. Gordon, 1989, 1999*b*; Karsai & Wenzel, 1998). Overall, task partitioning has the potential to greatly enhance task performance efficiency but mostly so in complex societies.

(3) Nest complexity

Individual ability to cooperate as groups and teams and partition tasks in complex societies may have implications for where they live. We suggest that complex ant societies tend to construct nests for

themselves rather than utilizing existing crevices and that these nests are relatively complex. One possible reason is that suitable natural nest cavities are more limiting for large colonies than for small; unfortunately, testing this is not straightforward. Alternatively, complex colonies have greater potential for tackling tasks that are beyond the abilities of an individual, such as the construction of tailor-made nests (e.g. Bonabeau *et al.*, 1999; Anderson & Franks, 2001).

What constitutes a complex nest? There are many features associated with increased nest complexity. Foremost, we see partitioning of the nest into two or more chambers. This is usually associated with some spatial specialization of colony activity. For instance, in *Atta* leaf cutter ants some chambers contain the fungal garden and brood whilst others solely contain refuse material (e.g. Weber, 1972). In many ant species, brood is piled in specific areas of the nest and in termites the queen is physically entombed in one chamber and the eggs that she lays are taken to other chambers (e.g. Wilson, 1971). In the seed harvester ant *Pogonomyrmex barbatus* (Gordon, 1999*a*), piles of seeds accrue only in certain parts of the nest.

In addition to the points made above, this physical segregation of workers in a multi-chambered nest has an important implication in the degree of control a queen has over a complex society. In a multi-chambered nest, any regulatory pheromones the queen releases are unlikely to diffuse rapidly throughout the nest and so her ability to control colony activity will be greatly reduced. In addition, more complex societies exhibit a greater degree of morphological skew. Thus, workers could potentially very easily exclude the queen(s) from certain areas of the nest by restricting the size of entrances to particular chambers (Howse, 1970), in the extreme, completely entombing the queen in a single chamber. Not only will the diffusion of any of the queen's pheromones be restricted but this could also be true of alarm pheromone: recruitment of additional defenders when the colony is attacked could be limited by the layout of the nest. Thus, in complex societies we expect some localisation of specialized defenders near the nest entrance(s) as in *Camponotus* (*Colobopsis*) *fraxinicola* ants discussed in Section IV.4.

Complex nests may contain additional adaptive structural features not found in simple nests. Starr (1991: p. 523) lists a number of nest features that are believed to have originated to serve secondary functions. In ant societies, these include fungus gardens (leaf cutter ants), auxiliary silk bowers used as shelters for homopterans (e.g. weaver ants) and

windows or tunnels used for the escape of sexuals for mating flights (fire ants). Here, we also include the specialized repletes who act as living storage vessels in the honey pot ants (*Myrmecocystus mimicus*, Hölldobler & Wilson, 1990) and 'turrets' at the nest entrance of *Acromyrmex landolti* nests which may prevent inundation during sheet flooding (Navarro & Jaffe, 1985). Despite the apparent complexity of some nests, it should be stressed that it is not necessary to invoke complexity at the individual level during their construction: the complexity may be an emergent property of a collection of interacting simple builders (e.g. Théraulaz & Bonabeau, 1995; Théraulaz, Bonabeau & Denubourg, 1998; Karsai, 1999).

Specific testing of our prediction – that complex societies construct their own nests and that these nests are more complex – may be difficult. First, the three-dimensional aspect of an excavated nest will probably be difficult to preserve. Second, to understand how features of the nest impact on colony activity requires observation of undisturbed colonies and the attempt to observe will probably affect its behaviour. Third, an insect society may move into an existing crevice but modify it specifically for their needs. Consider a honey bee colony, a complex society, whose swarms move into natural tree cavities but add their own wax combs. In the case of the honey bee, these modifications may be easy to detect, but in other instances they may not; an enlarged natural chamber in a log may be indistinguishable from an unenlarged one.

(4) Defence

We suggest that simple ant societies with few workers react to intruders, usually by stinging, as and when the need arises. Stinging is presumably the major ancestral ant defence mechanism as ants evolved from wasps (Hölldobler & Wilson, 1990) and stinging is the main, but by no means only, defence in wasps (e.g. Hermann, 1981). By contrast, in more complex societies, which have many individuals, the colonies can afford to allocate workers to specific defensive roles and defence mechanisms are more likely to be varied. For instance, they may post workers at entrances to check 'colony membership' of individuals going into the nest [e.g. *Camponotus* (*Colobopsis*) *fraxinicola* ants; Wilson, 1974]. Alternatively, they may employ workers to patrol around the nest looking for intruders. For instance, *Pseudomyrmex ferruginea* ants patrol the foliage around the *Acacia* thorns in which they live (Janzen, 1983).

Polymorphism, a complex-society trait, opens up the possibility of producing workers morphologically specialized for defence. Defence is one of the three main proposed roles of majors in ants, the other two being seed milling and food storage (Hölldobler & Wilson, 1990). In many polymorphic species majors possess particularly large and strong mandibles (e.g. *Pheidole pallidula* majors who decapitate intruders; Detrain & Pasteels, 1992). Some species, such as *Camponotus truncatus* and *C. ephippium*, possess specially shaped 'phragmotic' which can plug nest entrances, either individually or working with others to function as a living door (Hermann, 1981; Fig. 8–33 of Hölldobler & Wilson, 1990). In this situation, nest complexity itself also plays its part in colony defence by only having nest entrances that are just one individual wide. Similar behaviour is also known in some social wasps, such as in *Chartergus chartarius* (Jeanne, 1991), in which the passages between combs can be blocked by a single individual.

(5) Foraging strategies

As well as the existence of group, team and partitioned tasks in complex societies, another facet of higher-level functionality is a shift from individual to group foraging strategies. Beckers *et al.* (1989) identified six foraging strategies in ant colonies: (1) 'individual foraging' – foraging without cooperation and communication with others; (2) 'tandem running' – a scout guides one recruit to the food source with or without trail laying; (3) 'group/mass recruitment' – the scout guides a group of recruits to the source, usually laying a trail to the nest; (4) 'mass recruitment' – the scout lays a trail while returning to the nest which guides recruits to the food source; (5) 'trunk trail' – semi-permanent trails guide foragers to long-lasting food sources; and (6) 'group hunting' – a group leaves the nest and forages collectively in a swarm along a well-defined trail system. It is reasonable to assume that the order of strategies above (1–6) represents an increase in reliance on chemical communication between workers; assuming that this ordering is correct, then a trend of increasing use of chemical communication with increasing colony size is unmistakable (Beckers *et al.*, 1989; Fig. 1B). (See also Ruano, Tinaut & Jose Soler, 2000 for effects of temperature upon foraging strategy.) In addition, these strategies also appear to be correlated with a decrease in the autonomy of the individual foragers themselves (cf. Jaffe & Hebling-Beraldo, 1990 and also see Section IV.6). That is, there is a shift from information

processing by individuals to emergent properties of a set of essentially probabilistically behaving individuals mediated through signals, i.e. a set of trail pheromones. For instance, in an individual foraging strategy the worker must rely on its own information, navigating back to the nest using the sun or other landmarks (e.g. the desert ant *Cataglyphis bicolor*). In tandem running, a successful returning forager can recruit just one individual and passes on information of where the food source is by physically leading the recruit to the source (e.g. *Leptothorax* spp.). However, with more complex strategies trail pheromones can pass the information not just to one other recruit but to many. There is no need for an individual to be able to navigate back to the nest using the sun or a prominent rock but can simply orient ('smell') their way along a chemical trail (e.g. *Atta* spp.). Despite the apparent simplicity of this task, foragers experience a constant probability per unit distance of losing the trail. Seemingly counterintuitive, this apparently errant behaviour has been shown to be very adaptive at the group-level (Deneubourg, Pasteels & Verhaeghe, 1983; Deneubourg *et al.*, 1987; Fletcher, Blackwell & Cannings, 1995). Once lost, these workers become scouts who can search for new sites. However, it appears that the error rate is sufficiently tuned so that enough foragers do not lose the trail and thus can exploit the source whilst enough become scouts enabling a constant supply of new sources. [Parallel behaviour is known in honey bee foraging in which the directional information in waggle dances is imprecise (Weidenmüller & Seeley, 1999).] It seems that the complexity emerges at the level of the trail network (or group) which can adaptively adjust to fluctuating food dispersion or density (e.g. Bernstein, 1975). Thus, the foragers are a 'group-level adaptive unit' (*sensu* Seeley, 1995, 1997; see also Bonabeau, 1998).

(6) Tempo, reliability and efficiency

There are some interesting relationships between colony 'tempo', individual reliability, foraging strategy, metabolic rate and social complexity, in particular, colony size. Oster & Wilson (1978), without supporting data, suggested that colony tempo increases with colony size. Tempo was defined simply as 'activity level' and thus is presumed to incorporate both amount of activity, e.g. proportion of time spent inactive and the speed and efficiency of task completion when active. Oster & Wilson (1978) suggested that workers of 'cool' species, such as many ponerine, dacetine and basicerotine ants –

which we suggest are simple societies – are slow and deliberate and conservative in their use of energy. 'Hot' species, on the other hand, such as army ants, fire ants and members of the genera *Conomyrma*, *Forelius* and *Iridomyrmex* – which we suggest are complex societies – bustle with activity, 'seethe with rapid motion' and 'waste substantial amounts of time canceling out another's actions' (Oster & Wilson, 1978: p. 282). On this basis, we can formulate two non-exclusive hypotheses. First, the amount of inactivity decreases with increasing colony size (hypothesis 1). Second, running speed increases with colony size (hypothesis 2).

Hypothesis 1 was examined by Schmid-Hempel (1990). He demonstrated a highly significant decrease in the proportion of time spent inactive and the proportion of acts of self-grooming (a low-energy activity), with increase in colony size for a variety of ant species. See Fig. 1C. Running speed was shown to increase with colony size in *Aphaenogaster rudis* and *Myrmica punctiventris* by Leonard & Herbers (1986) and in colony fragments of *Pheidole dentata* by Burkhardt (1998). Thus, there are limited data supporting the hypothesis that within a species, running speed is correlated with colony size. We compared running speed among 26 taxonomically diverse ant species (from 11 genera) and found a highly significant relationship between running speed (cm/s) and $\log_{10}$(colony size) ($F = 5.03$, $r^2 = 0.326$, $N = 26$, $P < 0.02$) thus confirming hypothesis 2 (Fig. 1D). In response to Tschinkel's (1991) plea for publication of sociometric data, the raw data appear in the Appendix. (Two desert-dwelling species, *Cataglyphis bicolor* and *Ocymyrmex barbiger*, which live in very hot climates and run fast to minimize time spent outside in the intense heat, were not included in the analysis. Their running speeds are an order of magnitude greater than most of the other species studied.) Thus, the available data – although uncorrected for body size, phylogenetic relationships and ambient temperature – appear to support Oster & Wilson's (1978) assertions.

Why should tempo and colony size be correlated? There are at least three main hypotheses. The first considers foraging strategy and reliability theory (Barlow & Proschan, 1975; Oster & Wilson, 1978; Herbers, 1981). The second considers thermodynamics of far-from-equilibrium systems (Jaffe & Hebling-Beraldo, 1990, 1993). The third considers pheromone concentration.

The first argument is based upon Oster & Wilson's (1978) proposal that the correlation between tempo and colony size can be explained by diet. Their

argument, now backed with more recent research (Herbers, 1981), goes as follows: in Section IV.5 we explained that there is a correlation between colony size and the type of foraging strategy, ranging from individual foraging in species with small colonies to group hunting in species with very large colonies. Herbers (1981) used reliability theory to consider selection pressures upon individual competence for five ant foraging strategies. She demonstrated that strategies associated with larger colonies – strategies in which foragers have a high rate of encounter with their prey (high tempo) – result in high system reliability, even if individual competence is low. So, species with large colonies, which are catholic in their selection of prey (i.e. broad diet; Oster & Wilson, 1978), can afford some inefficiency at the individual level. Even though retrieval rate per encounter is relatively low because of poor individual competence, the net energy influx is high because of the sheer numbers of workers involved (Oster & Wilson, 1978). Herbers (1981: p. 185) even argues that colony selection will itself result in workers with low competence (see also Karsai & Wenzel, 1998). Her argument is based on the assumption that selection maximizes benefit minus cost, where 'benefit' is the system reliability and the 'cost' is individual competence in which it is assumed that more reliable individuals are more costly to produce. Species with few foragers on the other hand, tend to have a more restricted diet and rely on stealth to catch their prey; Peeters (1997: p. 377) states that 'All "primitive" ants are armed with a sting and hunt arthropods'. The loss of one forager in a small colony will have a large effect upon the colony's foraging success and so they are selected to have high individual competence. In short, species with few foragers have to be relatively reliable whereas foragers in large colonies tend to be less reliable because they are able to exploit such a strategy. It could be argued, although little data exist, that less reliable foragers, such as blind army ants who follow chemical trails and overcome prey by sheer weight of numbers (e.g. Schneirla, 1971; Franks, 1989) may be cheaper to produce than highly competent individuals who stealthily track down and overcome prey individually. However, incompetent workers can only 'pay their way' if they are especially active, i.e. are high tempo, so that their rate of encounters, despite their incompetence during an encounter, generates a sufficient supply of prey items.

A second explanation for the correlation between tempo and colony size can be formulated, without reference to diet, by considering (neg)entropy and

far-from-equilibrium thermodynamics. The more ordered and complex a system is, the further it is from equilibrium (disorder) and the higher the amount of energy required to maintain the system in that ordered state (e.g. Nicolis & Prigogine, 1977). In a static equilibrium, such as a wood ant colony's nest – the equilibrium state being disordered pine needles lying on the ground – the energy required to order the system is normally only a one-time investment: the effort to construct the nest. However, with a dynamic equilibrium, such as the far-from-equilibrium order of an ant society (i.e. the workers themselves) – the disordered state being anarchic activity, each individual operating independently and without cooperating with others – a constant stream of energy is required to maintain that state. Jaffe & Hebling-Beraldo (1990, 1993 and references therein) argue that this should be reflected in a higher metabolic rate and greater energy consumption per unit mass. In short, they argue that a correlation should exist between social complexity and (1) the colony's overall energy content and (2) the rate of energy use by workers, which may be reflected in tempo. They found that basal metabolic rate increased with colony size and the number of morphological castes in eight attine species from four genera (Jaffe & Hebling-Beraldo, 1993). However, these results hold for the genus level but not when comparing castes within a species. That is, complex colonies as a whole should have a higher metabolic rate with increasing colony size, but there may be variation in the partitioning of energy within the colony. For instance, colonies may contain minims who have a high metabolic rate and large soldiers with a low metabolic rate. Karsai & Wenzel (1998) point out that one way of increasing the 'tempo of interaction', assuming that the queens' resources for worker production are limited, is to increase colony size through reduced body size of workers. We suggest that if the almost universal '0.75 scaling rule' for metabolic rate – i.e. metabolic rate scales with the $\frac{3}{4}$ power of body mass (see Schmidt-Nielsen, 1984) – applies to workers, then metabolic rate per unit mass increases as workers are reduced (on average) in size and overall metabolic rate for the colony as a whole increases. In effect, we suggest that the increase in colony metabolic rate is achieved by partitioning a colony into smaller and higher metabolic-rate units. This is supported by the findings of Calabi & Porter (1989) who showed that in the fire ant *Solenopsis invicta*, large workers have approximately a 30% lower respiration rate per milligram of tissue than smaller ants.

A third possibility and fairly speculative hypothesis is that higher running speed might be a secondary effect of colony size. The suggestion is that colony size correlates with a larger absolute number of workers on a foraging trail, which in turn may correlate with total pheromone concentration. If running speed is positively correlated with pheromone concentration – as an experimental study of *Eciton burchelli* trails suggests (Franks *et al.*, 1991) – then we might expect higher tempo in larger colonies. However, further study is required to test this hypothesis at the cross-species level because if members of larger and more complex colonies lay pheromone with higher volatility (and thus lower *per capita* concentration) then this could ameliorate or even reverse this effect. A relationship between colony size and trail pheromone volatility has not yet been investigated, but doing so should be straightforward.

Irrespective of the underlying reasons for the correlation between tempo and social complexity the same conclusions can be drawn. Individuals from larger colonies are more active and tend to be less reliable, yet the colonies can afford to waste energy at the individual level. However, as noted earlier, larger systems are inherently more homeostatic and predictable than equivalent smaller systems (e.g. more predictable food influx) and species with larger colonies tend to rely on recruitment during foraging. Karsai & Wenzel (1998) also argue that parallel-processing systems in insect societies are more efficient *per se* in that it allows behavioural specialization of individuals and greater buffering of stochastic fluctuations. Schmid-Hempel (1990) notes that this creates an interesting paradox. Larger colonies may be able to afford a reserve forager force. Some of the workers could remain in the colony saving energy until demand for their labour is required when effective recruitment can be used. [See model and review in Anderson (2001).] However, on energetic grounds workers in larger colonies are shown empirically to be and from theory may be required to be, more active than in simple societies, i.e. there is an ergonomic cost. This cost is contrary to complex societies' greater potential for efficient cooperative work organization, i.e. an ergonomic benefit. We suggest that far-from-equilibrium dynamics – that larger colonies waste energy as a cost of 'order' – may be a causal factor of Michener's (1974) much cited but puzzling decrease in *per capita* productivity with increasing colony size, but this will be difficult to test.

(7) Intermediate-level parts

Groups, teams and possibly nests are examples of intermediate-level 'parts' (*sensu* McShea 2000; McShea & Venit, 2001; C. Anderson & D. W. McShea, in preparation), or adaptive structures or behaviours in an aggregate which are larger than a single lower-level individual but a subset of the whole. Such structures occur at the level of the organism as well as that of the colony and are possible only where there is a high degree of cooperation and coordination among lower-level individuals. They are important for several reasons. First, they confer a higher level of functionality, meaning that they allow individuals or colonies to achieve things collectively that a single individual cannot. Second, they introduce new organizational levels. This has important implications in the way that communication and feedbacks are effected among individuals (see Section V). Third, some of the structures are clearly associated with a reduction in autonomy: in many self-assemblages, each individual is effectively reduced to a construction component equivalent to a building brick or scaffolding pole (C. Anderson, G. Théraulaz & J. L. Deneubourg, in preparation). For instance, the primary role of an individual ant within a *Solenopsis invicta* raft or *Eciton burchelli* bridge is to hold on to other ants and so help to form and maintain the structure.

Intermediate-level parts can arise in at least three ways. One is as a connected group of lower-level individuals, a subgroup of the entire aggregate in the same manner as an army ant bivouac. Also, most metazoan tissues and organs would qualify as intermediate-level parts. Or at the colony level, a non-social-insect example might be the clusters of non-feeding zooids (or clusters in which density of feeding zooids is lower), i.e. maculae, which in some cyclostome bryozoan species may function as ex-current chimneys for the colony as a whole (Banta, McKinney & Zimmer, 1974).

Alternatively, an intermediate-level part may consist of a single lower-level individual which is hypertrophied or elaborated in various ways to attain intermediate size. For example, in eukaryotic cells, the portion of the cell that is homologous with the original eubacterial host, plus subsequent additions – e.g. microtubular structures, Golgi apparatus and so on – constitutes an elaborated lower-level individual. Notice that this set does not include the former endosymbionts, such as mitochondria and chloroplasts, which (historically) are different individuals. At the colony level, modern chondrophorines, such as *Velella* and *Porpita*, consist of a large pneumatophore, or float, overlying a central gastrozooid, ringed by smaller medusa-shaped gonozooids (Hyman, 1940; Mackie, 1959); the gastrozooid by itself constitutes an intermediate-level part. This type of intermediate-level part appear to be absent in insect societies. This may be so because of several reasons. First, developmental constraints may limit the size and form that ants may take (Wheeler, 1991). Second, large elaborate individuals may be too costly. Calabi & Porter (1989) analyzed the energetic costs – longevity, respiration rates and 'energy content' of worker tissue – in various sizes of workers in the fire ant *Solenopsis invicta*. They concluded that although larger workers have a lower respiration rate per milligram of tissue their larger biomass means that 'one large worker must provide services equivalent to at least four small workers, to justify the colony's energy investment' (Calabi & Porter, 1989: p. 643). Third, elaborated individuals may reduce the increased reliability effects of system redundancy. That is, assuming that these individuals are relatively rare, they become 'key individuals' (see Robson & Traniello, 1999). 'Failure' by a single key individual may have a large effect upon the overall efficiency of the group and makes the system less robust and reliable.

Finally, many of the various inanimate structures produced by higher-level entities would count as intermediate-level parts. At very low hierarchical levels, such structures might include the sheaths that enclose filamentous cyanobacterial colonies, or at the eukaryotic cell level, the nucleus (assuming it is not a former endosymbiont). In multicellular organisms, shells and exoskeletons and in colonies – in addition to nests in social insects – the various non-zooidal support structures (Boardman & Cheetham, 1973) count as intermediate level.

Bonner's (1988) argument that size increases favours internal division of labour and therefore differentiation, can be extended to predict intermediate-level parts. As lower-level individuals aggregate to form a whole, selection favours the emergence of functional capabilities in the whole. But as the whole grows, lower-level individuals become less competent to perform higher-level functions on account of their small size (Bell & Mooers, 1997). Thus, selection favours collaborations among a number of lower-level individuals (perhaps with subdivision of labour), the elaboration of single ones, or the production of larger inanimate structures in order to magnify their effects. Also, the argument

for the production of heterogeneity among individuals, namely the various advantages that flow from the cooperative division of labour, predicts that labour will be divided among intermediate-level parts and therefore they will become differentiated from each other. Notice that the main difference between this argument and Bonner's original is that intermediate-level parts – unlike lower-level individuals (cells in multicellular individuals, or colony members in colonies) – have no autonomous existence. A team in an insect colony, or a macula in a bryozoan colony, has no autonomous existence; even the elaborated archaebacterial host has lost much of its historical autonomy. However, autonomy is not a prerequisite for collaboration and differentiation.

V. COMMUNICATION AND FUNCTIONAL INTEGRATION

In the previous section, we suggested three different task types (group, team and partitioned tasks) in which coordination of multiple individuals is required for successful task completion. More generally, most, if not all, aspects of colony life require coordination of individuals for successful colony operation. Mechanisms exist to coordinate effort, e.g. recruit additional help when required, with the result that complex colonies can often exhibit group-level adaptive behaviour (see Seeley, 1997; Bonabeau, 1998). It is these mechanisms – mechanisms that are used functionally to integrate individuals and thus the colony – which are considered in this section.

We consider these mechanisms of functional integration under Seeley's (1995: p. 248) broad definition of communication: 'information transfer *via* cues as well as signals'. It is important to distinguish cues from signals because, as we show below, cues play a relatively more important part in complex society communication and integration than in simple societies. According to Lloyd (1983) a signal is an act of communication that has been shaped by natural selection. An example of a signal is alarm pheromone. When signaling occurs, natural selection acts upon both the signal sender, e.g. by canalizing the behaviour so that it is more stereotyped and also upon the receiver, e.g. increasing sensitivity to that behaviour pattern. A cue on the other hand, is a structure or behaviour that conveys information, but only incidentally and has not been shaped by natural selection (at least not directly). For example, intranidal temperature and the number of brood are both cues. Clearly, as information

from cues is incidental and may originate from inanimate objects, such as the nest, natural selection may only act upon the information receiver.

(1) Signal range and system connectedness

The first signaling characteristic we consider is signal range: that is, local *versus* global. Some types of signal are expected to be global regardless of social complexity. In particular, we refer to defence behaviour and alarm pheromones. If a colony is under attack it is imperative that this information is conveyed to all members of the colony as quickly as possible so that individuals can become involved in colony defence, or in some cases escape or hide inside the nest. [In several ant species, young workers react to an alarm signal by retreating into the nest while older workers – a 'disposable caste' (Porter & Jorgensen, 1981) who are more likely to have degenerate ovaries – move out and defend the nest (Hölldobler, 1984a).] Consequently, these signals are expected to be volatile chemical signals or mechanical signals, such as rapping the nest substratum or jittering (Wilson, 1976), with 'one-to-many' effects, which will reach a large proportion of the individuals quickly.

Signals for other colony functions, however, are expected to differ among simple and complex societies. In a small simple society, local signals could potentially reach a relatively large proportion of the colony. Also, direct one-to-one interactions with individuals, such as antennation, as they move around the nest may also mean that individuals in simple societies interact with a relatively large proportion of the colony. However, in a complex society, individuals are spatially separated. For instance, they may be segregated among different nest chambers. We suggest that this does not imply that signals should be necessarily be long range as one might initially expect. We have argued (Sections II and IV) that in complex societies, individuals exhibit division of labour and specialization, work more cooperatively and also that work tends to be concentrated in different sections of the nest [which would favour 'foraging for work' (Tofts 1993; Franks & Tofts, 1994)]. This means that individuals should primarily interact with others in the local vicinity, i.e. other individuals who may have the skills and opportunity to help with a task. In short, we should expect the existence of 'cliques': a group of individuals who preferentially interact with each other rather than with others outside the group. Thus, the term clique is used here *sensu* Moritz &

Southwick (1992: p. 145) rather than Hölldobler & Wilson's (1990: p. 343) more stringent – and from our current knowledge of social insect cognitive abilities, unrealistic – definition: a 'group of workers whose members recognize one another as individuals to accomplish some task'.

It is not clear whether the average signal range, the physical distance, in a simple society is greater than in complex societies. Indeed, simple societies may rely more on direct one-to-one interaction. However, we do expect signaling behaviour and interaction in complex societies to be relatively more locally concentrated and organized. One way of quantifying this is to consider the average system connectedness (or ASC; Moritz & Southwick, 1992). The basis of this analysis is to consider all the possible interactions between pairs of individuals, or 'dyads'. Given n individuals, there are $n(n-1)/2$ possible pairings. If one can observe interaction behaviour and quantify the number of unique pairs of individuals that actually interact within a colony, then the ASC is the observed number of dyads divided by the possible number of dyads. ASC values range from 0 to 1; a value of 1 means that all individuals are fully connected to each other. We would expect a high ASC value when considering alarm pheromones. A low ASC would be expected when interaction patterns are very localized, i.e. cliques occur and members within a clique interact with each other but cliques have little interaction with other cliques. On this basis, we make the following prediction: with the exception of important necessarily global signals such as alarm pheromones, ASC for other tasks is expected to decrease with increasing social complexity. This is not to say that individuals are not highly connected in a complex society, but simply that for a given task, a relatively small and exclusive group of individuals will be involved in tackling that task. More specifically we predict that patterns of interaction, as reflected by ASC, are more heterogeneous in complex societies than in simple ones. This pattern of interaction does not necessarily reflect the total number of interactions among individuals which is a function of signaling rate, or the strength of interaction, simply who is communicating with whom. Moritz & Southwick (1992: pp. 149–150) provide some estimates of ASC for various tasks in the honey bee. Thus, as expected, an ASC of 1 (100 %) was observed for defensive behaviour but the ASC was very low, only 3.1 %, for water-handling behaviour. These methods could be used to compare the ASC in simple *versus* complex societies.

(2) Signals *versus* cues

We predict that communication in simple societies makes relatively little use of cues whereas they are of much greater importance in more complex societies. Unfortunately, it is not possible to make a more explicit prediction, e.g. concerning the ratio of communication that flows through cues rather than signals since the effects of confounding variables, such as the rate of signaling and existence of modulatory signals (see below), are not clear. We make the above prediction on the basis that we expect a vastly different pattern of social regulation in simple versus complex societies. Social regulation in complex societies is based upon feedback from groups to individuals and also from groups to groups [see Wilson & Hölldobler (1988) and Seeley (1995)], while regulation in simple societies occurs mostly through direct worker-worker interaction and feedback is primarily from individual to individual.

Wilson & Hölldobler (1988) talk of 'dense heterarchies' and mass communication as the basis of organization in ant colonies. (We suggest that this applies only to relatively complex ant societies.) Their findings are mirrored by Seeley's (1995) analysis of honey bee social integration. A heterarchy is a communication network in which interaction occurs between different levels of the system or subsystems. Thus, feedback occurs from higher-level 'parts' (*sensu* McShea, 2000; McShea & Venit, 2001), such as intermediate-level parts, including groups and teams, to lower-level parts, such as individual workers. In turn, lower-level parts have effects upon the higher-level parts. For instance, low food reserves in the nest could influence a worker to forage and collect more food. The lack of stored food may influence many individuals to forage and as the forage reserve within the nest increases this may inhibit further foraging. Thus, there is interaction from the group-level summed foraging effort, i.e. the food pile (an intermediate-level part) and the lower-level individual foragers. Notice that this example used a cue – the amount of stored food – to influence individual activity. Seeley (1995) argues that cues are relatively important in complex social systems, for at least three reasons. First, the group-level cues are effectively a summation of many individuals' inputs and thus are expected to be accurate indicators. Second, cue-based communication means that information may be conveyed to many individuals at once. Third, cues are probably more easily sensed than the underlying variables of supply and demand. For instance, it should be easier to

assess the size of a seed pile than to directly assess the flow of returning foragers adding to the pile and other individuals depleting the resource (see Anderson & Bartholdi, 2000).

The honey bee society is probably our most well-understood complex insect society. Seeley (1998) reviewed the state of our current knowledge of cues and signals in honey bee colonies and found that there are twice as many known cues as signals (34 *vs*. 17). Unfortunately, the ant literature lacks this degree of detail for any ant species and is certainly an area where more research is needed.

(3) Modulatory signals

Hölldobler (1999) reviewed the complexity of signals (in general) in ant communication. One important aspect of that review which relates to social complexity is the existence of modulatory signals. Hölldobler (1995: p. 20) explicitly states that 'communication in complex social systems is not always characterized by a deterministic releasing process but sometimes plays a more subtle role'. He proceeds to explain the concept of a modulatory signal – a signal that does not necessarily evoke a behavioural response in itself from the recipient, but does alter the way that the recipient responds to another signal (Markl, 1985). For instance, in *Camponotus* spp. ants, workers may strike the nest substratum during alarm behaviour. This signal does not necessarily induce aggressive defensive behaviour *per se* but appears to act as a modulatory signal. Ants that have first received this drumming signal react more aggressively to their alarm pheromone than ants that have not (See Hölldobler, 1999 and references therein). Many other examples of modulatory signals are known (see Hölldobler, 1999) and we suggest that they are more likely to be found in complex societies than in simple societies. Their primary function appears to be in fine-tuning. Through the use of these signals, the colony is able to alter its level of response to the same stimulus depending upon other colony needs and circumstances. Thus, a *Camponotus* spp. colony may increase its defensive response by using the drumming signal in conjunction with the alarm pheromone to elicit a large response or can use the alarm pheromone by itself for a smaller reaction.

We predict that these modulatory and other fine tuning signals will tend to be lacking in simple societies because they are generally less integrated, more conflict ridden, more susceptible to stochastic fluctuations and tend to be composed of relatively autonomous generalists rather than cooperative specialists. In order to test this, we need to detect these signals; one approach to doing so is that of Anderson & Ratnieks (1999*c*) in their analysis of the coordination of nectar foragers and nectar receivers in the honey bee. In their study, they estimated the minimum set of signals and feedbacks that are needed to regulate a society or an aspect of a society and then compared it with the actual set of signals exhibited. They found that only three different signals and feedback mechanisms should be needed to regulate the number of honey bee nectar foragers and the number of receiver bees [to whom the foragers regurgitate their nectar for storage (e.g. Seeley, 1995)]. However, in reality, honey bee colonies use five different signals and feedbacks, two more than the minimum. One of these two additional signals was a modulatory signal, the shaking signal, which was used to 'fire up' the forager-receiver system after nectar dearth by altering the probability that individuals will respond to the forager re-cruitment signal (waggle dance). The other signal, the stop signal, was used to counteract effects of heterogeneity on the dance floor in an attempt to prevent both forager and receiver recruitment dances occurring simultaneously. Thus, both these additional signals were fine-tuning signals.

(4) Integration and connectedness

The above predictions are tentative at best. There are many aspects of signaling behaviour and colony functional integration that are not at all clear. For instance, we do not understand how the overall rate of signaling should vary with social complexity. Complex societies may rely more on cues rather than signals for direct feedback but they may also employ modulatory signals. Increased cooperation and co-ordination when tackling tasks in complex societies may require more communication than in simple societies. On the other hand, larger systems are more homeostatic and are less prone to stochastic fluctuations (thus requiring recruitment), than smaller systems. The net effect of these various factors is unknown. Sensing a cue is an act of communication and possibly individuals of more complex societies may test their environment very frequently, perhaps more frequently than sensing signals: for example, perhaps one waits to be antennated in a simple society. Specificity of signals may vary with social complexity. It is possible that simple societies use generic 'help me with my task' signals whereas more complex societies with their reduced individual

behavioural flexibility, meaning individuals cannot switch to all tasks, may need more specific signals such as 'help me with a task of class x' (see Hölldobler & Carlin, 1987). This too is currently unknown.

Two aspects of signaling, however, are well understood. The first aspect concerns the changes in foraging strategy with increasing colony size (Section IV). It is clear that 'low complexity' strategies such as tandem running employ mechanical one-to-one signals, and as the 'complexity' of the strategies increases and more and more individuals are involved in a foraging group, such as in mass recruitment, these individuals are coordinated by chemical signals with one-to-many effects, such as trail pheromones. The second aspect concerns the regulation of interaction rates with increasing colony size. This solely concerns direct interaction among individuals through antennation. Gordon (1999 b and references therein; see also Mangel, 1995) have shown that as group size increases ants reduce their density in the nest which in turn reduces their *per capita* interaction rate. Under the assumption that environmental stimuli, such as the demand for a task, increase roughly linearly with colony size, theory predicts (see also Bonabeau, Théraulaz & Deneubourg, 1998 a) and experiments show, that ants should reduce their density to reduce *per capita* interaction. The reason is that interaction rates are expected to scale at a greater rate than environmental stimuli (under random Brownian motion they would scale as the square of the number of individuals) and thus could swamp out the environmental stimuli effects.

More generally, connectedness is expected to be a function of differentiation and of individual autonomy. Harvell (1994) pointed out that in polymorphic marine invertebrate colonies, individuals specializing for functions other than food gathering (in bryozoans, polymorphs), tend to lose food-gathering capability and therefore their activities must be subsidised by the colony as a whole. In other words, connections among individuals must be available for sharing resources. On the other hand, Harvell (1994) also raised the possibility that over-connectedness may present a barrier to differentiation. She rejected the notion ultimately, because it appears to be falsified by the Siphonophora and the Hydroida, in which polymorphism is high and individuals are highly connected, sharing a common gut. However, there are theoretical reasons to think that the notion may be worth exploring further. Kauffman (1993) has shown that in N-K Boolean networks, stable cycles of activation emerge only at intermediate levels of connectivity. More particularly, in organisms, proper function in a specialist individual would seem to require at least a modicum of isolation and therefore a constraint on connectedness, in order to limit outside interference with internal flows of signals and materials. Thus, cell boundaries would seem to be necessary to maintain cellular differentiation; or, to put it another way, a prediction is that syncytial forms should be less differentiated.

VI. DISCUSSION

In this study, we have attempted to broaden our understanding of social complexity in insect societies and where possible to draw parallels with coloniality at other hierarchical levels. Our study is organized in a particular manner to tell a 'story' such that each section is a consequence of changes in social organization in the previous section(s). Thus, differentiation (Section II) has implications for specialization (Section II) – the greater the differentiation, the greater the specialization. In turn, both differentiation and specialization have consequences for intracolony conflict, totipotency and individual constraint (Section III) – the larger and more differentiated the society, the more specialized individuals become such that a reduction in an individual's capacities may follow. The ability to shift to a higher degree of cooperative activity when tackling tasks (Section IV) is a direct consequence of reduced intracolony conflict (Section III), colony size and differentiation (Section II). Finally, increased cooperation, specialization and spatial segregation of activity in the nest require enhanced coordination and functional integration (Section V). We present the whole suite of social correlates in Table 1 to summarise our findings and in the hope that the high degree of interdependence and connectedness among these correlates will be apparent.

One of our major themes has been the reduction of complexity of lower-level individuals with increases in social complexity. Our findings support Jaffe & Hebling-Beraldo's (1990, 1993) claims about insect societies in this respect and we extend their arguments with additional correlates, causal relationships and parallels with other social entities. One reason we consider it an especially significant trend is that it runs contrary to the conventional wisdom (e.g. Seeley, 1995: pp. 254–255) and perhaps contrary to intuition as well. Another reason is that in most

Table 3. *Various ant species mentioned in the text assigned to five levels of complexity (first column). Some of the major reasons for placing the particular individuals within a complexity class are given in the second column. This is a subjective procedure in which consideration of different aspects may place species in different classes. The third column shows mature colony size for the species and shows that colony size generally increases with complexity but there is large variation due to other correlates such as work organization or totipotency. Colony sizes are taken from Beckers* et al. *(1989), Table 3.2 of Hölldobler & Wilson (1990), or Kaspari & Vargo (1995), except where indicated otherwise.*

Degree of complexity and species	Reasons for placing in particular complexity level	Colony size
High		
Atta colombica	Agriculture, polymorphism	1 750 000
Eciton burchelli	Teams, polymorphism	825 000
Oecophylla	Teams, polymorphism	480 000
Pheidole pallidula	Teams, polymorphism	5000
Medium/high		
Acromyrmex landolti	Agriculture and polymorphism (but small colony size)	1000
Daceton armigerum	Task partitioning, majors that cannot feed themselves	10 000
Pogonomyrmex badius	Polymorphism and trunk trails	4300
Medium		
Camponotus truncatus	Working as group (as living door)	50
Megaponera foetans	Polymorphism and task partitioning	518
Low/medium		
Aphaenogaster rudis	Small colony size	303
Cataglyphis	Autonomous individuals, no recruitment	5000
Colobopsis fraxinicola	Small colony size, but guards at nest entrance	165[a]
Myrmica punctiventris	Small colony size	86
Low		
Amblyopone pallipes	Very small colony size and lack of division of labour	18[b]
Dinoponera quadriceps	Small colony size, loss of queen caste, high intracolony conflict	89[c]

[a] Wilson (1974); [b] Traniello (1978); [c] Monnin & Peeters (1999)

treatments of the advent of new hierarchical levels, including the origin of multicellularity as well as of complex societies, the focus has been on the accompanying increase in complexity (e.g. Stebbins, 1969; Bonner, 1988; Maynard Smith & Szathmáry, 1995). Indeed, it seems clear that complexity does increase in these transitions in two senses. There is the obvious increase in a hierarchical sense, simply on account of the advent of a new level, but also an increase in a non-hierarchical sense, on account of the increase in number of different types of parts, i.e. differentiation among individuals at the same level. Here, we have drawn attention to the fact that certain decreases are also expected to accompany these increases, in particular, the number of different functional capabilities of lower-level individuals – as reflected in numbers of parts, physiological capacities and distinct behaviours – is expected to decline. In sum, the suggestion is that as the complexity of the whole rises, the complexity of its components decreases (presumably with some limits) (McShea, in press *a*).

Exceptions to this general rule may occur and may be worth further study for the insight they offer into it. Possibilities include species in which in individuals spend significant amounts of time away from the nest working alone. This may be true of species that fly to forage sites, such as bees and wasps and thus cannot rely on interaction with other colony members on some trail. For instance, the evolution of the waggle dance in the honey bee means that individuals can forage significantly further from the nest and therefore are required to be more individually capable (Beekman & Ratnieks, 2000).

Our treatment of social complexity is intentionally agnostic on the subject of causes of complexity change. That is, it seems clear that the correlations we discuss and their tendencies to change in particular ways with increasing social complexity, could be understood as the product of selection and thus throughout the discussion we have offered a number of possible selective mechanisms (primarily for heuristic purposes). However, non-selective

routes are also possible. In principle, for example, behavioural differentiation could be the result of self-organizing properties that emerge when colony size passes some crucial threshold (Bonabeau *et al.*, 1997; Bonabeau, 1998; Camazine *et al.*, in press). Still, causes aside, it also seems clear that increases in social complexity provide an opportunity for selection. That is, the increases in differentiation and integration, as well as the losses of individual functional capability, that accompany the formation of a complex society, whatever their sources, produce among individuals a condition of extreme dependency, of shared fate, which in turn makes selection at the level of the whole possible.

Also, our discussion has been agnostic on the subject of evolutionary trends, on whether or not any tendency exists for social complexity to increase. The focus of many treatments of trends has been on increases (Bonner, 1988; Maynard Smith & Szathmáry, 1995), but it is well known that decreases also occur (e.g. Wcislo & Danforth, 1997). However, no systematic study has been carried out to determine whether increases occur more frequently than decreases, either among the social insects or among social metazoans generally (although see D. W. McShea, in preparation). Moreover, we are currently unable to demonstrate that 'primitive' (in the sense of lacking derived characters) equals 'simple', and 'advanced' (having many derived characters) equals 'complex'. For instance, are agrarian attine species, such as *Atta* and *Acromyrmex*, both socially complex and more advanced? We suspect that this is the case, but without a sufficiently detailed phylogeny this is currently untestable. We make a number of other predictions throughout the study which are potentially testable – e.g. that complex societies tend to construct their own nests, and that ASC should decrease with colony size – but for which there is currently insufficient data. (To help readers less familiar with particular ant species, in Table 3 we have placed a number of ant species discussed above in five categories of social complexity and given some reasons for their placement – alternative reasons or a different focus could reorder the list. Colony sizes are also reported to make the point that this in general does correlate well with social complexity but there is much variation.) Some genera and species, such as *Atta* and *Oecophylla* have been studied intensively, while others, such as *Amblyopone* and *Aphaenogatser* have received far less attention. It is not always the case that the research has not been conducted, but that it has not been published. Thus, we reiterate Tschinkel's (1991) plea for publication of sociometric data and, ideally, the establishment of a social insect sociometric data bank so that broad comparative studies, such as ours, can be carried out and thus provide further insights into sociality in insect societies.

VII. CONCLUSIONS

(1) We review the relationships among various correlates of social complexity and in particular focus on ant colonies as an explicit 'test case'.

(2) Social complexity is positively correlated with differentiation among individuals. That is, individuals in larger more complex societies may differ from each other in three main ways: polymorphism (caste), physiological specialization and behavioural specialization.

(3) Individuals in complex societies tend to be less 'totipotent'. That is, they are somehow restricted from being generalist fully-functional individuals, e.g. by not possessing functional ovaries, or by possessing certain physiologically or morphologically adaptations which favour them adopting certain specialised roles in the colony.

(4) Complex societies, which tend to have relatively little intracolony conflict, often tackle colony tasks in a highly cooperative manner, e.g. by working as groups or teams or using group foraging strategies and constructing tailor-made nests.

(5) Complex societies tend to be 'high tempo' comprising very active and fast-running individuals.

(6) Complex societies are highly 'integrated' involving a sophisticated and heterogeneous communication network of signals and importantly, modulatory signals and cues.

(7) Our conclusions support Jaffe & Hebling-Beraldo's (1990: p. 538) hypothesis that 'individuals of highly social ant species are less complex than individuals from simple ant species'.

VIII. ACKNOWLEDGEMENTS

IX. APPENDIX

Tempo, as measured by running speed (cm s⁻¹) versus colony size in 26 species of ants. The species are grouped by subfamilies from Hölldobler & Wilson (1990: pp. 9–19). Colony size data are taken from the running speed reference, Beckers et al. *(1989), Boomsma (1982), Table 3.2 of Hölldobler & Wilson (1990), or Kaspari & Vargo (1995). Where an expression relating running speed and worker size was given, e.g. Lighton* et al., *(1987), the mean or median worker size was used. The data are plotted in Fig. 1D and discussed in Section IV.6.*

Species	Colony size	Running speed (cm s⁻¹) and Reference
Ecitoninae		
Eciton burchelli	425 000	5.2 Franks *et al.* (1991)
E. burchelli	425 000	8.4 Franks (1986)
E. hamatum	300 000	8.92 Bartholemew *et al.* (1988)
Myrmicinae		
Acromyrmex lundi	1500	2.6 Roces (1993)
Aphenogaster rudis	145	1.02 Leonard & Herbers (1986)
Atta cephalotes	500 000	3.78 Rudolph & Loudon, 1986
A. colombica	1 750 000	5.2 Lighton *et al.* (1987); Burd (1996)
Monomorium pharaonis	800	3.29 Ross, Shimabukuro & Dixon (1992)
Myrmica punctiventris	145	1.16 Leonard & Herbers (1986)
M. rubra	1000	1.1 Cammaerts *et al.* (1981)
M. ruginodis	2000	1.06 Cammaerts *et al.* (1981)
M. sabuleti	3000	0.72 Cammaerts *et al.* (1981)
M. scabrinodis	2000	0.96 Cammaerts *et al.* (1981)
Ocymyrmex barbiger	200	30.6 Marsh (1985)
Pogonomyrmex barbatus	12 358	2.3 Morehead & Feener (1998)
P. desertorum	500	2.3 Morehead & Feener (1998)
P. maricopa	400	2.9 Weier *et al.* (1995)
P. occidentalis	3024	2.3 Morehead & Feener (1998)
P. rugosus	7740	3.95 Lighton & Feener (1989)
Veromessor pergandei	27 500	3.64 Rissing (1982)
Formicinae		
Camponotus hurculeanus	13 376	2.0 Jensen & Holm-Jensen (1980)
Cataglyphis bicolor	2000	14.4 Wehner & Srinivasan (1981)
Formica aquilona	400 000	1.4 Holt (1955)
F. fusca	500	2.7 Jensen & Holm-Jensen (1980)
F. lugubris	40 000	3.2 Breen (1976)
F. polyctena	450 000	2.3 De Bruyn & Kruk-De Bruin (1972)
F. rufa	150 000	0.98 Holt (1955)

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