The complexity and hierarchical structure of tasks in insect societies

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To understand the functioning and organizational complexity of insect societies, a combination of different approaches is needed. One such approach, which we adopt in this study, is to consider tasks in insect societies not based upon their function, as is traditional, but upon their structure. Four types of task in insect societies have been proposed: individual, group, team and partitioned tasks. We examine the relationships among these four task types and consider 'task complexity' to mean the degree of cooperation and coordination required to complete a particular task successfully. In this respect, individual tasks are considered the simplest (low complexity), group tasks are more complex (medium), and team and partitioned tasks the most complex (high). We decompose tasks into their component subtasks to understand how the demands of a task influence how workers must work together to complete it successfully. We describe a simple method to measure the complexity of tasks using task deconstruction. Points are assigned to each subtask within the task and summed to give a total score. This measure, the task's score, allows objective comparison of tasks (different tasks may be ranked in order of their complexity) within and between species, or even higher taxa, and we hope it will be of practical use to researchers. We propose that both team and partitioned tasks may contain individual, group, team and partitioned subtasks. We examine each of the possible task–subtask relationships and provide examples from known social insect behaviour.

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Insect societies (colonies of ants, bees, wasps and termites) are extremely successful in the majority of terrestrial ecosystems (Wilson 1990). Undoubtedly, one of the major factors contributing to their success is the ability of individuals to work together and cooperate when tackling tasks. Great effort has been made to understand the inner workings of insect societies. Traditionally, this research has focused on task function, for example compiling behavioural catalogues, and also related issues of division of labour and how individuals are divided among these tasks. Only more recently has attention been paid to the structure and demands of the tasks themselves (Anderson & Ratnieks 1999, 2000; Bonabeau et al. 1999; Karsai 1999;

Ratnieks & Anderson 1999; Anderson & Franks, in press). That is, how does the set of skills needed to complete a task influence the organization of workers around that task?

Adopting this perspective, that is task structure rather than task function, Anderson & Franks (in press) identified four types of task in insect societies: individual, group, team and partitioned tasks. We examine the relationship between these four task types and, in particular, the hierarchical structure within tasks, that is, among the tasks and their component 'subtasks'. On the basis of proposed task type definitions (Ratnieks & Anderson 1999; Anderson & Franks, in press), we list the various possible task–subtask relationships and illustrate these relationships with examples from the social insect literature. Anderson & Franks (in press; see also Anderson & McShea 2001) suggested that analysis of teams may be a useful way of objectively evaluating the complexity of an insect society. This claim is supported and widened in this study, and we also suggest how task complexity can be measured.

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We propose a simple method of measuring 'task complexity', specifically meaning the degree of cooperation and coordination required for successful task completion, based upon the deconstruction of a task into its component tasks and subtasks. Anderson & Franks (in press) proposed 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)'. Sometimes a subset of the behaviours required to complete a task may appear as a discrete unit in themselves, a subtask. For instance, when killing intruding ants, a group of *Pheidole pallidula* ants will work together to immobilize, 'pin down', the intruder (Detrain & Pasteels 1992). However, this is classed as a subtask because it must be followed by the separate act of decapitation (which can be carried out only by a major) or it will make no contribution to enhancing colony fitness. By assigning points to different (sub)task types, we propose a measure in which the total task complexity can be assessed. Our measure is based upon certain intuitions: for example, that a task composed of several different types of subtask seems more complex than one with no subtask distinction, that a team in which the members are groups is more complex than one in which they are individuals and so on.

Our measure allows the relative complexity to be assessed and therefore means that tasks can be ranked in terms of their complexity. Thus, it can be used to assess objectively the complexity of different tasks within a colony or species, and even how different species tackle the same task. We hope that this approach will be of practical use in the study of social complexity in insect societies. For instance, Cole (1985) found a relationship between behavioural repertoire and brain volume to the 3/2 power in ants; our measure could be used to extend this analysis and examine task complexity: do ants with larger brains tackle more complex tasks?

Our approach is similar to and builds upon that of Cisne (1974), Bonner (1988), McShea (1993), Valentine et al. (1994) and Bell & Mooers (1997), who understood the complexity of a system as a function of the number of different types of parts. Our measure adds a hierarchical dimension, taking into account the contribution to complexity conferred by the nesting of parts within parts (McShea 1996), or rather, in our scheme, tasks within tasks.

TASK TYPES AND THEIR RELATIVE COMPLEXITY

In this section we briefly describe the four task types and consider their relative complexity, assigning them to three distinct complexity levels. (Greater detail and additional examples of these task types are to be found elsewhere: individual tasks: Hölldobler & Wilson 1990; partitioned tasks: Ratnieks & Anderson 1999; Anderson & Ratnieks 2000; group and team tasks: Anderson & Franks, in press; Anderson & McShea, in press) Our focus, which provides some insight into the hierarchical structuring and organization within insect societies, is the degree of cooperation and coordination required to complete a particular task successfully. This is our proxy for 'task complexity'.

Individual Tasks

Individual tasks are tasks that can, or can only, be satisfactorily performed by an individual. For instance, *Cataglyphis* workers forage alone (without any help from nestmates) for other arthropods that have succumbed to heat exhaustion (e.g. Wehner et al. 1983). In the honeybee, *Apis mellifera*, workers put their heads into cells to regurgitate food to the growing larvae. This is a task that is clearly an individual task (only a single head can fit into the cell at a time) and is therefore an example of a task that can only be tackled as an individual task. Because these tasks do not need cooperation for their completion, we suggest that individual tasks are 'low complexity'. When individuals work in a parallel-series arrangement (Oster & Wilson 1978), that is with each worker tackling its own task simultaneously, this may entail some coordination among workers. For instance, many workers may regurgitate to different larvae simultaneously. Importantly, however, unlike groups (see below), such cooperation and coordination is not crucial for successful task completion and thus it is still an individual task.

Group Tasks

Anderson & Franks (in press) proposed that group tasks require many workers operating concurrently for successful task completion. In a group task there is no division of labour and each individual performs the same task. Crucially though, individuals must work concurrently or the task cannot be completed. Examples of group tasks include *Apis dorsata* bees that link legs to form a living curtain around brood (Dyer & Seeley 1991), group ambush of prey in *Azteca* ants (Morais 1994), and nest construction in many, if not most, insect societies (Bonabeau et al. 1999; Karsai 1999).

Although there is no division of labour within a group (every individual within the group acts similarly and tackles the same task) concurrent activity is necessary because the combined effort of all the individuals must exceed some threshold to complete the task. Importantly, this threshold is higher than a single individual's capability. For instance, large prey items are often retrieved by a group in ants. When a single ant is too small or too weak to move the prey by itself, it may be able to recruit nestmates to help. If several ants pull on the prey concurrently their combined effort can exceed the frictional forces across the ground and the prey is moved. There is no implication that division of labour occurs, simply that at some point the ants pull or push at the same time. In fact, group retrieval in ants is often poorly coordinated with some individuals pushing and pulling against each other (see Sudd 1965, 1967). As a greater degree of cooperation is required to complete group tasks than individual tasks we suggest that they are 'medium complexity'.

Table 1. A selection of examples from the social insect literature of a particular colony task, 'defence', that are identical in task function but that differ in task structure

Behaviour (and task type)	Species	Source
Individual task		
Squirting foam over victim	*Pachycondyla tridenta*	Maschwitz et al. 1981
Abdominal bursting	*Globitermes sulfureus*; *Camponotus* sp.	Oster & Wilson 1978
Nest blocking by an individual	*Chartergus chartarius*	Jeanne 1991
Group task		
Visual warning and defensive alignment	*Dendromyrmex chartifex*; *Apoica pallens*	Wilson 1981; Hermann & Blum 1981
Balling (i.e. 'cook' predator in a ball of bees)	*Apis cerana japonica*	Ono et al. 1995
Nest blocking by 2 or more individuals	*Colobopsis truncatus*	Anderson & Franks, in press
Synchronized mobbing	*Polistes annularis*	Starr 1990
Team task		
Decapitation	*Pheidole pallidula*; *P. punctulata*	Detrain & Pasteels 1992; Way 1953

Team Tasks

A team task requires two or more different subtasks to be performed concurrently for successful task completion (Anderson & Franks, in press). That is, team tasks require the cooperation of many individuals to complete a task successfully, and there is a necessary division of labour. Decapitation of intruders by *P. pallidula* (Detrain & Pasteels 1992) mentioned earlier is one such example. It is crucial that both pinning down by a group of minors (the first subtask) and decapitation by a major (the second subtask) occur concurrently for the task (decapitate intruder) to be completed. Thus, we suggest team tasks are of 'high complexity': not only must many individuals work concurrently but also, unlike group tasks, members of a team must coordinate their different contributions.

Partitioned Tasks

The subtasks in a team task are concurrent but in a partitioned task they are sequential. A task is said to be partitioned when it is split into a number of sequential subtasks and material is passed from one worker to another (Jeanne 1986; Ratnieks & Anderson 1999). For instance, in the termite *Hodotermes mossambicus*, one set of workers climbs up grass stems, cuts off pieces of grass, and drops them to the ground below (subtask 1) while a second set of workers transports the material back to the nest (subtask 2; Leuthold et al. 1976). Thus, the different subtasks (cutting and transport) are clearly distinguished, and explicitly linked, by the act of transfer which may be direct (the material is handed directly to another individual) or indirect (the material is left in a pile or 'cache' on the ground). As there is usually both division of labour and material transfer, a partitioned task requires multiple individuals working together for successful task completion.

Partitioned tasks require multiple individuals and undoubtedly involve some differences in work contribution. Often the initial stage of a partitioned task involves collection of a resource. Intermediate stages usually involve transport and final stages the processing, storage, or use of the material (see Ratnieks & Anderson 1999; Anderson & Ratnieks 2000). Partitioned tasks are characterized by the act of transfer itself, which clearly involves coordination of individuals: direct transfer requires that two individuals must meet at the same point in space and time whereas indirect transfer requires that 'collectors' from a cache must know, or at least be likely to encounter, where the 'depositors' have placed their material. These two factors, probable differences between subtasks and coordination required during transfer, suggest that a partitioned task is at least a high-complexity task.

Team and partitioned tasks have been placed at the same level of complexity. Is there any reason to suppose that one of these two task types is consistently more complex than all instances of the other task type? (In which case we could assign the four task types to four different complexity levels.) We suggest that this is not so. Below we propose that a team task may contain a partitioned subtask and a partitioned task may contain a team subtask. Consequently, there is no a priori reason to suppose that team tasks are always more complex than partitioned tasks or vice versa.

That task structure is an important but separate issue from task function can readily be appreciated in Table 1. We list examples of the same insect society task in terms of function, i.e. that of 'defence', but that vary in their structure. (Defence strategies in insect societies are reviewed in Hermann & Blum 1981; see also Evans & Schmidt 1990.) This list is somewhat tentative in that detailed behavioural observations may elevate some of the group tasks to team tasks if crucial division of labour is discovered. However, despite this, it is clear that diversity of task structure for a certain colony function exists.

TASK–SUBTASK RELATIONSHIPS IN INSECT SOCIETIES

When a task contains subtasks, for example in a team, the overall complexity of the task is only sensibly defined as the maximal amount of cooperation and coordination required in any part of the task, that is all of its constituent subtasks. Figure 1 illustrates the relationships between the four task types and details the possible subtask types that they may logically contain. In this section we
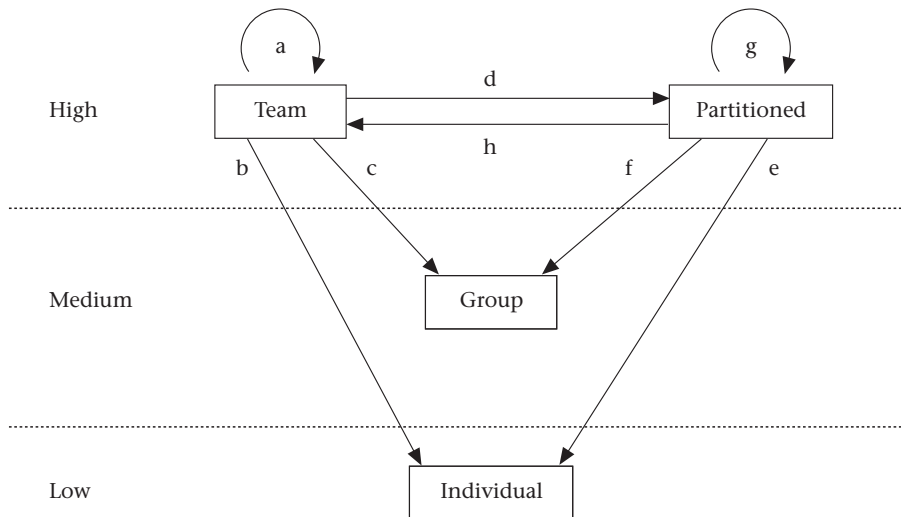
Figure 1. The relationships between the four task types proposed in insect societies: individual, group, team and partitioned tasks. We assign these four task types to three levels of complexity: low, medium and high (left). Individual tasks are of low complexity, group tasks are medium complexity, and team and partitioned tasks are high complexity. The arrows point to the different subtasks that may be contained within a task type, i.e. each logically 'allowable' (sub)task–subtask relationship. For example, arrow b pointing from 'team' to 'individual' suggests that a team task may contain a group subtask. Thus, both team and partitioned tasks may contain individual, group, team and partitioned subtasks. Each arrow a–h is discussed in the text.

examine this set of possible relationships in the light of examples drawn from the social insect literature.

A team task may potentially include team, individual and group subtasks (Fig. 1: arrows a, b and c, respectively). Nest construction in the African weaver ant *Oecophylla longinoda*, a proposed team task (Anderson & Franks, in press), exemplifies these three relationships. The nest is formed in a tree or bush by pulling neighbouring leaves together and gluing them with larval silk (Hölldobler & Wilson 1977, 1983). There are two main subtasks: workers must pull the leaves together (subtask 1), a group subtask (arrow c; the 'group' box in Fig. 2a), and at the same time they must be glued (subtask 2; Fig. 2a). This latter component is a team subtask (arrow a; the lower 'team' box in Fig. 2a) because to glue the leaves together requires two concurrent subtasks. First, a larva must produce the glue (silk) and at the same time a worker needs to move the larva around the region to be glued. These two individuals, the gluer and the larva work together as a functional unit. They each have a different subtask to perform, both of which are individual subtasks (Fig. 1 arrow b; the two 'individual' boxes in Fig. 2a), and they must be performed concurrently. In summary, the team task in *Oecophylla* nest construction is composed of a group subtask and a team subtask, the latter composed of two individual subtasks.

A team task containing a partitioned subtask (Fig. 1 arrow d) may occur during guarded slave maker raids, but further observations are needed to confirm this. Anderson & Franks (in press) suggested that slave-making ants may sometimes act as a team. During a raid, host workers tend to grab their brood and flee the nest. However, in some slave maker species, in particular *Protomognathus* (=*Harpagoxenus*) *americanus* and *Leptothorax* (=*Myrafant*) *duloticus*, a member of the raiding party acts as a guard at the nest entrance (Alloway 1979; Foitzik

et al. 2001). The guard prevents host workers escaping with brood thus ensuring there is brood to steal while other ants from the slave-making nest steal the brood. Structurally this is a team task, 'steal brood', with two individual subtasks: 'guard entrance' and 'capture brood' (Fig. 2c). Alloway (1979, page 206) and Wesson (1939, page 115) both mentioned that during raids that captured items, usually the less valuable items such as eggs or small larvae, were dropped outside the nest entrance. It is likely that these are later collected by members of the slave-making colony and taken back to the nest, and, if these are collected by a worker other than the one that dropped them, then it is a partitioned subtask (Fig. 1 arrow d). In laboratory colonies of *P. americanus*, brood items were sometimes abandoned, but were always collected later (S. Foitzik, personal communication). This issue will be resolved only by careful observations in which the identity of different individuals is distinguished.

Partitioned tasks certainly contain individual subtasks (Fig. 1 arrow e). Foraging in *H. mossambicus*, described earlier, is an example with two sequential individual subtasks (cutting and transport). Leaf retrieval in the leafcutter ant *Atta sexdens* is sometimes a partitioned task. One group of workers, 'arboreal harvesters', climbs trees and clips off leaves, which then fall to the ground. A second group, 'cache exploiters', collects the leaves and carries them to the main trail, leaving them in a 'cache' next to the trail. Finally, a third group, 'carriers', takes the leaves to the nest (Fowler & Robinson 1979). Thus, this is a three-stage process in which each stage is an individual subtask (Fig. 2d). Lastly, the seed-harvester ant *Messor barbarus* sometimes partitions forage retrieval with up to five transfers (Reyes & Fernández-Haegar 1999).

Group subtasks of a partitioned task (Fig. 1 arrow f) may occur in leafcutter ants (*Atta* spp.). Groups of workers will sometimes work together to drag a particularly large leaf
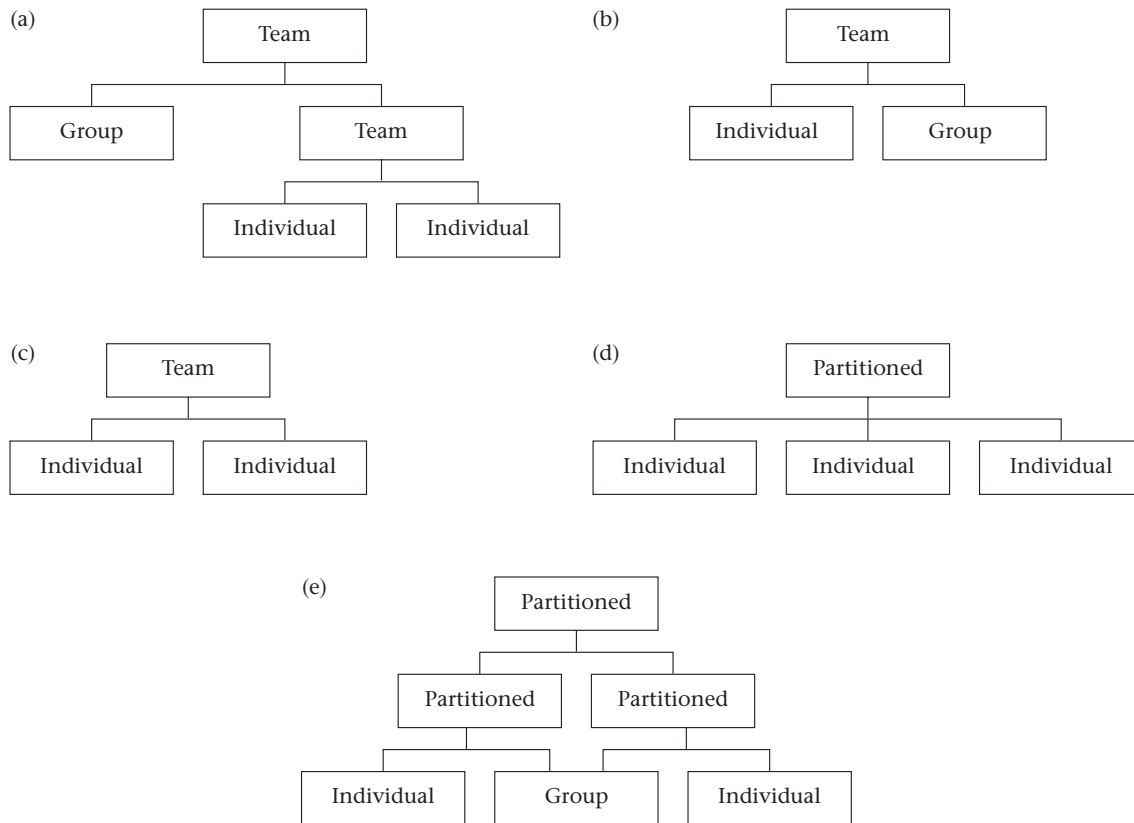
Figure 2. The hierarchical structure of various team and partitioned tasks. Each box represents a discrete task or subtask. (a) *Oceophylla* nest construction. (b) *Pheidole* decapitation, or prey retrieval in *Eciton* when there are several followers. (c) *Protomognathus* slave raid, or prey retrieval in *Eciton* when there is a single follower. (d) Leaf retrieval in *Atta*. (e) *Lasius* nest construction. See text for details. The complexity of a particular task can easily be quantified: substitute 3 points for each 'Team' or 'Partitioned', 2 points for a 'Group', or 1 point for an 'Individual'; the task's total score is a measure of task complexity.

or piece of stem towards the nest. If the material is abandoned and picked up and moved by another individual or group of individuals then this would qualify as a partitioned task with a group subtask.

Partitioned tasks may contain other partitioned tasks (Fig. 1 arrow g). One instance is nest construction in *Lasius fuliginosus* ants (Fig. 2e). One group of workers collects honeydew and regurgitates the material to builders back at the nest. This is the first partitioned subtask. At the same time, another group of ants collects soil particles and deposits them at the nest. The same builders take some soil and some honeydew and add this sticky substance to the nest (Dobrzańska 1966; see Figure 1 of Ratnieks & Anderson 1999). This is the second partitioned subtask. Thus, the whole partitioned task is composed of two partitioned subtasks, one for each of the two materials used. In addition there are three interacting groups of workers: honeydew regurgitators performing an individual subsubtask, soil depositors performing a different individual subsubtask, and finally builders performing a group subsubtask.

An example of a partitioned task containing team subtasks (Fig. 1 arrow h) may occur in *Eciton burchelli* army ants. During a raid, prey retrieved by *Eciton* transport teams is sometimes dumped in a booty cache. From here, it is either processed into smaller pieces or is later carried off. It is extremely unlikely that exactly the same ants would return to the cache to deal with the prey item; almost inevitably other ants will handle the item after it has been placed in the cache and therefore it is almost certainly a partitioned task (personal observation).

Team tasks are based upon concurrent action whereas partitioned tasks are based upon sequential action. If a team task were to contain a partitioned subtask would this be consistent with the task type definitions? We suggest that it would. For instance, suppose that *Oecophylla* nest construction is still a team task but instead individuals use pieces of spider's web to bond the leaves together (c.f. Baroni Urbani 1978; Hölldobler & Wilson 1983, page 490). Subtask 1 is a group subtask: 'bring the leaves together'. Subtask 2 is 'add spider's web to the seam'. The latter could be an individual subtask: each individual goes away and searches for a piece of web and adds it to the joint. There is no loss of concurrency: the leaves must be brought together as the web is added. However, subtask 2 could also be performed as a partitioned task: the material is supplied along a chain of individuals. This does not affect the concurrency issue of the task in question, the top-level team task. Whenever a task contains a team (sub)task and a partitioned (sub)task (as above), both high-complexity elements, it is the

(sub)task that is highest in the hierarchy that determines the overall task type.

Anderson & Franks (in press) stated that group tasks do not contain subtasks. We qualify this by stating that it is logically possible for a group task to contain a group subtask but it is unlikely to occur in practice, particularly for social insects. What would a group within a group involve? Such a task structure would require that each 'individual' of the top-level group is in fact a group of cooperating members in itself, but crucially there is no division of labour among all of the workers at all levels. Imagine a group of individuals constructing a tepee-like nest. Suppose that there are three groups of workers, each of which must position a stick against the other two sticks to form a tripod structure. Each of the three groups of individuals is performing the same subtask as the other two groups, positioning their stick. Thus, at this level there is no division of labour. If there is no division of labour within each of the three groups and so they simply need the combined effort of several workers to move and position the stick, then at this lower level there is also no division of labour. This multilevelled coordination, both within and between groups, is unlikely to occur in insect societies without some degree of specialization of the workers.

A MEASURE OF TASK COMPLEXITY

In the previous section we deconstructed tasks into their component subtasks, thus illuminating the hierarchical interrelationships among these subtasks, some of which are shown in Fig. 2. This deconstructionist approach provides a simple way of measuring task complexity. We assign 1 'complexity point' to an individual task or subtask, 2 points to a group (sub)task and 3 points to a team or partitioned (sub)task, thus reflecting the complexity level in which these tasks or subtasks have been assigned (Fig. 1). The focal task is deconstructed into its component subtasks one hierarchical level at a time (as above and in Fig. 2), the relevant points are assigned, and the number of complexity points is summed. The final result is a 'total score' which operates on an interval scale, meaning that it has properties of 'measures' and 'intervals' but not 'rational zero' (Stevens 1951). An example of a measure on this scale is 'degrees Celsius' in which 20 °C is hotter than 10 °C, but not twice as hot. Similarly, we do not claim that a 10-point task is twice as complex as a 5-point task, but the measure can be used to rank tasks in terms of their complexity.

Adopting the above procedure (formulating a task hierarchy, as in Fig. 2, and substituting '3' for every 'Team' or 'Partitioned' (sub)task, 2 for every 'Group' (sub)task, and 1 for each 'Individual' (sub)task), we find that nest construction in *Oecophylla* (Fig. 2a) is a team task (3 points) composed of a group subtask (2 points) and a team subtask (3 points). The team subtask is composed of two individual subtasks (2 × 1 point). Totalling these points gives a score of 10 points. Decapitation of intruders in *Pheidole* (Fig. 2b) scores only 6 points; it is a team task (3 points) composed of a group subtask (2 points) and an individual subtask (1 point). Slave maker raids with

guards (Fig. 2c) score 5 points: a team task (3 points) with two individual subtasks (2 × 1).

Quantifying the complexity of partitioned tasks is particularly straightforward since the act of transfer defines the top level of subtasks (but not subtasks within subtasks). Thus, forage retrieval in *H. mossambicus* scores 5 points: 3 because it is a partitioned task and 2 further points, one for each of the two individual subtasks. Similarly, the three-stage partitioning in *A. sexdens* (Fig. 2d) scores 6 points: 3+3 × 1. Almost all partitioned tasks are composed solely of individual subtasks, usually individual transport (see Ratnieks & Anderson 1999), thus the task complexity score for a partitioned task is usually 3 plus the number of stages. The minimum complexity score for both partitioned and team tasks is 5 points: the least complex forms of these tasks involve two individual subtasks (e.g. Fig. 2c).

Within a colony or species, some tasks may result in different scores in different situations. Army ant prey retrieval, another proposed team task (Franks 1986, 1987; Franks et al. 1999; Anderson & Franks, in press), is one such example. In both *Eciton burchelli* and *Dorylus wilverthi* a definite team structure occurs (Franks et al. 1999, 2001) in which there are two subtasks, 'front running' and 'following'. In *Eciton*, a single submajor, the 'front runner', tends to initiate the prey retrieval process by starting to move the prey (Franks 1986). Other ants, the followers, then join in to help. Often a group of followers is required to move the prey at the standard retrieval speed (Franks 1986). (There is a positive correlation between the mass of ants moving a prey item in a team and the weight of the prey, Franks 1986; Franks et al. 1999.) Thus, this has the same task structure as *Pheidole* decapitation: a team task (3) with one group subtask (2) and one individual subtask (1; Fig. 2b), thus scoring 6 points. However, at other times, a single additional ant, such as another submajor, is sufficiently large to perform the 'follower' subtask. In this situation then, prey retrieval is a team task (3) but with two individual subtasks (2 × 1; Fig. 2c) and scores only 5 points.

As this measure operates on the interval scale, averages can be meaningfully calculated, just as they can for temperature. For instance, 88% of *E. burchelli* teams contain a single follower (Franks 1986) with the remainder containing a group. Thus, the average complexity score is 0.88 × 5+0.12 × 6=5.12. What is not allowable, however, is to consider ratios of scores, for example to state that *Oecophylla* nest construction (10 points) is 10/6=66% more complex than *Pheidole* decapitation (6 points). The main use of this measure is to rank tasks; thus, of the four social insect team tasks discussed above we can objectively say that nest construction in *Oecophylla* is the most complex (10 points), followed by decapitation of intruders in *Pheidole* (6 points), then army prey retrieval (5 or 6 points), and finally guarded slave maker raids (5 points).

At first sight it may seem that our method contains some double counting of subtasks. For instance *Oecophylla* nest construction has just three 'terminal' subtasks (Fig. 2a: pulling leaves [Group], silk production

Table 2. Summary of the task complexity of some of the tasks discussed in the text

Task	(Sub)task type				Complexity score
	I (1)	G (2)	T (3)	P (3)	
Lasius fuliginosus nest construction	2	1	0	3	13
Oecophylla longinoda nest construction	2	1	2	0	10
Messor barbarus forage retrieval (when there are 5 transfers)	6	0	0	1	9
Atta sexdens forage retrieval (3-stage)	3	0	0	1	6
Decapitation of intruders in *Pheidole pallidula*	1	1	1	0	6
Eciton burchelli forage retrieval (when there is a group of followers)	1	1	1	0	6
Average *E. burchelli* prey retrieval team	1.88	0.12	1	0	5.12
Eciton burchelli forage retrieval (when there is a single follower)	2	0	1	0	5
Guarded slave-making raids	2	0	1	0	5
Hodotermes mossambicus foraging	2	0	0	1	5
Apis dorsata curtain	0	1	0	0	2
Cataglyphis foraging	1	0	0	0	1

I, G, T, and P represent the four (sub)task types, i.e. individual, group, team and partitioned, respectively. Numbers in parentheses signify the score associated with each (sub)task type.

[Individual] and moving larvae around the seam [Individual]) yet we add another two scores (of 3 points each) to the total, one for each 'team' component. This is not double counting but reflects the hierarchical structure of the task. A set of subtasks can be arranged in different ways, and a deeper or more complex hierarchy must surely generate a higher complexity score. This can easily be seen by comparing Fig. 2a (*Oecophylla*) with Fig. 2e (*Lasius*). Both these examples of nest construction contain two terminal individual subtasks and one terminal group subtask. However, *Lasius* clearly has a more sophisticated hierarchical structure and consequently scores 13 points ($3 \times 3 + 2 \times 1 + 2$) to *Oecophylla*'s 10 points.

DISCUSSION

In this study, we have examined the relationships between the four proposed task types in insect societies. The relationships are summarized in Fig. 1, and the hierarchical structure of various tasks is shown in Fig. 2. This technique of deconstructing tasks into their component subtasks enables the complexity of the task to be examined objectively. Table 2 summarizes the task structure and relative task complexity of a number of tasks discussed above. Importantly, this procedure is generic and taxon independent implying that if sufficient detail is known about the way any particular task in any particular taxon is tackled, then its task complexity can be assessed.

We have examined all of the possible hypothetical relationships between (sub)task types (Fig. 1). We find that insect societies could in principle exhibit all logically allowable relationships. There is no a priori reason to suspect that social insects are constrained to some subset of these relationships. Indeed, we have highlighted known examples for the majority of these relationships and suggest situations in which the few other relations not currently confirmed may occur (Fig. 1, arrows d, f and h). Thus, from theory and now specifically for

insect societies, we suggest that team tasks may contain individual, group, team or partitioned subtasks. In practice, neither group nor individual tasks contain subtasks.

That different species, or the same species or colony, may tackle a task in different ways at different times is not a concern (Anderson & Franks, in press). How a task is tackled ultimately depends upon the skills of the individuals available to perform the task. For instance, an ant may struggle inefficiently to drag a prey item by itself along a sparse trail, thereby classifying as an individual task, but work with others as a group or team on a busy trail when other workers are available. And what may be a group task in a monomorphic ant species may be a team task in a polymorphic species in which differing abilities between workers are more pronounced. (These issues are discussed further in Anderson & Franks, in press.) It is these differences that this measure is designed to capture, and allows one, potentially, to consider such questions as whether task complexity increases as an incipient colony grows and matures and its cast structure changes.

A related concern may be that our measure is sensitive to variation in descriptions of behaviours, and that behavioural descriptions, and therefore the complexity values associated with them, are in some sense arbitrary. Indeed, in the social insect literature, descriptions of behaviours in ant behavioural catalogues vary enormously yet comparisons of the 'same' task are often made (C. Anderson, unpublished data). The problem is well known in the morphological literature: how to identify and describe 'characters' in nonarbitrary ways (e.g. Wagner 2001). Thus, a necessary assumption here is that behaviours, or in morphological studies, characters, have some real structure to them, that the apparent structure is not imposed arbitrarily by our linguistic choices, and further that our impressionistic assessments, or gestalts, provide real access to that structure. In this view, variation in behavioural description is a source of noise, but the assumption is that a strong 'signal' can be deciphered.

Another possible concern is that colony complexity has a number of different aspects which our measure overlooks, such as degree of polymorphism, difficulty of tackling a particular subtask (individual tasks may well require higher cognitive abilities and greater information processing than group tasks and the subtasks within team tasks), number of types of interactions among individuals, and others (see Anderson & McShea 2001). Actually the omission is deliberate: our concern is only with behaviours, and in particular with the hierarchical organization of behaviours in the performance of colony tasks. Except for individual tasks, these units lie at a hierarchical level between an individual ant and the colony as a whole, and thus constitute what might be called 'intermediate-level parts' (Anderson & McShea 2001, in press; McShea 2001). Thus, we are not concerned (at least not directly) with complexity at lower levels, for example, with number of castes or even number of different task types; nor are we concerned with the complexity of individual ants, for example, with the number of different behaviours an individual is capable of performing (Anderson & McShea 2001). In principle, we might be able to design a single measure that combines all of these aspects, to produce a measure of what might be called 'overall colony complexity'. However, combining multiple independent aspects in a single measure would render it analytically unwieldy. And, if a correlation were found between overall complexity and another variable, say between overall complexity and colony size, we would then need to dissect complexity into its component parts to understand it. Our view is that it is more useful to treat each aspect separately, to develop a kind of tool kit of complexity measures and to apply them independently to investigate possible relationships with other variables. The measure developed here, which captures the hierarchical structure of intermediate-level task-performing units, or parts, is one such tool.

Our measure is promising as a useful metric for two reasons. First, its components (group, team and partitioned tasks) have already been shown to be significant in other contexts (Ratnieks & Anderson 1999; Anderson & Franks, in press; Anderson & McShea, in press). Second, and more generally, our hierarchical–deconstructionist approach to complexity has been used successfully elsewhere. For instance, Saunders (1995) used a hierarchical measure of sutural complexity to disprove Buckland's (1836) longstanding hypothesis that more complex ammonoid shells (in terms of septal folding) were both stronger and lighter. Also, Brakefield et al. (1996) made an intensive genetic study of eyespot patterns and their formation in the butterfly *Bicyclus anynana*. Based upon assessing the hierarchical structure of these eyespots, Yagil (1998, 1999) predicted that eight genes were required to produce such a pattern. His prediction falls within the empirical estimates from genetic backcrosses, i.e. 6.4–9.9 genes for females and 7.5–10.8 genes for males (Brakefield et al. 1996). Consequently, Yagil (1999, page 26) concluded that 'the utility of the complexity concept is in its ability to predict instructional requirements for pattern generation, in particular to predict coding requirements for patterns that have a code or blueprint behind them'. Drawing parallels, we ultimately hope that this hierarchical–deconstructionist approach will lead to a greater understanding of the number of different types of behaviours required in an insect society to achieve the complex and adaptive higher-level behaviour of the colony.

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