

## Review article

# Task partitioning in insect societies

F.L.W. Ratnieks<sup>1</sup> and C. Anderson<sup>2,3,\*</sup>

<sup>1</sup> Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK, e-mail: F.Ratnieks@sheffield.ac.uk

<sup>2</sup> School of Mathematics and Statistics, University of Sheffield, Sheffield, S3 7RH, UK

<sup>3</sup> Current address: Department of Zoology, Duke University, Durham, NC 27708, USA, e-mail: stp95ca@Sheffield.ac.uk

Received 22 June 1998; revised 14 October 1998; accepted 20 October 1998.

**Summary.** Task partitioning is the name given to the phenomenon in which a piece of work is divided among two or more workers, such as the partitioning of the collection of a load of forage between a forager and a storer or transporter. This study 1) reviews empirical data concerning the occurrence of task partitioning in insect societies with the general aim of drawing broad conclusions about its prevalence and diversity, and 2) considers the potential costs and benefits of task partitioning. The data show that task partitioning occurs in many species, with examples in ants, bees, wasps, and termites. The general impression is that it is an important and widespread feature of work organisation in insect societies. Nearly all examples concern foraging. There is much variation on the main theme. For example, in the number of intersecting cycles (2, 3 linear, 3 all interlocking), where transfer occurs (at the nest, at the forage site, on the trail back to the nest), whether transfer is direct or indirect (liquids such as nectar, water, and honeydew are always transferred directly whereas solids are transferred both directly and indirectly). Task partitioning is always subject to time costs. Benefits occur either through enhancement of individual performance (e.g., where task partitioning permits greater division of labour thereby utilising consistent differences in worker abilities caused by morphology or experience) or through enhancement of the overall system (e.g., where partitioning itself eliminates a constraint affecting task performance, such as when a forager can collect sufficient material for several builders). By causing a series organisation of work, task partitioning reduces system reliability but this effect may be minimal in all but very small colonies.

**Key words:** Task partitioning, foraging, task efficiency, task reliability, transfer.

## Introduction

The organisation of work in insect societies can be viewed in two main ways. Traditionally, a division of labour perspective has been adopted (Jeanne, 1986a) and has focused attention on individuals and the tasks they perform over a period of time ranging from hours to the whole working life (Oster and Wilson, 1978; Jeanne, 1986a; Robinson, 1992). Attention can also be directed onto the work itself, particularly towards a feature of work organisation called “task partitioning”, a novel term coined by Jeanne (1986a) that describes the situation in which two or more individuals contribute sequentially to a particular task or piece of work (Jeanne, 1986a, 1991).

The difference between division of labour and task partitioning is perhaps most easily visualised as follows. Division of labour is the division of the workforce among the range of tasks performed in the colony, whereas task partitioning is the division of a discrete task among workers. That is,

$$\text{division of labour} = \frac{\text{workers}}{\text{tasks}},$$

and

$$\text{task partitioning} = \frac{\text{task}}{\text{workers}}.$$

A straightforward example of task partitioning occurs in nectar collection in the honey bee. At the nest, foragers transfer their nectar to bees working within the nest, known as storers or receivers, who then deposit the nectar into cells (shown schematically in Fig. 1; Fig. 2c). Nectar collection is therefore partitioned between foragers and receivers, with each load of nectar being partitioned. Honey bees also show division of labour between foragers and receivers, with the latter being younger bees (Seeley, 1985; Winston, 1987; Seeley, 1995). This illustrates an important point. Task partitioning and division of labour are not mutually exclusive alternatives in the organisation of work (Jeanne, 1991). In fact, by divi-

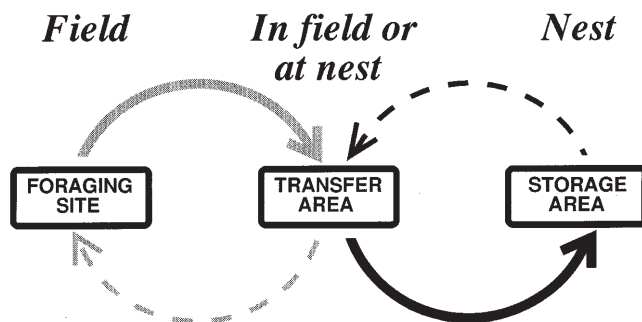
\* Author for correspondence.

ding the nectar collection task into the separate subtasks of foraging and receiving, task partitioning can facilitate greater division of labour (Fig. 1). In addition to dividing nectar collection into two subtasks, task partitioning also causes a novel feature to appear: transfer between forager and receiver. Moreover, it is the material itself that is required to link the various subtasks in a partitioned task. Division of labour can occur with unrelated tasks but task partitioning requires explicit linking of related tasks, i.e., sequential stages in the handling and processing of material.

Implicit in the definition of task partitioning is the definition of a task. We consider a task to be a discrete unit of work that must be completed. In foraging, the complete task is the collection, retrieval, and use or storage of a load of forage. Clearly, the task is incomplete if forage is collected but brought only part way to its point of use or storage. In foraging, the task is both unified and discretised from other tasks by the physical nature of the forage. In this sense the total work of foraging is composed of many tasks – the individual loads of forage being connected.

It may be helpful to define three categories of tasks:

1. *partitioned task* – a task divided sequentially among two or more workers (Jeanne, 1986a), such as the collection and storage of nectar by the honey bee.
2. *group task* – a task requiring the cooperation of several workers in order for successful completion of the work. For example, during the establishment of a dominance hierarchy in *Dinoponera quadricaps* several workers may work together to immobilise a nestmate (T. Monnin and C. Peeters, unpubl. manuscript).
3. *team task* – a group task which requires a combination of workers with particular skill, such as size or strength. That is, “members of different castes that come together for highly coordinated activity in the performance of a particular task” (page 343 of Hölldobler and Wilson, 1990). For example, in *Pheidole pallidula* minor workers immobilise conspecific intruders and a major worker then cuts off its head (Detrain and Pasteels, 1992). Teams may be “superefficient” (Franks, 1986) in that the combined abilities of the group is more than simply the summed total of individual abilities.



**Figure 1.** A schematic representation of a two-stage partitioned task. The solid lines represent the flow of material (task partitioning) and the grey and black lines the flow of collectors and users (division of labour) respectively

Task partitioning is a relatively new subject. The purpose of this paper is to broaden the empirical and conceptual base of task partitioning. We do this by addressing two important areas. The first is empirical data, for which we provide a general review of examples of task partitioning. These examples have been obtained from a scattered literature, with the relevant information frequently mentioned only in passing as part of a broader study. The aim is not to provide a complete survey of all existing data, which would in any case be nearly impossible given its scattered and fragmentary nature, but to provide examples illustrating the diversity of task partitioning patterns that occur. The second area addressed is the costs and benefits of task partitioning, including the effect of task partitioning on system reliability.

### Examples of task partitioning

All the examples of task partitioning below concern the collection of food and other materials, and typically involve partitioning between foragers and storers or transporters. The only examples of task partitioning not in foraging that we are currently aware of are in the excavation of nest chambers in *Pogonomyrmex* (D.M. Gordon, pers. comm.) and the removal of old fungus garden in *Atta* (J. Bot, pers. comm.). These examples still concern the movement of material in and out of the nest but whether there are examples of a partitioned task performed entirely within the nest is unknown. Possibly, this lack of knowledge is due to deficiencies in our survey of the literature, or due to the literature itself being biased towards studies of foraging. However, we think it is more likely that the apparent importance of task partitioning in foraging but not in other areas of work is a real phenomenon. One reason for this is that although many non-foraging tasks involve multiple workers, the “units” of work are relatively independent of each other. For example, a larval honey bee will be fed many times during its life by nurse workers. However, the degree to which a later nurse worker continues or completes the task of an earlier nurse is much lower than in foraging, in which the collection, retrieval and storage of the foraged material unifies the subtasks and the partitioning of the overall foraging task among more than one worker. Nevertheless, despite our failure to find examples we feel it is probable that examples of task partitioning do occur outside foraging and encourage others to seek and publish them.

Below we discuss task partitioning in foraging under a number of headings relating principally to variation in transfer of the foraged material. The categories chosen are not all mutually exclusive, as in 2) with 5) and 6). One most important feature of transfer, direct versus indirect transfer, is not used at all in this categorisation but is referred to, and later more specifically addressed in “Transfer and handling properties of the material” (also Table 1). Direct transfer means transfer between two individuals (or groups), as when a honey bee receiver takes nectar regurgitated from the mouth of a forager. Indirect transfer

**Table 1.** Task partitioning in foraging for a variety of materials, and the relationship between the mode of transfer (direct and indirect) and the physical properties of the material (solid and liquid). In the category titles *a)–f)*, *C* and *U* denote the collection and use of the material, *i. e.*, the source and final destination of the material, arrows represent the transport of the material to the next stage, and *D* and *I* represent direct and indirect transfer

Material	Phase	Taxon	Reference
<i>a) Two stages with indirect transfer: C → I → U</i>			
Grass	Solid	<i>Hodotermes mossambicus</i>	Leuthold et al., 1976
Millipedes	Solid	<i>Probolomyrmex dammermani</i>	Ito, 1998
Termites	Solid	<i>Megaponera foetens</i>	Longhurst and Howse, 1979
Termites	Solid	<i>Leptogenys ocellifera</i>	Maschwitz and Mühlenberg, 1975
<i>b) Two stages with direct transfer: C → D → U</i>			
Nectar	Liquid	<i>Apis mellifera</i>	Seeley, 1995
Nectar	Liquid	<i>Vespula</i>	Jeanne, 1991
Honeydew	Liquid	<i>Oecophylla longinoda</i>	Hölldobler, 1984
Honeydew	Liquid	<i>Formica obscuripes</i>	King and Walters, 1950
Honeydew	Liquid	<i>Formica rufa</i>	Stäger, 1935, 1939
Honeydew	Liquid	<i>Myrmecocystus mimicus</i>	Hölldobler and Wilson, 1990
Water	Liquid	<i>Apis mellifera</i>	Seeley, 1995
Seeds	Solid	<i>Messor</i>	Sudd, 1965
Insect prey	Solid	<i>Daceton armigerum</i>	Wilson, 1971
Propolis	(Solid)	<i>Apis mellifera</i>	Ribbands, 1953
Cocoons	Solid	<i>Polyergus rufescens</i>	P. D’Ettorre, pers. comm.
(Intruders)	Solid	<i>Pheidole pallidula</i>	Detrain and Pasteels, 1992)
<i>c) Two stages with direct and indirect transfer: C →<sup>D</sup> →<sub>I</sub> → U</i>			
Insect prey	Solid	<i>Ectatomma ruidum</i>	Schatz et al., 1996
Insect prey	Solid	<i>Ectatomma quadridens</i>	Schatz et al., 1996
<i>d) Two stages with direct or no transfer: C →<sup>D</sup> →<sub>→</sub> U</i>			
Insect prey	Solid	Polistinae and Vespinae	Jeanne, 1991
Nectar	Liquid	Polistinae and Vespinae	Jeanne, 1991
Water	Liquid	Polistinae	Jeanne, 1991
<i>e) Two stages with direct, indirect, and no transfer: C →<sup>D</sup> →<sub>→</sub> U</i>			
Leaves	Solid	<i>Atta cephalotes</i>	Hubbell et al., 1980
<i>f) Three (or more) stages with indirect transfer: C → I → I → U</i>			
Leaves	Solid	<i>Atta sexdens</i>	Fowler and Robinson, 1979
Leaves	Solid	<i>Atta saltensis</i>	Daguerre, 1945
Insect prey	Solid	<i>Lasius fuliginosus</i>	Dobrzańska, 1966
Insect prey	Solid	Polistinae	Jeanne, 1991

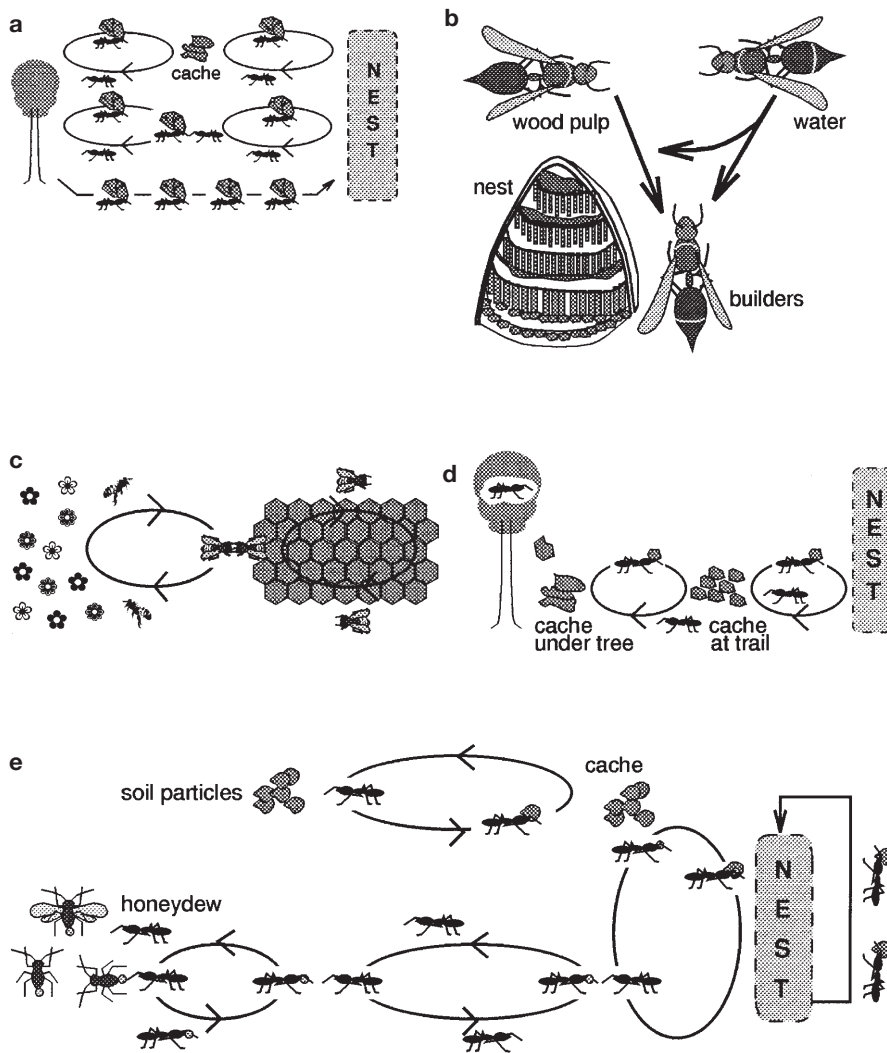
means transfer via a temporary cache or dump site as when a leaf cutter ant places a leaf fragment on a pile on the ground near the trail for others to collect. Only direct transfer requires physical pairing between workers.

### 1. Tasks not partitioned

Foraging without task partitioning is extremely common, and may be the sole means of handling forage, as in bumble bees, *Bombus*, which transfer neither pollen nor nectar (Michener, 1974). Of the four materials collected by honey bee foragers (nectar, pollen, water, propolis) only pollen is not partitioned, the other materials all being transferred directly to receivers in the nest (Fig. 2 c).

### 2. Tasks sometimes partitioned

Foraged material may sometimes, but not always, be transferred. In *Vespula* wasp colonies, nectar is directly transferred in large colonies but not in small colonies (Akre et al., 1976; Jeanne, 1986b). *Vespula* colonies grow from a single queen and zero workers in spring to as many as 5000 workers at the end of the ergonomic phase of their annual life cycle (Greene, 1991) suggesting that this changeover from no transfer to transfer is an adaptive response to changing colony size. Similarly, Schatz (B. Schatz, pers. comm.) reports that in *Ectatomma ruidum* ant colonies of less than 16 workers, “hunters” always hunt for insects and transport the prey back to the nest themselves. However, in colonies of 21 workers or more, the task becomes partitioned between



**Figure 2.** Examples of task partitioning. a) direct, indirect, and no transfer of leaves in *Atta cephalotes*, b) nest construction in *Polybia occidentalis*, c) nectar transfer in the honey bee, d) three-stage indirect transfer of leaves in *Atta sexdens*, and e) direct and indirect transfer of the two materials used in nest construction in *Lasius fuliginosus*

hunting by “stingers”, with direct or indirect transfer of prey to a second group, “transporters”, who carry it to the nest (Schatz et al., 1996). There is an intermediate response in colonies of size 17–20 where there is some partitioning of the task. Data in Table 11.2 of Jeanne (1991) suggest that in polistine wasps, both transfer and no transfer occur in swarm-founded and independent founded species, and it is common for returning foragers to share pulp, prey and water with nestmates. In swarm-founded species transfer is the rule and no transfer rare, with the reverse in non-swarm-founded species such as *Polistes*.

Figure 2a shows the case of the leaf cutter ant *Atta cephalotes* (Hubbell et al., 1980) in which direct, indirect, and no transfer occur simultaneously. The first foragers at a new patch do not carry their leaf fragments back to the nest, but only as far as the main trail, where fragments are usually either dropped or transferred to other “carrier” workers who take them back to the nest (Hubbell et al., 1980). However, first foragers sometimes take their leaf fragments all the way back to the nest themselves. The proportion dropping or transferring their load decreased from 89% to 25% from the

first to the fifth ten-minute period following the discovery of an artificial food patch of bread crumbs. It is suggested that first foragers transfer their loads in order to return to the newly established food patch more quickly and easily, given that the new patch is at first only tenuously linked to the main trail by a pheromone trail laid by just a few ants.

### 3. Transfer at the foraging area

Transfer of material may take place at the foraging area. *Hodotermes mossambicus*, a harvesting termite, partitions foraging for grass stems. Workers of one group climb grass stems and cut off pieces 2–6 cm long and deposit them in a pile below, which are carried back to the nest by other workers (Leuthold et al., 1976). Minor workers of *Oecophylla longinoda*, the African weaver ant, transfer honeydew gathered from scale insects directly to major workers for transport back to the nest (Hölldobler, 1984; Fig. 13–38 of Hölldobler and Wilson, 1990). This is also true of *Formica obscuripes* (King and Walters, 1950). Wilson (1971) suggests



that the minor workers, being smaller, are more efficient at extracting the honeydew from the homopterans than the majors, whereas the major workers can carry a greater volume in their crops and so are more efficient at transport. Size differences also appear to be important in *Megaponera foetens*, an obligate termite-hunting ant. Major workers open up a termite nest and the smaller minor workers enter it to hunt for termites (Levieux, 1966; Longhurst and Howse, 1978; Brian, 1983). Minor workers deposit the termites in a pile outside the prey's nest and major workers carry them home. This is also similar to termite hunting in the ant *Leptogenys ocellifera* (Maschwitz and Mühlenberg, 1975).

#### 4. Transfer en route to the nest

Transfer of material may also take place en route to the nest and may involve many stages. In *Atta sexdens* (Fig. 2d; Fowler and Robinson, 1979) leaf fragments are transferred indirectly between “arboreal cutters” and “cache exploiters”, and “cache exploiters” and “carriers”. The cutters climb trees and cut leaves. The leaves fall to the ground, which acts as a cache, where they are retrieved and cut up by the exploiters, who take the pieces to the foraging trail for transport to the nest by carriers (Fowler and Robinson, 1979). Similar organisation of leaf foraging in *Atta* is found in *A. saltensis* (Daguerre, 1945), and Hubbell et al. (1980) report that dropping leaves from trees sometimes occurs in Costa Rican *A. cephalotes*. This process in which an item is sequentially passed from one group to another has been dubbed “bucket brigade” (Fowler and Robinson, 1979), “relay principle” (Goetsch, 1934), and “chain transport” (Stäger, 1935; Dobrzańska, 1966). (See Wilson, 1971, pages 292–293.)

*Lasius fuliginosus* a monomorphic ant, demonstrates an additional advantage to this type of relay mechanism. Foragers spend several days on end patrolling a section of the colony's foraging area and rest in “outstations” (Dobrzańska, 1966). When an insect is captured, it is taken to the nearest outstation and transferred directly or indirectly to workers within the station who then relay it to the next station where it is transferred to another group and so on until the material reaches the nest. Thus, workers specialise spatially and shuttle between two outstations on a trail which allows them to move over the ground “efficiently and faultlessly” (Dobrzańska, 1966). Whereas *L. fuliginosus* uses a series of transfer sites at “known” locations, the outstations, to transport prey back to the nest, in other species direct transfer can occur at various locations on the way back to the nest on a more flexible basis. For instance, in *Daceton armigerum*, medium-sized workers usually capture prey, but when they encounter a larger worker on their return journey, usually at an outstation, the item is taken off them with the bigger forager completing the journey, presumably “close to the maximum possible speed” (Wilson, 1962, 1971). Sudd (1965) reports that in *Messor* seed-harvester ants, returning foragers readily give up their seeds to “newcomers” travelling in the opposite direction. This may have some unknown

informational benefit, such as the availability of certain seed species, especially as *Messor* are known to specialise on individual seed species even if presented with a mixture of three species (Rissing, 1981).

#### 5. Transfer at the nest

Some foraged items are collected and transported to the nest by one individual and then transferred to intranidal workers for immediate use, further processing, or storage. One example is nectar collection and storage in the honey bee described previously (Fig. 2c). Similar examples are found in *Polybia* and *Polistes* wasps (Jeanne, 1991). Foragers of the ponerine ant, *Probolomyrmex dammermani*, specialise on preying millipedes (Ito, 1998). A forager captures the prey and carries it back to the nest chamber itself where other workers remove setae and legs, and dump the waste material at the nest entrance. In many of the examples described so far, it is conceivable that there are further stages of the partitioned task, concerned with the processing of the foraged items, inside the nest. For instance, in *Atta*, leaves brought back to the nest are cut into finer pieces by small nest workers for cultivating fungi (Hölldobler and Wilson, 1990).

We have recently come across an example of a partitioned task with transfer at the nest which constitutes a new form of task partitioning as it involves two species: the first species is found in the foraging group and the second is the forage material itself. Raiding parties of the slave-making ant *Polyergus rufescens* retrieve cocoons which are deposited outside the nest and which are then brought into the nest by other workers (P. D'Etorre, pers. comm.). We encourage other researchers to document other such examples.

The bounds of task partitioning are open to interpretation and some examples are less obvious, or even arguable, cases of task partitioning. For instance, in the honeypot ant, *Myrmecocystus mimicus*, returning foragers regurgitate nectar and honeydew to “repletes” or “honeypots”, members of a caste who act as living storage vessels (Hölldobler, 1984). Clearly, there is direct transfer from one group of workers, foragers, to another, honeypots, and these two groups perform different roles, collection and storage. This example appears to fulfill the general criteria for a partitioned task. However, as the honeypots' job is literally to hang around and do nothing, it is arguable that they are a passive component of the task. This situation is equivalent to nectar foraging in *Bombus*, which is not partitioned, and where nectar is stored in a wax pot. The only difference is that honeypot ants use a living “pot”. A second example is found in *Pheidole pallidula* in which minor workers pin down intruding ants and later major workers arrive to decapitate the intruders (Detrain and Pasteels, 1992). In this example there are elements of a partitioned task, group task, and team task. The partitioning element occurs in that the first subtask (pinning down) is performed by one group before the second subtask (decapitation) is performed by a second group or individual. The group element is provided by the cooperation of several workers. The team element is the cooperation of physically different workers

with synergistic skills, such as the ability of soldiers but not workers to decapitate intruders.

### 6. Tasks involving more than one material

Foraged items required in nest construction may also be partitioned, and may involve more than one material, typically a solid and a liquid, and several groups of workers. *Polybia occidentalis* (Fig. 2b) and *Lasius fuliginosus* (Fig. 2e) both forage for two types of material to use in nest construction and involve three groups of workers. Note that in comparison to *A. sexdens* (Fig. 2d) these examples are not linear in their task partitioning. In *P. occidentalis* there are two groups of foragers collecting building materials, wood pulp and water. On returning to the nest, foragers directly transfer wood pulp and water to receivers, who then build nest carton and comb (Jeanne, 1986b). At the nest, water foragers also directly transfer water to pulp foragers who use the water to soften the wood they are collecting. In *L. fuliginosus* there are also two independent sets of foragers, collecting honeydew from aphids and particles of soil or organic matter (Hölldobler and Wilson, 1990). The honeydew is transferred directly to builders. Particles are indirectly transferred after being dumped near the nest carton within the nest cavity.

### 7. Conclusions

The above examples show the great diversity that exists. Within a single species different materials may be transferred or not (e.g., nectar vs. pollen in the honey bee). Within a single species (e.g., honeydew vs. particles in *L. fuliginosus*) or even a single type of material (leaf fragments in *A. cephalotes*) there may be both direct and indirect transfer. The two most complex systems, involving two cycles of foragers interlocking with one of receivers, both occur for building materials. This complexity almost certainly reflects the nature of building, which in both cases requires builders to use two materials simultaneously. Conversely, food materials such as pollen and nectar need not be combined before storage or use, and the task partitioning is primarily a relay mechanism.

### Transfer and the handling properties of material

Given the diversity described above, what are the factors that determine whether or not transfer occurs, and whether transfer is direct or indirect? In species with trophallaxis, liquids such as nectar, honeydew, and water can presumably be directly transferred simply, quickly, and without spillage or waste. Liquids are straightforward to transfer, but this may not always be the case with solids. One possible reason that honey bees do not transfer pollen is that this would be difficult given the physical properties of the pollen. A foraging honey bee combs the pollen adhering to her body hairs into the pollen baskets (corbiculae) on her hind legs, where it is

compressed and mixed with nectar to form a pellet. Setae surrounding and inside the pollen basket help to keep the pellet in place (Michener, 1974). It would be very difficult to transfer the pellet from the pollen baskets of a forager to the pollen baskets of a receiver. Possibly, a receiver could remove pollen pellets using her mandibles and then transfer the pellet to a storage cell, but this would not be an efficient process because two receivers would be needed, one to unload each of the forager's two pollen baskets.

Foraging honey bees also collect propolis (sticky tree resin) in the pollen baskets. But unlike pollen, the propolis is transferred to receivers at the nest (Huber, 1814; Butler, 1949; Ribbands, 1953). Why is propolis but not pollen transferred from the pollen baskets? It has been suggested that a forager cannot easily unload the sticky propolis herself (Alphonsus, 1933). In some cases a propolis forager waits many hours, or even overnight, to be unloaded, suggesting that propolis transfer is subject to relatively great transfer inefficiencies. However, propolis is collected by a very small proportion of foragers, so that inefficiencies in its collection will not greatly reduce the ergonomic efficiency of the colony as a whole.

Although solid, leaves (*Atta cephalotes*), seeds (*Messor*), wood pulp (*Polybia*), and insect prey (*Polybia*, *Daceton*, and *Ectatomma*) are transferred directly between workers in some species, but they could in principle be transferred indirectly. These materials are held in the mandibles by foragers and transfer is presumably easy and efficient, perhaps even easier than the transfer of liquids given that a reasonably discrete object is being handled and is held outside and not within the forager's body. In *P. occidentalis*, Jeanne (1986b) reports that transfer of pulp (6.7s, 16.1s) is quicker than transfer of water (35s, 45s) (durations are for "large" and "small" colonies, and include time searching for a transfer partner). Average nectar transfer durations in the honey bee range from 40s to 80s depending on study and experimental conditions (Seeley, 1986; Kirchner and Lindauer, 1994). In addition, direct transfer may incur fewer losses of material than indirect transfer in material which is potentially prone to theft from competitors and other types of loss. Direct transfer may take place only when a worker encounters another who can increase the task efficiency, i.e., the speed at which the task is performed, such as in the larger workers of *Daceton armigerum* who run faster than the medias (Wilson, 1971). Also, as hinted earlier, in *Messor* direct transfer may have some informational benefit. The costs and benefits of task partitioning are specifically discussed later.

Direct transfer is the rule with liquids. Obviously, direct transfer of nectar and water in the honey bee is an effective way of preventing these liquids from being lost, but, in principle, a system of indirect transfer could also work. For example, a wax "trough" just inside the nest entrance into which foragers unload, and from which receivers fill up. However, such indirect transfer of liquids could not occur without the evolution of a new structure built by the bees, or the change in use of an existing structure. In the honey bee, returning nectar foragers could easily regurgitate their load into designated "transfer cells" near the nest entrance, elimi-

nating search and queueing delays. Receivers could then transfer the nectar to other areas of the hive.

In contrast to liquids, the physical properties of some solid materials are well suited to indirect transfer. Indirect transfer of leaves occurs in *Atta* (Figs. 2a and d) and of grass stems in *Hodotermes* (Table 1) and obviously the physical properties of these materials lend themselves well to being dropped or placed on the ground for later retrieval. The ground serves as an effective and convenient dump site or cache. In *A. cephalotes*, both direct and indirect leaf transfer (and also no transfer) occur. It is likely that direct transfer results in fewer leaf fragments being lost, but the co-occurrence of the two transfer methods seems to indicate that no one method is necessarily superior. A great loss of forage material during indirect transfer occurs in *A. sexdens* because only 53% of the leaf material dropped from the trees by arboreal cutters is collected (Fowler and Robinson, 1979). Dropping whole leaves eliminates a great deal of time-consuming walking up and down trees. Because leaves must be cut into small fragments to be carried, each leaf that is dropped takes the place of not one but many round trips up and down the tree. The ergonomic benefits to be gained from having arboreal cutters and indirect transfer by leaf dropping can be appreciated by realising that only 0.1–0.5% of foragers are arboreal cutters (Fowler and Robinson, 1979). A second factor reducing the cost of transfer loss to the ants is that the loss occurs early in the collection process, before much work has been put into each item of forage. A similar transfer loss occurring at the nest would be more costly, because each item of forage would by then have had additional work put into it.

In summary, when liquids are transferred, they are necessarily passed directly between workers. Some solid materials are too difficult to transfer, such as pollen, or virtually impossible to collect and use *without* direct transfer, such as propolis. However, most solid materials could in theory be transferred indirectly but may not be for a variety of reasons.

### Costs and benefits of task partitioning

Task partitioning and division of labour open new opportunities for increasing the efficiency with which forage is collected and processed (Jeanne, 1986a). However, as hinted in the previous two sections, there are costs as well as benefits. These costs and benefits are discussed in detail in this section and are divided into three broad categories: factors which affect task *efficiency* (Table 2), i.e., the amount of material that can be processed per unit time or effort; factors which affect task *reliability*, i.e., factors that affect the probability of material completing the task sequence; and *others*. Some of the major costs and benefits are shown schematically in Table 3.

The aim is to set out all of the possible factors that may affect efficiency or reliability of partitioned tasks. Unfortunately, it is difficult to predict a priori which are the most important because costs and benefits differ among species. However, some generalisations are made, where possible. Efficiency gains of task partitioning were briefly discussed by Jeanne (1986a) and Wilson (1971), the only two previous discussions of the subject. We take the opportunity here to re-examine Jeanne's claims in the light of the further knowledge and broader context presented in this paper.

**Table 2.** The costs and benefits of factors that affect task efficiency, i.e., the amount of material processed per unit time or effort

Category	Costs and Benefits
i. Specialisation (performance efficiency)	<b>Benefits:</b> through morphological or behavioural specialisation, some workers may be more suited to a task than others and perform it more quickly or efficiently. <b>Costs:</b> a worker may become overspecialised and become less efficient at other tasks if required to perform them.
ii. Differential abilities	<b>Benefits:</b> a worker who specialises on a task, and happens to have innately above average skills will be more efficient than the average worker. <b>Costs:</b> conversely, specialisation by below-average workers will reduce average efficiency.
iii. Differential experience	<b>Benefits:</b> a worker who has particularly good knowledge, such as a short-cut to a food patch, will perform tasks more quickly. <b>Costs:</b> conversely, workers with poor knowledge may expend unnecessary time and effort to perform the task.
iv. Material handling efficiency	<b>Benefits:</b> by decoupling the tasks, the task with the lowest performance efficiency no longer limits the efficiency of the whole sequence, and the efficiency of the task can rise to limits of the constraints imposed by that task.
v. Search delays	<b>Costs:</b> time spent searching for a transfer partner.
vi. Transfer delays	<b>Costs:</b> time spent transferring material.
vii. Unavoidable queueing delays	<b>Costs:</b> even at optimal worker allocation queueing delays occur due to stochastic arrival of workers.
viii. Avoidable queueing delays	<b>Costs:</b> if the colony is not at optimal worker allocation, the group in excess experiences queueing delays which reduce ergonomic efficiency which could be avoided by appropriate recruitment and task-switching.
ix. Recruitment costs	<b>Costs:</b> recruitment mechanisms, such as dancing in honey bees, take time and effort.
x. Recruitment errors	<b>Costs:</b> inappropriate recruitment, such as recruiting workers to the group in excess, can reduce ergonomic efficiency.

**Table 3.** Interplay of performance efficiency, material handling efficiency, and material processing rates. Assume there are two subtasks: collection ( $C$ ) which takes a generalist  $t_1$  seconds to complete, and utilisation ( $U$ ) which takes a generalist  $t_2$  seconds to complete. Secondly, assume that if there is task partitioning, then there is a delay  $d$  which incorporates search delay, unavoidable queuing delay and transfer delay. Lastly, assume that if there is specialisation, then there is some performance efficiency factor  $\theta_i > 1$  which determines how much better specialists are at performing a task than generalists. Thus, if  $\theta_1$  is 2 then first subtask specialists are twice as good as generalists and thus it only takes  $t_1/\theta_1$  seconds to complete the first subtask

Category	Schema $t_0 \longrightarrow$ time	Efficiency costs and benefits	
		A) time required to process 1 unit of material	B) # items processed by colony/unit time
a) No task partitioning		$t_1 + t_2$ : “standard”	# foragers/ $(t_1 + t_2)$ : “standard”
b) TP with no performance efficiency, i.e., $\theta_1 = \theta_2 = 1$ .		$t_1 + d + t_2$ : the additional delay $d$ makes it longer than standard	less than standard: reduced by a factor of $\frac{t_1}{t_2 + d}$ for collectors and $\frac{t_2}{t_2 + d}$ for users
i) optimal worker allocation			
ii) excess of collectors		$t_1 + d + q + t_2$ : the additional delays $d$ and the unavoidable queuing delay $q$ make it longer than standard	less than standard: users work at full capacity but collectors are slowed by a factor of $\frac{t_1}{t_1 + d + q}$
iii) excess of users		as standard	less than standard: collectors work at full capacity but users are slowed by a factor of $\frac{t_2}{t_2 + d}$
c) TP with performance efficiency, i.e., $\theta_1 > 1$ and/or $\theta_2 > 1$		$\frac{t_1}{\theta_1} + d + \frac{t_2}{\theta_2}$ : faster than standard more standard if $\frac{t_1(\theta_1 - 1)}{\theta_1} + \frac{t_2(\theta_2 - 1)}{\theta_2} > 2d$	more than standard if $\frac{t_1(\theta_1 - 1)}{\theta_1} + \frac{t_2(\theta_2 - 1)}{\theta_2} > 2d$
d) TP with handling efficiency, e.g., pulp forager can collect 3 units of pulp		$t_1 + 2d + t_2$ on average: slower than standard	collector can collect more loads per trip
e) TP with handling efficiency and performance efficiency		$\frac{t_1}{\theta_1} + 2d + \frac{t_2}{\theta_2}$ on average. Faster than standard if: $\frac{t_1(\theta_1 - 1)}{\theta_1} + \frac{t_2(\theta_2 - 1)}{\theta_2} > 2d$	more than standard as collector can collect more loads per trip and complete more trips/hr

## Task efficiency

According to Jeanne (1986a), the efficiency of a task can be increased in two main ways (see Box 1 right). Firstly, gains in efficiency may arise from gains in individual performance, i.e. factors that are independent of what others are doing. Jeanne classifies these as “efficiency gains at the level of the individual” and incorporates “performance efficiency” and “spatial efficiency”. Secondly, gains can arise from the overall organisation of the task, “efficiency gains through organisational changes” (Jeanne, 1986a), and are independent of the gains at the level of the individual. These include “material handling efficiency” and “worker allocation efficiency”. Each of these four sub-categories will be discussed as well as the additional factors that affect task efficiency in Table 2.

The first three categories in Table 2i–iii, specialisation and differential abilities and experience, are classified under “performance efficiency” – how well an individual performs a task – by Jeanne (1986a). Task efficiency can be increased by some form of morphological or behavioural specialisation

### Box 1: Efficiency gains arising from task partitioning as hypothesised by Jeanne (1986a)

- efficiency gains at the level of the individual
  1. performance efficiency
    - (a) increased skill through repetition
    - (b) differential experience
    - (c) differential abilities
  2. spatial efficiency
- efficiency gains through organizational changes
  3. material handling efficiency
  4. worker allocation efficiency



which increases the ability of an individual to perform a task (Table 3: a) vs. c)). Task partitioning enhances division of labour with resulting efficiency gains through specialisation. Examples discussed in the earlier examples section include: 1) foraging in *Formica obscuripes* and *Oecophylla* in which small workers, because of their size, are more efficient at milking scale insects than larger and faster running transporters; 2) *Daceton armigerum* medias who relinquish their prey to larger foragers who run faster; and 3) foraging in *Lasius fuliginosus* in which prey are transferred to workers familiar with a particular patrolling area and who consequently run faster. Jeanne (1986a) states “if the worker specializing in the task happens to have above average innate ability to perform the task, efficiency will be greater than if performed by the average worker”. This is true. However, by chance below-average workers may also specialise on that task and cause decreased efficiency. If we consider differences among workers within a caste, but not between members of different castes then “differential abilities” and “differential experience”, which reflect variation in individuals arising from morphology and learning, are likely to be selectively neutral. This is because it is just as likely that a below-average worker, whether in terms of knowledge or innate ability, will specialise on a particular task than an above-average worker. On average there will be no net effect.

Concerning spatial efficiency, Jeanne (1986a) notes,

“If a worker specializes on the cluster of tasks performed in a given location in the nest and the sites for these tasks are interspersed, the worker can reduce the time spent searching for the next task by performing each task as it is encountered, rather than sticking to one task.” (Also, see Seeley, 1982.)

Jeanne considers this an efficiency gain but we disagree with this and consider it as a way of minimising costs, in terms of search delays and travel time, that are directly caused by task partitioning. This is discussed in more detail later.

The fourth category in Table 2 is “material handling efficiency” and operates through the organisation of multiple individuals (Jeanne, 1986a; see Table 3: a) vs. d) and e)). Consider a sequence of two subtasks. If one individual performs both subtasks then the efficiency of the whole task is constrained by the limiting task. For example, in *Polybia* a forager can collect more pulp than can easily be handled by a single builder. By partitioning this into subtasks of foraging and building, building is no longer a constraint on foraging and less pulp collecting trips need to be made per unit of nest construction. Note that this example does *not* require any gains in individual abilities: pulp foragers and builders could periodically switch between tasks and task partitioning would still be beneficial. Basically, the novel organisation makes better use of individual abilities. A similar situation occurs with *Atta sexdens*. By partitioning between arboreal cutters and cache exploiters, efficiency is increased. (However, in *A. sexdens* there may also be individual efficiency gains because the two types of workers were of different sizes (Fowler and Robinson, 1979).) In the honey bee, partitioning

between foragers and receivers reduces the amount of time a forager needs to spend in the nest at the end of a foraging trip. Task partitioning will increase the number of trips a forager can make to a current known patch before that patch declines and a forager needs to locate a new patch. (Flower patches turn over rapidly and recruitment through waggle dancing is quite unreliable as often the advertised patch is not found by the recruit (Seeley, 1995).) The partitioning will increase efficiency because it will increase the number of foraging trips made during a lifetime as time is saved both from less time searching for new patches and less time spent in the nest per foraging trip. This is shown schematically below where a nectar foraging trip is represented by ■■■, a scouting trip for a new forage site by ■■■■, and the period spent in the nest between trips by a gap:

a) no task partitioning



b) task partitioning



The main novel feature of task partitioning in foraging is transfer, and this introduces time costs not found in unpartitioned tasks. Task partitioning introduces time costs in terms of 1) search delays (time spent searching for a transfer partner); 2) queueing delays (both “avoidable” and “unavoidable” time spent waiting for the arrival of partners at the transfer area, Anderson and Ratnieks, 1999a, b); and 3) transfer delays (time spent transferring the material between workers). The magnitude of these costs depends on whether the transfer is direct or indirect, the nature of the material being transferred (solid vs. liquid), and the relative work capacities of interacting groups (Table 3b). Generally, unless access to the cache is restricted, workers depositing material in a cache experience no delay and workers collecting material from a cache experience a delay only if the cache is empty. This assumes that cache location is fixed so that collectors do not waste time searching for the cache, which is not necessarily true in *Ectatomma ruidum* (Schatz et al., 1996). With direct transfer the queueing delays, which are absent from direct transfer, may provide good information about the relative work capacities (Anderson and Ratnieks, 1999b). However, the size of the cache itself may also provide useful information. A large or rapidly increasing cache is probably a good indicator that the work capacity of the “depositors” exceeds that of the “collectors”. Transfer delays may be negligible, especially with respect to solid materials such as direct transfer of leaves in *Atta* and seeds in *Messor*. Even when transfer delays occur, they may be relatively small in relation to the total length of the whole partitioned task. Because the arrival of workers at the transfer area is stochastic there will always be some queueing delays as workers wait for partners when indirect transfer occurs. These delays will be minimised, but still present (unavoidable delays) when the work capacities of the two groups are matched, and will rapidly increase in magnitude as the difference in work capacities of the two groups increases (avoidable delays). These ideas are devel-

oped by Anderson and Ratnieks (1999a, b). Another potential recruitment cost is that individuals must act on information, which is unlikely to be perfect, in order to make recruitment decisions. There are likely to be recruitment errors, for example recruitment of workers to the subtasks already with excess work capacity.

Task partitioning requires recruitment or task-switching mechanisms to maintain appropriate worker allocation between subtasks in order to minimise search and queueing delays. Costs arise here from the time and effort required in performing the recruitment procedure, such as dancing in honeybees.

With respect to worker allocation efficiency, Jeanne (1986a) considers two groups of workers, foragers and builders, and states that “how well their activities are coordinated affects the efficiency of the whole operation” and that “Just the right proportions of foragers and builders must be engaged to *minimize the waiting times* experienced by workers at each task...” [our italics]. Although we agree with these statements, we feel that the focus should be on the fact that waiting times arise as a direct result of task partitioning and in that sense, ignoring any individual level efficiency gains, task partitioning will always be less efficient than no task partitioning (Table 3: a) vs. b)). Altering worker allocation at best minimises these delays and thus should be considered as a cost of task partitioning. Any delay in achieving optimal allocation will result in avoidable queueing delays thereby reducing task efficiency (Anderson and Ratnieks, 1999b).

### Task reliability

Specialisation by workers may enhance not just the speed at which a task is completed (performance efficiency), but also individual reliability: the probability of completing the task correctly. In this respect, individual reliability is directly analogous to individual performance. Experience through repetition at performing a task may improve an individual’s skills so that it is more reliable. For example, by knowing how to collect or transport a specific forage item. However, as with performance efficiency there is a potential cost if that worker switches to another task.

Another aspect of reliability is the reliability of the whole “system”. One of the proposed major advantages of sociality is that a series-parallel arrangement of tasks (Oster and Wilson, 1978) increases the reliability of the whole task sequence (e.g., nest construction, provisioning, etc.) in comparison to that of the nest of a single female. In the case of a forage collection system, task partitioning can break this into two subsystems, collecting and storing. How does this affect foraging system reliability? Reliability has been defined (Oster and Wilson, 1978) as the probability that the work can be performed, meaning that there is at least one worker performing each essential task. For example, when task partitioning occurs forage collection is possible if there is at least one collector and one storer. However, without task partitioning forage collection is possible with only one worker

who performs both subtasks. This suggests that task partitioning actually reduces system reliability. This is illustrated in Box 2.

Formally, it can easily be shown that task partitioning reduces reliability. Consider a situation in which  $n$  workers are available and can be allocated in one of two ways. Either (case 1, no task partitioning) all  $n$  are collector/storers or (case 2, with task partitioning)  $k$  are collectors and  $n-k$  are storers. In case 1 all the workers work in parallel. In case 2 there is a series-parallel arrangement. Within a subtask workers are in parallel, but the two subsystems are linked in series (see also Oster and Wilson, 1978, page 12). We assume that one of the subtasks is performed within the nest, e.g. storage, and the other is performed outside the nest, e.g. collection. Defining  $f$  as the probability that any one worker fails (e.g., dies) on the external subtask and workers never fail on the internal subtask, the probability that the whole system in case 1 fails is  $f^n$ . In case 2 the system fails if either subsystem fails. (For example, there are collectors but no storers, or storers but no collectors). The probability that a sub-system in case 2 fails is greater than the probability that the whole system in case 1 fails. This is because each sub-system has fewer than  $n$  workers in it. This case is general for all  $n$  and any number of series-linked subsystems.

However, even if reliability is reduced by task partitioning, the effect will be minimal in all but very small colonies. With  $n$  large the probability of failure in both cases 1 and 2 is close to zero. In making this conclusion we have assumed that individual failure is not affected by task partitioning. However, if task partitioning reduces individual failure task partitioning could give a more reliable system. For example, in *Lasius* task partitioning between different groups of transporters may decrease individual failure, because transporters only work within an area they know well and therefore have a reduced probability of becoming lost and dying. Task switching may also reduce the cost of task partitioning on subsystem reliability. For example, if many foragers die then storers switch to foraging to maintain system reliability until only one worker remains at which point the system fails.

Another dimension of reliability is retrieval reliability: the probability that an item of forage is actually brought back to the nest and used or stored. In *Atta sexdens*, only 53% of leaves cut by arboreal cutters were retrieved by cache exploiters, and so forage reliability of this first stage of foraging is low. However, as leaves were not in limiting supply and leaves are relatively easy to cut the cost is low and there is probably a benefit in that cache exploiters can more easily locate fallen leaves. (Leaves are presumably easier to find in the canopy of a tree than on the ground below.) In this example it is probably important that losses occur early in the sequence when little collection effort has been invested into the material.

## Box 2: system reliability

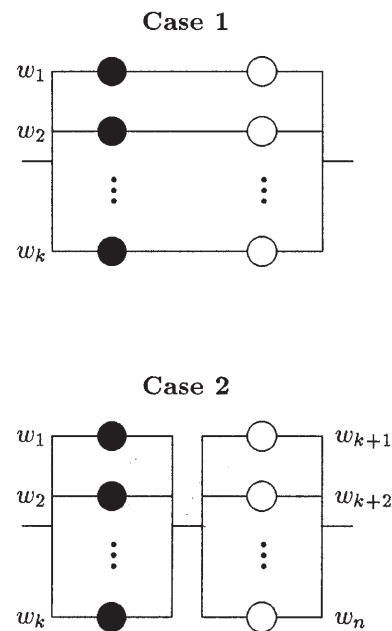
Consider a task such as nectar collection and processing in the honey bee. Assume that there are  $n$  workers available and that these can be organised in one of two ways:

Case 1 — there is no task partitioning and all  $n$  workers perform both tasks, i.e. a parallel-series arrangement (Oster and Wilson, 1978).

Case 2 — task partitioning occurs and there are  $k$  foragers (sub-system 1) and  $n - k$  storsers (sub-system 2), i.e. a series-parallel arrangement (Oster and Wilson, 1978). Because workers only perform a single task, they complete twice as many single tasks per unit time than workers in case 1.

Assume that there is constant probability of failure, e.g. death per foraging trip (Visscher and Dukas, 1997) which we denote as  $f$  (a “failure”). In case 1, failure occurs if all  $n$  workers die and this occurs with probability  $f^n$ . In case 2, failure of the system occurs if sub-system 1 fails. Sub-system 2 never fails as there is no mortality of storsers. To compare failure rates between case 1 and case 2 we must consider the probability that a forager dies during the two trips (which is equivalent in time to a single combined foraging/storing trip in case 1) which is  $2f - f^2$ . Therefore the failure rate of the system in case 2 is  $(2f - f^2)^k$ . Case 2 is thus less reliable as  $f < 2f - f^2$  (they are exposed to a higher death rate per unit time) and  $k < n$  (there are less workers in the group) and so  $(2f - f^2)^k > f^n$ .

More generally, if the two tasks vary in danger, then we have the situation in which the individual mortality in case 1 is intermediate between the individual mortalities in subsystem 1 and subsystem 2. Because both subsystems 1 and 2 have fewer than  $n$  workers, at least one of the case 2 subsystems has greater failure than the overall case 1 system. If mortality is random, i.e. unconnected to work, then case 2 is still less reliable as there are fewer workers in each sub-system.



## Miscellaneous costs and benefits

Task partitioning increases worker-worker interaction through direct transfer of material and recruitment mechanisms. This has a potential benefit in the spread of information through the colony. In the honey bee, this could be the sugar concentration of the collected nectar (Seeley, 1995) or possibly even the smell of the flower species that the forager has been collecting from. However, on the downside, a potential cost of this increased rate of interaction between workers is increased spread of parasites and disease. This could come about through indirect transmission via the material, or the interaction between workers when direct transfer occurs. See Schmid-Hempel (1998).

Lastly, one other benefit of task partitioning is that it may allow novel materials to be used which would otherwise be

unworkable or unfeasible in the absence of this type of organisation. One suggested example is that of propolis collection in the honey bee in which workers are unable to unload themselves (Ribbands, 1953).

## Discussion

The review section of this paper presents examples of task partitioning in ants, bees, wasps, and termites. The data show that task partitioning is a taxonomically widespread feature of foraging in insect societies and has evolved multiple times. Although our data do not allow us to determine what proportion of insect societies have task partitioning in foraging, the general impression we have gained is that it occurs in a substantial proportion of species, but probably not in the majori-

ty. As researchers who began to study task partitioning approximately two years ago we have been surprised at the large number of examples that we have found.

When task partitioning in foraging occurs there is considerable diversity in the details. Where transfer takes place and whether it is direct or indirect both vary among and even within species, even for the collection of the same material. This diversity is not surprising, and much of it reflects the varying contingencies and biology of different species and types of forage. Drawing together overall principles is not easy. One that is quite apparent is that when task partitioning occurs in winged species (wasps and bees) transfer is always at the nest. However, in species with walking foragers (ants and termites) transfer may also occur away from the nest. Typically, this occurs in order to allow a group of workers that are more efficient at retrieval, either due to their superior local knowledge of the way to the nest (*Lasius fuliginosus*, Dobrzańska, 1966) or more suitable morphology (honeydew collection in *Oecophylla* (Hölldobler, 1984) and *Formica* (King and Walters, 1950)), to carry out this subtask. There are probably two main reasons why winged species do not have transfer away from the nest. First, workers in bees and wasps show much less morphological variation than do ants and termites so there will be reduced individual efficiency gain. Secondly, retrieval by flying offers less opportunity for meeting nestmates on the way to the nest.

Additional principles appear in relation to the type of forage and direct versus indirect transfer. Direct transfer is always used for liquids whereas solids are transferred both directly and indirectly. Even for the same species and the same material, such as leaf fragments in *Atta* (Hubbell et al., 1980), there may be both direct and indirect transfer. However, this is not necessarily a complication in the actual performance of the transfer. It may simply mean that a forager about to put forage in a cache will also give it to another worker if there is one waiting at the cache location. In the honey bee, it seems that transfer has proceeded as far as it can usefully do so, with pollen pellets, which we argue cannot easily or efficiently be transferred, being the only material that is not transferred. Nectar, water and propolis are all transferred. It is perhaps surprising that indirect transfer of liquids apparently does not occur in bees, which could use cells as a dump site. Obviously, in the absence of a suitable dump site liquids cannot be cached, whereas solids can simply be cached on the ground.

Turning to the costs and benefits of task partitioning, work efficiency can be enhanced by effects of task partitioning at both individual and organisational levels. Organisational effects work primarily through a specific benefit of the transfer itself. Good examples of the latter are *Polybia occidentalis* (Jeanne, 1986b), in which task partitioning allows foragers to collect larger wood pulp loads because they can now unload to multiple receivers, and *Atta sexdens* (Fowler and Robinson, 1979), in which partitioning between arboreal cutters and cache exploiters, together with the help of gravity, allows a great saving in walking up and down tree trunks. In many cases the benefits are much harder to pinpoint. In the honey bee, we suggest that nectar collection may be parti-

tioned because it allows foragers to work fewer patches of flowers in their foraging career, thereby reducing the number of costly patch changeovers. Much of the benefit from task partitioning through individual level effects arises through enhancement of division of labour. We are at least hopeful that our listing of the various costs and benefits is fairly complete and provides, together with Jeanne (1986a), a starting point for further study.

One important point about task partitioning is that it always results in some time being wasted such as in searching or queueing for a transfer partner. In this respect indirect transfer is more efficient because a cache can serve to even out fluctuations in the arrival rates of foragers and receivers. Especially in the honey bee and also in *Polybia occidentalis* there is good evidence that delays in waiting for a transfer partner are used by foragers to optimise the foraging system, either by recruitment (honey bee) or by task switching (*Polybia*, Jeanne, 1986b). Although it is tempting to consider this as a benefit of task partitioning, it is more logical to consider it as a means of reducing the costs. In a system where each individual is both a forager and a receiver or builder then the system is automatically balanced, at least in those species in which a forager and a receiver can handle equal amounts of material. This is likely to be the case in honey bees because the crops of foragers are unlikely to be different in capacity to those of receivers. However, as mentioned above foragers and builders do have different material handling capacities in *Polybia*.

Reliability is a factor which looms large in discussions of the benefits of sociality (Oster and Wilson, 1978). In particular, the reliability of a colony of a few individuals is likely to be much greater than the reliability of a single insect, in the building and provisioning of a nest. The greater reliability arises from the parallel operations in insect societies which introduces redundancy. Task partitioning introduces a series arrangement into a task, and on the surface this would seem to reduce reliability. However, in societies that are medium-sized or large the reliability of each subtask-group will only be slightly lower than if task partitioning did not occur. Furthermore, this effect is only a problem in species in which each subtask is composed of workers who show division of labour and cannot easily be replaced. For example if one subtask is carried out by morphologically specialised workers. Where no division of labour occurs then task switching could quickly cause additional workers to perform the other subtask. Similarly, when division of labour without morphological specialisation occurs recruitment can replace missing workers. Where colonies are large or even medium sized reliability in the sense of "at least one worker left to perform the task" is not really an issue – obviously one nectar forager would not do much for a honey bee colony. When reliability is considered not at the level of the whole colony but at the level of the collection of each item of forage, there is even a good example of low reliability being efficient, in the case of leaves dropped by arboreal cutters in *Atta sexdens*. Leaves are not in limiting supply and can cheaply be cut, so it is of little consequence that only about half are retrieved.



In the areas covered by this study, task partitioning offers considerable scope for further study. On the one hand there is a need for more “alpha” studies, which report on the existence of task partitioning. This will help to determine the importance of task partitioning in insect societies as a whole. Allied to this is the possibility of discovering general patterns that fall outside those we have reported. For example, task partitioning not in foraging, indirect transfer of liquids, the intersection of four cycles. Another area of great interest is studies which go beyond documenting the existence of task partitioning, but gather quantitative data on the various costs and benefits, such as the quantification of performance efficiency ( $\theta$  in Table 3). In this respect, of particular use as model systems are societies in which the mode of transfer or the actual occurrence of task partitioning is variable within a species for a single type of forage. As we show in Table 1 several such societies are already known. However, even if costs and benefits can be quantified, it may be difficult or impossible to translate them to a fitness measurement. One area of task partitioning has already received much study. The regulation of the numbers of workers performing foraging and receiving in the various subtasks (Seeley, 1995; Jeanne, 1986; Anderson, 1998).

## References

- Akre, R.D., W.B. Garnett, J.F. MacDonald, A. Greene and P. Landolt, 1976. Behavior and colony development of *Vespula pensylvanica* and *V. atropilosa* (Hymenoptera: Vespidae). *J. Kansas Entomol. Soc.* 49: 63–84.
- Alphonsus, E.C., 1933. Some sources of propolis. Methods of gathering and conditions under which this work is done. *Gleanings in Bee Cult.* 61: 92–93.
- Anderson, C., 1998. *The Organisation of Foraging in Insect Societies*. Unpublished Ph.D. Thesis, School of Mathematics, University of Sheffield, UK. 224 pp.
- Anderson, C. and F.L.W. Ratnieks, 1999a. Task partitioning in foraging: general principles, efficiency and information reliability of queueing delays. In: *Information Processing in Social Insects* (C. Detrain, J.-L. Deneubourg, and J.M. Pasteels, Eds.), Birkhäuser Verlag, Basel, (in press).
- Anderson, C. and F.L.W. Ratnieks, 1999b. Task partitioning in insect societies (I): effect of colony size on queueing delay and colony ergonomic efficiency. *Am. Nat.*: (in press).
- Brian, M.V., 1983. *Social Insects. Ecology and Behavioural Ecology*. Chapman and Hall, London. 372 pp.
- Butler, C.G., 1949. *The Honeybee: An Introduction To Her Sense-physiology and Behaviour*. Oxford University Press, Oxford. 226 pp.
- Daguerre, J.B. 1945. Hormigas del género *Atta* Fabricius de la Argentina. *Revta Soc. argent. Ent.* 12: 438–460.
- Detrain, C. and J.M. Pasteels, 1992. Caste polyethism and collective defense in the ant, *Pheidole pallidula*: the outcome of quantitative differences in recruitment. *Behav. Ecol. Sociobiol.* 29: 405–412.
- Dobrzańska, J., 1966. The control of the territory by *Lasius fuliginosus* Latr. *Acta Biol. exp. (Warsaw)* 26: 193–213.
- Fowler, H.H. and S.W. Robinson, 1979. Foraging by *Atta sexdens*: seasonal patterns, caste, and efficiency. *Ecol. Entomol.* 4: 239–247.
- Franks, N.R., 1986. Teams in social insects: group retrieval of prey by army ants (*Eciton burchelli*, Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 18: 425–429.
- Goetsch, W., 1934. Untersuchungen über die Zusammenarbeit im Ameisenstaat. *Z. Morph. ökol. Tierre* 28: 319–401.
- Greene, A., 1991. *Dolichovespula* and *Vespula*. In: *The Social Biology of Wasps*, (K.G. Ross and R.W. Matthews, Eds.), Cornell University Press, Ithaca, New York. pp. 263–308.
- Hölldobler, B. 1984. The wonderfully diverse ways of the ant. *Nat. Geog. mag.* 165: 778–813.
- Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, Mass. 732 pp.
- Hubbell, S.P., L.K. Johnson, E. Stanislav, B. Wilson and H. Fowler, 1980. Foraging by bucket-brigade in leaf-cutter ants. *Biotropica* 12: 210–213.
- Huber, F., 1814. *Nouvelles Observations sur les Abeilles*, II. 2nd Ed., English translation by C.P. Dadant (1926). Dadant and Sons, Hamilton, Illinois. 314 pp.
- Ito, F., 1998. Colony composition and specialized predation on millipedes in the enigmatic ponerine ant genus *Probolomyrmex* (Hymenoptera, Formicidae). *Insectes soc.* 45: 79–84.
- Jeanne, R.L., 1986a. The evolution of the organization of work in social insects. *Mon. Zool. Ital.* 20: 119–133.
- Jeanne, R.L., 1986b. The organization of work in *Polybia occidentalis*: the costs and benefits of specialization in a social wasp. *Behav. Ecol. Sociobiol.* 19: 333–341.
- Jeanne, R. L., 1991. Polyethism. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, Eds.), Cornell University Press, Ithaca, New York. pp. 389–425.
- King, R.L. and F. Walters, 1950. Population of a colony of *Formica rufa melanotica* Emery. *Proc. Iowa Acad. Science* 57: 469–473.
- Kirchner, W.F. and M. Lindauer, 1994. The causes of the tremble dance of the honeybee, *Apis mellifera*. *Behav. Ecol. Sociobiol.* 35: 303–308.
- Leuthold, R.H., O. Bruinsma and A. van Huis, 1976. Optical and pheromonal orientation and memory for homing distance in the harvester termite *Hodotermes mossambicus* (Hagen) (Isopt., Hodotermitidae). *Behav. Ecol. Sociobiol.* 1: 127–139.
- Levieux, J., 1966. Note préliminaire sur les colonnes de chasse de *Megaponera foetens* F. (Hymenoptera Formicidae). *Insectes soc.* 13: 117–126.
- Lindauer, M., 1961. *Communication Among Social Bees*. Harvard University Press, Cambridge, Mass. 143 pp.
- Longhurst, C. and P.E. Howse, 1979. Foraging recruitment and emigration in *Megaponera foetans* (Fab.) (Hymenoptera: Formicidae) from the Nigerian Guinea savanna. *Insectes soc.* 26: 204–215.
- Maschwitz, U. and M. Mühlenberg, 1975. Zur Jagdstrategie einiger orientalischer *Leptogenys*-Arten (Formicidae: Ponerinae). *Oecologia* 20: 65–83.
- Michener, C.D., 1974. *The Social Behaviour of Bees: a Comparative Study*. Harvard University Press, Cambridge, Mass. 404 pp.
- Oster, G.F. and E.O. Wilson, 1978. *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton, New Jersey. 352 pp.
- Ribbands, R., 1953. *The Behaviour and Social Life of Honeybees*. Bee Research Association, London. 352 pp.
- Rissing, S.W., 1981. Foraging specializations of individual seed-harvester ants. *Behav. Ecol. Sociobiol.* 9: 149–152.
- Schatz, B., J.P. Lachaud and G. Beugnon, 1996. Polyethism within hunters of the ponerine ant, *Ectatomma ruidum* Roger (Formicidae, Ponerinae). *Insectes soc.* 43: 111–118.
- Schmid-Hempel, P., 1998. *Parasites in Social Insects*. Princeton University Press, Princeton, New Jersey. 392 pp.
- Seeley, T.D., 1986. Social foraging by honeybees: how colonies allocate foragers among patches of flowers. *Behav. Ecol. Sociobiol.* 19: 343–354.
- Seeley, T.D., 1989. Social foraging by honeybees: how nectar foragers assess their colony’s nutritional status. *Behav. Ecol. Sociobiol.* 24: 181–199.
- Seeley, T.D., 1995. *The Wisdom of the Hive*. Harvard University Press, Cambridge, Mass. 295 pp.

- Stäger, R., 1935. Über Verkehrs- und Transportverhältnisse auf den Strassen der Waldameise. *Rev. Suisse Zool.* 42: 459–460.
- Stäger, R., 1939. Neue Beobachtungen und Versuchsanstellungen mit Ameisen. *Mitt. Naturforsch. Ges. Bern, 1938*: 1–15.
- Sudd, J.H., 1965. The transport of prey by ants. *Behav.* 25: 234–271.
- Visscher, P.K. and R. Dukas, 1997. Survivorship of foraging honey bees. *Insectes soc.* 44: 1–5.
- Wilson, E.O., 1962. Behavior of *Daceton armigerum* (Latreille), with a classification of self-grooming movements in ants. *Bull. Mus. Comp. Zool.* 127: 403–422.
- Wilson, E.O., 1971. *The Insect Societies*. Harvard University Press, Cambridge, Mass. 548 pp.