REVIEW

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Task partitioning in leafcutting ants

Abstract A task is said to be partitioned when it is split into two or more sequential stages and material is passed from one worker to another; for instance, one individual collects a material from a source and passes it to another for transportation back to the nest. In this study, we review the existence of task partitioning in leafcutting ants (Attini) and find that, across species, this form of work organisation occurs in all stages of leaf collection, leaf transportation, and leaf processing within the nest; in the deposition of refuse (leaves and spent fungal garden) to internal or external dumps; and in colony emigration. Thus, task partitioning is shown to be a very important component of work organisation in leafcutting ants. Examples mostly concern *Atta* but task partitioning is also known in *Acromyrmex*. The costs and benefits of task partitioning of the various stages are discussed and suggestions for further research are highlighted.

Keywords Task partitioning · Material transfer · Leaf processing · Waste management · *Atta* · *Acromyrmex*

Introduction

Colony work organisation is a dominant theme in social insect research (Oster and Wilson 1978). One major study area has been division of labour (e.g., Oster and Wilson 1978; Frumhoff and Baker 1988; Robinson and

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Page 1988; Tofts 1993; Franks and Tofts 1994; reviewed in Beshers and Fewell 2001). However, division of labour studies are primarily concerned with how the workforce is divided among different tasks. This is only one aspect of work organisation. A complementary aspect that focuses on the organisation of the work itself is task partitioning. Task partitioning (Jeanne 1986) describes situations in which tasks are subdivided into sequential subtasks linked by material transfer (Ratnieks and Anderson 1999a, b). Thus, task partitioning concerns how a task is divided among workers. Partitioned tasks are considered one of four fundamental task types, the others being individual tasks, group tasks, and team tasks (Anderson and Franks 2001; Anderson et al. 2001; see also Anderson and McShea 2001).

One example of a partitioned task is observed in the polymorphic weaver ant *Oecophylla longinoda* in which small workers collect honeydew from scale insects and regurgitate it to larger workers for transportation back to the nest (Hölldobler 1984). [Note that this example also includes division of labour, with different-sized workers specialising upon a particular subtask. In fact, task partitioning often enhances division of labour (Ratnieks and Anderson 1999b).] However, just because a colony partitions one of the materials it collects does not necessarily mean it partitions all materials. For example, honey bee (*Apis mellifera*) foragers collect nectar, water, propolis, and pollen. Whereas the collection and storage of nectar, water, and propolis are partitioned between foragers and nest-based receiver or food-storer bees, the collection and storage of pollen is not partitioned, with foragers storing pollen loads directly in cells themselves (Seeley 1995). In task partitioning, transfer may be of two types, direct, as in *Oecophylla* and all the honeybee examples above, or indirect, in which material is placed on the ground in a cache (an example of which will be discussed in detail below).

Ratnieks and Anderson (1999b) consider task partitioning an overlooked aspect of work organisation and deserving of further study. Recent studies have shown that task partitioning is of particular significance in leaf-

cutting ants (Attini: *Atta* and *Acromyrmex*). These New World ants live in large colonies [10^4–10^6, with *Atta sexdens* reaching perhaps 8 million workers (Hölldobler and Wilson 1994)] and cultivate a symbiotic fungus in underground fungus gardens (Weber 1972). The ants are obligately dependent upon the fungus as food for brood and to a lesser extent for adults, who also derive some nutrition from leaf sap. The fungus is grown on highly processed mulch prepared in the fungus gardens from plant material collected by foragers. This enterprise inevitably produces waste in the form of exhausted fungus garden and culture medium. A leafcutting ant colony can, therefore, be thought of as a factory orchestrating a flow of material from the environment, through the fungus gardens, and back to the environment as waste.

Our aim in this review is to bring together both recent work and scattered examples from the literature to provide an overview of task partitioning in leafcutting ants. Most of the data available concern *Atta*, but wherever possible we provide data on *Acromyrmex*. A further aim is to draw attention to promising areas for future research, as well as to highlight novel features of task partitioning in leafcutting ants. Examples include task partitioning within the nest and in the removal of waste, and novel advantages of task partitioning such as for nest hygiene. Task partitioning has now been studied in almost all aspects of material handling in *Atta* and these studies have decisively shown it to be a sophisticated, important, and sometimes crucial feature of work organisation.

Task partitioning in foraging

We define foraging as the collection and transport of plant material to the nest. Collection often involves cutting leaf or petal fragments directly from a plant but also includes scavenging material lying on the ground (e.g., fallen petals, seeds, and fruits), especially during the dry season (Weber 1972). Task partitioning in foraging can occur both between initial cutting or collecting from the plant or ground and transportation, and also within the transportation stage itself, for example, when a leaf fragment is transferred between two or more ants as it travels to the nest.

Task partitioning between collection and transport

Task partitioning with indirect transfer at the leaf source

Foraging without task partitioning between cutting/collection and transport (i.e., non-partitioned forage retrieval) is the usual situation in leafcutting ants (Weber 1972; Hölldobler and Wilson 1990; Hart and Ratnieks 2001a). That is, a forager collects a piece of forage and carries it back to the nest. However, as early as 1831, an alternative strategy involving two-stage task partitioning between arboreal leaf 'cutters' and terrestrial leaf 'carriers' had been observed:

Lund states that, when on a voyage of exploration in Brazil, he was very much astonished to hear, during calm weather, a noise like rain, caused by leaves falling to the ground. He was standing under a laurel tree 12 feet high, having coriaceous leaves which were detached, although having their natural green color, thus having no resemblance to diseased leaves. He saw then that each petiole had upon it an ant that was trying to cut it off. Each leaf severed and thrown to the ground was seized by the *Oecodomas* [*Atta cephalotes*], who immediately cut it up and carried the fragments to their nest. In less than an hour the tree was stripped and resembled a gigantic broom. (Heim 1898, reporting Lund 1831a, b)

Two-stage partitioning between cutting and carrying also occurs in *A. sexdens* (Fowler and Robinson 1979; also stated without reference in Vasconcelos 1990). Furthermore, it appears that in this species the roles of cutter and carrier are partly size defined, showing that some division of labour occurs, with arboreal cutters significantly smaller and more variable than leaf carriers. The opposite size specialisation occurs in *A. laevigata* where arboreal cutters are larger workers (Vasconcelos and Cherrett 1996). Leaf dropping is also found in *A. cephalotes* (Hubbell et al. 1980), *A. colombica* (A.G.H, personal observation), *A. laevigata* (Vasconcelos and Cherrett 1996), *A. saltensis* (Daguerre 1945), and *A. texana* (McCook 1909). In addition, leaf dropping occurs in *Acromyrmex*: in the desert-dwelling leafcutting ant, *A. versicolor versicolor*, 30 of 60 ants studied cut a leaf and transported it back to the nest without partitioning and 14 of 60 leaves were cut and fell to the ground with the ant still attached and without partitioning. However 16 of the ants cut leaves that were allowed to drop to the ground and "were collected by foraging colony members on the following day prior to any resumption of cutting" (Gamboa 1975, p. 108).

Interestingly, Fowler and Robinson (1979) state that the probability of dropped leaf retrieval is low in *Atta sexdens*, with an estimated recovery efficiency of 49%. A similar retrieval probability (53%) is calculated by Hubbell et al. (1980) for *A. cephalotes* and Gamboa states that dropped leaves were "commonly lost" during retrieval in *Acromyrmex versicolor versicolor* (Gamboa 1975, p. 108). The low retrieval efficiency associated with dropping leaves from trees is a potential confounding effect when quantifying the ecological impact of leafcutting ants, which are the major neotropical herbivores, because estimates of leaf cutting taken at the nest entrance are likely to underestimate total cutting.

There are several likely advantages of partitioning cutting and carrying: *Atta* are highly polymorphic (Hölldobler and Wilson 1990) and so task partitioning can be coupled with a size-based division of labour to ensure that each subtask is performed by suitably sized foragers. This may be what is occurring in *A. sexdens* (Fowler and Robinson 1979) and *A. laevigata* (Vasconcelos and Cherrett 1996), although with opposite patterns of size distribution between cutters and carriers – meaning that cutters are larger than carriers in one spe-

cies but it is the carriers that are larger in the other species; the possible adaptive benefit of this, if any, is unclear. It could, in fact, indicate that size is relatively unimportant. Furthermore, measurements of worker size have not been followed up with an analysis of the efficiency with which different-sized ants can perform the cutting and carrying tasks. Probably of greater, and certainly clearer, likely adaptive significance, task partitioning allows gravity to carry leaf material to the ground, thereby reducing the amount of time, walking, and carrying required. In addition, Burd (1996) suggests that carrying fragments down vertical or steep tree trunks is difficult, because of the torque exerted by the leaf load on the mandibles prising the ant from the trunk. Field work on leaf fragment dropping in *A. colombica* confirms that dropping is more common around the base of source trees, lending support to Burd's hypothesis (Lugo et al. 1973; Hart and Ratnieks 2001a; also in *A. texana*, U.G. Mueller and F.L.W.R., personal observations).

The nature of the dropped load is important in an analysis of ergonomic efficiency. Some studies state that whole leaves are cut at the petiole and dropped intact to the ground (Lund 1831a, b; Fowler and Robinson 1979; Vasconcelos and Cherrett 1996) but dropping cut fragments is also reported (Hubbell et al. 1980; A.G.H., personal observation). Leaf recovery from caches on trails (described later) has been shown to be suboptimal, with foragers carrying fragments picked up from caches walking slower than foragers carrying fragments they have cut themselves. This is because there is a mismatch between forager size and load, which does not occur when foragers cut their own fragment (Wetterer 1990; Hart and Ratnieks 2001a). Therefore, it may be more efficient to cut and drop whole leaves, allowing foragers on the ground to cut fragments of an appropriate size to carry.

Whether ants drop leaves or fragments, Hubbell et al. (1980) calculate that employing leaf dropping will be less costly than non-partitioned foraging when

$$C/T < (n-1)/m,$$

where C is the cutting cost, T is the cost of travelling up and down the tree, n is the number of fragments or leaves cut, and m is the number of additional fragments or leaves cut for each n found. [In fact, Hubbell et al.'s (1980) analysis is formulated for dropping fragments but applies equally well to whole leaves.] This leads to the conclusion that "there is likely to be a selection pressure to increase the probability of pick-up and transport of cut leaf fragments" (Howse 1990, p. 430). Leaf recovery is discussed further below in the context of trail caching. Overall, it may be that the low retrieval efficiency (around 50%, see above) is not important since leaves are usually not limiting and can be cut cheaply. However, partitioned foraging could be abandoned if leaves become a limiting resource, for example during the dry season.

Vasconcelos and Cherrett (1996) suggest a further advantage offered by leaf dropping. In *Atta laevigata*, leaves severed at the petiole and dropped to the ground were frequently left to wilt until the next foraging day (or even later) before recovery. Gamboa (1975) reports a similar recovery delay for leaves dropped by *Acromyrmex versicolor versicolor*. Vasconcelos and Cherrett (1996) suggest that wilting enhances leaf palatability by reducing the effects of repellent or toxic substances in the leaves. Alternatively, or additionally, wilting may effect changes in the nutrient and water content of leaves thereby increasing palatability. However, these hypotheses have not been tested by toxicological analysis. It may simply be that wilting makes the leaf lighter to carry. Depending on the environmental conditions, the colony may need more or less moisture and this would also affect the costs and benefits of allowing leaves to wilt before collection.

Suggestions for further study

Further work would be valuable to determine the factors that result in the switching from non-partitioned (no transfer) to partitioned (direct and/or indirect transfer) foraging and the relative efficiencies of partitioned and non-partitioned organisation. Factors that may prove important include leaf source height and distance from the nest, which would both affect the time required to forage. Exclusivity of foraging territory is also likely to be important. If a colony has exclusive use of a foraging territory then they may be more likely to drop leaves than if the foraging territory is shared with other leafcutting ant colonies (competition for cached resources is discussed below). Simple field studies quantifying the costs and benefits of partitioning, for example, the cost (in time and energy currencies) of tree climbing and the relative predation and parasitism risks of tree-based cutters and trail-based foragers, are likely to be particularly important.

There seems good reason to suppose that leaf-dropping behaviour is found in most, if not all, *Atta* spp. that harvest arboreal leaves and its occurrence in at least one species of tree-foraging *Acromyrmex* suggests it may be widespread within that genus also. Additionally, arboreal cutting is not the sole mode of foraging found in leafcutting ants. Grasscutting ants (e.g., *Atta capiguara*) may also employ fragment dropping although we have no data at present. The impact of *Atta* as a dominant herbivore means that a greater understanding of the organisation of foraging has wider applications both in environmental-impact assessment and pest management.

Task partitioning during transportation

Task partitioning with indirect transfer on trails

Leaf transport along trails is occasionally partitioned among two or more foragers with indirect transfer, as recorded in *A. cephalotes* (Hubbell et al. 1980; Hart and Ratnieks 2000), *A. colombica* (Hart and Ratnieks 2001a), *A. sexdens* (A.G.H., personal observation), and *A. texana* (Wheeler 1907). The transfer usually occurs at a cache, a

discrete pile of dropped leaves on the trail. Caches can accumulate over 1,000 fragments but the adaptive value, if any, of leaf caching is still not fully understood (Hart and Ratnieks 2000, 2001a). Most data relate to the locations of caches and the recovery of cached leaves.

Cache location. Leaf caching has been recorded along foraging trails (Emmel 1967; Lugo et al. 1973; Fowler and Robinson 1979; Hart and Ratnieks 2001a), at trail junctions (Hubbell et al. 1980), at trail blockages (Hart and Ratnieks 2001a), at the nest entrance (*Acroymrmex versicolor*, Wheeler 1907; Hart and Ratnieks 2000; *Atta cephalotes* and *A. colombica*, Hart and Ratnieks 2000), within the first chamber (*Trachymyrmex turrifex* and *T. septentrionalis*, Wheeler 1907, p. 758; A.N.M. Bot, personal communication reported in Hart and Ratnieks 2000), and during rainfall (A.G.H., personal observation). In the only field study of caching locations, Hart and Ratnieks (2001a) found that in *A. colombica*, 60% of caches were associated with topographical features that caused a discontinuity in the trail such as the intersection of ant and human trails, the base of steep slopes and changes in trail terrain (e.g., from earth trail to concrete path). [Similar observations have been made in *A. texana* (U.G. Mueller and F.L.W.R., personal observations).] Cache occurrence is also positively related to trail traffic and to distance from the nest. Hart and Ratnieks (2001a) conclude that changes in forager speed or ease of carriage coupled with high trail traffic and distance from the nest causes caching.

The potential and presumed costs and benefits of caching at different locations are varied and location specific. Caching at the junction between side and main trails allows workers to return to newly discovered leaf sources before the pheromone trail to the new source has dissipated (Hubbell et al. 1980). This in turn will lead to trail reinforcement and forager recruitment to the new site. Caching at trail blockages allows foragers to return to leaf sources and cut new leaves rather than waste time attempting to pass the blockage. Foragers on the trail can then recover the leaves when the blockage has disappeared. Interestingly, experimental blockages placed on trails only caused caching when the blockage was near the leaf source or near the nest entrance but not on the middle of the trail itself, which indicates that caching is facultative and may involve an investment/loss calculation in dictating whether caching is appropriate. Caching at the nest entrance occurs in *A. cephalotes, A. colombica* (Hart and Ratnieks 2000), *A. sexdens* (A.G.H., personal observation), and in *A. texana* (U.G. Mueller and F.L.W.R., personal observations). In the laboratory, nest entrance caching can be stimulated by partially blocking or restricting the nest entrance. This mimics the bottlenecks that may occur in the field when the rate of incoming forage exceeds a colony's leaf-handling capacity. However, nest entrance caches in field colonies may not always be a result of task partitioning. The symbiotic fungus produces chemical cues in response to unsuitable forage (North et al. 1999) that the ants could respond to by removing leaves from the nest and ceasing foraging on the unsuitable plant. It is possible, therefore, that leaf 'caches' at the nest entrance are fragments rejected as a consequence of the fungus's reaction to them. The failure of workers to collect leaf fragments that had accumulated outside the nest entrance (A.G.H., unpublished data) does suggest that some leaf accumulations at the nest entrance are mounds of unwanted leaves rather than part of a partitioned foraging system, but this is yet to be tested. Similarly, leaf fragments dropped in pools of water on foraging trails are not retrieved and may in fact be used as temporary pontoons to allow foragers to cross (Hart and Ratnieks 2000). Leaf dropping without task partitioning has also been seen in *A. cephalotes*. Hodgson (1955, p. 299) states that

[During heavy rain] the laden workers then drop their leaves and run until they reach a position where the rain no longer strikes them. It is common to find them by the hundreds to the sheltered side of a tree buttress or root along the foraging trail.

The implication is that when it starts raining the ants run off to a sheltered site without their leaves so that "the essential effect of rain, therefore, is the loss of an appreciable fraction of the day's foraging time" (ibid.; see also Weber 1972). However, Hodgson does not state whether the dropped leaves are subsequently recovered. An additional reason why leaves may be abandoned is attack by parasitic phorid flies (Tonhasca et al. 2001). Exposure to phorids led to an increase in abandonment from 10.3 to 17.5 leaves in a 0.25-m^2 quadrat (Bragança et al. 1998).

Cache exploitation. Dropping leaves in a small area to form a cache, rather than dropping them haphazardly along the trail, increases the probability that leaves will be recovered later in both laboratory and field colonies of *A. cephalotes* and *A. colombica* (Hart and Ratnieks 2000, 2001a). However, caching is not without its costs: it increases the time required to recover leaves in laboratory colonies of *A. cephalotes*, possibly because of interference between foragers on the cache (Hart and Ratnieks 2000). Furthermore, in field colonies of *A.colombica*, foragers collecting leaf fragments from caches walked at a lower mean speed than foragers who cut leaves for themselves (Hart and Ratnieks 2001a). The usually strong positive relationship between forager size and leaf load (Wetterer 1990, 1994; Vanbreda and Stradling 1994; Burd 1996) was not present for foragers collecting fragments from caches, indicating that the foragers were unable to select suitable loads for themselves from caches. Overall it took foragers at least 70% longer to transport leaves recovered from caches than leaves they had cut themselves. A further cost of caching is that cached resources can be stolen by other ants. For example, *Acromyrmex volcanus* has been reported stealing grass blade fragments cached at the entrance of a neighbouring *Atta cephalotes* colony (Wetterer 1993).
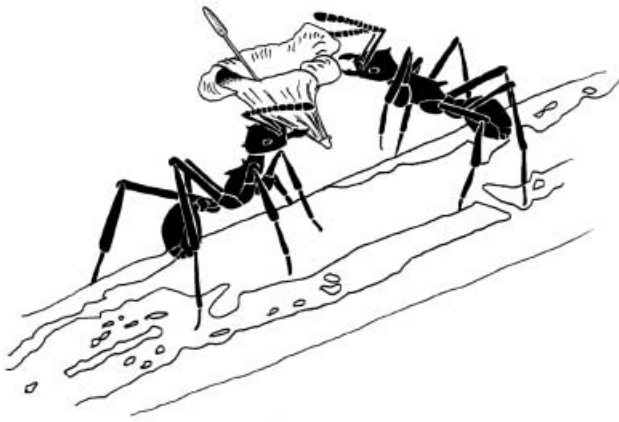
Fig. 1 An *Acromyrmex octospinosus* worker passes a flower to a nestmate for transportation back to the nest [Copyright: Carl Anderson, drawn from a film courtesy of S.R. Sumner and J.J. Boomsma (see Sumner 2000)]

Task partitioning with direct transfer on trails

Direct transfer of leaves between foragers on the trail occurs in *Atta* and *Acromyrmex*. *Atta cephalotes* foragers visiting a new leaf source carry leaf fragments back to the main trail where they may sometimes "antennate other ants and transfer their load to them" (Hubbell et al. 1980, p. 210). Anderson and Jadin (2001) report direct transfer in *A. colombica* where 9% of leaves were transferred directly to another individual on the trail at the base of the leaf-source tree. Furthermore, they found that with direct transfer the post-transfer speed was significantly faster than pre-transfer speed and matched those of material not-transferred, showing that leaf transfer was likely adaptive in terms of getting material back to the nest rapidly (Anderson and Jadin 2001). Further support for adaptive transfer is provided by Rudolph and Loudon (1986): they manipulated loads in *A. cephalotes* either by adding a weight or by snipping off a piece of leaf. They showed that not only did direct transfer occur but that three of four increased loads were transferred to larger ants and that all of eight decreased loads were transferred to smaller ants. These are interesting contrasts with Hart and Ratnieks' (2001a) data, which showed that with indirect transfer via a cache the recovery speed of leaves recovered from a cache was actually slower than that of leaves transported without partitioning. Presumably, ants must be assessing leaves more effectively, or there must be better information available to ants, in systems of direct transfer. Direct transfer has also been observed in *Acromyrmex octospinosus*. Laden foragers on a 3-mm-wide stem transferred flowers from their mandibles to the mandibles of an unladen forager coming the other way if one was encountered on the stem (Sumner 2000; A.G.H., personal observation; Fig. 1); after transfer, each ant about-turned and continued in the direction from which it had come, and as such the activity may qualify as a "bucket brigade" (sensu Anderson et al. 2002).

Suggestions for further study

Field studies focussing on the factors causing leaf caching in a range of species, including *Acromyrmex*, for a variety of foraging scenarios (e.g., different trail lengths and disturbance regimes) would greatly increase our understanding of the facultative and flexible nature of task-partitioned foraging. Such studies would combine observation with experimental manipulation and should also quantify more thoroughly the costs and benefits of leaf caching. The adaptive value or otherwise of nest entrance leaf 'caching' should also be explored, including the testing of the wilting hypothesis (Vasconcelos and Cherrett 1996) as an explanation for some leaf accumulations. It may be that leaf piles are adaptive in one species but not another, or that different types of leaf piles have different functions in different species. Additionally, direct transfer of leaf fragments occurs and determination of costs and benefits will add a further dimension to our understanding of facultative task partitioning in foraging.

Task partitioning in leaf processing

Foraged leaf pieces must be converted into mulch suitable for cultivating fungus. This entails processing the leaves within the fungus gardens in a process described as an "assembly line" (Wilson 1980; Hölldobler 1984; Hölldobler and Wilson 1990). Wilson (1980) classifies vegetation degradation as a two-stage process. The first stage entails workers within the fungus garden cutting and chewing leaf fragments shortly after they are brought into the garden to produce pieces of 2 mm or less. The second stage involves workers chewing and licking the reduced fragments. Finally, after this processing, the leaf pieces are inserted into the fungus garden. So, if leaf processing is taken as a task beginning when leaf fragments enter the fungus garden and ending at their point of insertion into the fungal substrate, then it involves at least four stages (movement into nest, degradation I, degradation II, insertion) linked by a flow of material between workers. Furthermore, Wilson shows that each stage is performed by sequentially smaller workers, mirroring the reduction in leaf fragment size. By this rationale, leaf processing is a multi-stage partitioned task coupled with a size-based division of labour. However, the situation may not be such a sequential "assembly line" process as Wilson's data suggest. Observations of *Acromyrmex echinator* have shown that foragers venture into the fungus garden where they directly transfer their leaf piece to a changing group of between three and seven smaller ants (A.G.H., unpublished data). These ants perform the duties of chewing and licking (Wilson's stages 1 and 2) concurrently, with ants joining and leaving the leaf piece as it is processed. In fact, there is no reason why small workers cannot lick and chew a leaf while larger workers cut the leaf into smaller pieces. Leaf processing is, therefore, a problematic example of task partitioning since, apart from the initial direct transfer between forager and

nest workers, it is without a well-defined material transfer from worker to worker. Rather, the material is kept stationary at a central place and the "sequential" subtasks (as implied by Wilson 1980) are performed concurrently (A.G.H., unpublished data).

Task partitioning in waste management

Leafcutting ant fungus gardens must be managed to keep the garden free of parasites and disease (Currie and Stewart 2001). One particular hazard is the fungus *Escovopsis*, a specialist parasite of the symbiotic fungus of leafcutting ants (Currie et al. 1999). *Escovopsis*, and other microorganisms, are weeded out of the gardens by minor workers (Currie and Stewart 2001). This results in the waste material being contaminated with pathogens that are undesirable and potentially fatal to the fungus garden (Bot et al. 2001). Furthermore, waste is also harmful to the ants themselves (Bot et al. 2001). In short, leafcutting ants produce large quantities of potentially hazardous waste requiring careful handling and processing. In *Atta*, there are two distinct waste disposal strategies: most species have dedicated underground waste chambers at a lower level than the fungus gardens and connected to them by tunnels. These waste chambers may contain 500 kg of waste (Fowler et al. 1994). However, some species (detailed below) have waste heaps outside the nest, similar to the middens of mediaeval castles. Task partitioning occurs in both disposal strategies.

Task partitioning in the internal waste chambers of *Atta cephalotes*

Internal waste organisation is difficult to study in the field because of the problems of observing chambers deep underground and can only realistically be studied in the laboratory. Fungus gardens are connected to chambers that the ants use for waste (Weber 1972). By using transparent plastic chambers and tunnels it is possible to observe the behaviour of workers transporting waste from the fungus gardens to the waste chambers.

Waste transport is a partitioned task involving at least two stages. Fungus garden workers carry waste particles along the tunnel connecting fungus garden and waste chamber. Just outside the waste chamber workers generally drop their waste load at a caching site and return to the fungus garden. Workers living in the waste chamber then collect particles from the cache and take them into the waste chamber. Ninety-four percent of all particles brought to the waste chamber are transferred indirectly in this way, with 4% of particles being transferred directly from transporting worker to waste heap worker. Rarely (2%), transporting workers enter the waste chamber, deposit their load and rapidly leave. In addition to task partitioning, there is a strong division of labour. Waste heap workers rarely leave the chamber and those that attempt to leave are usually met with aggression from nestmates, which may escalate fatally. Foragers experimentally contaminated with waste are frequently killed when reintroduced to nestmates (Hart and Ratnieks 2001b).

The combination of task partitioning and division of labour has a likely synergistic effect on colony hygiene. Task partitioning results in waste being dropped on a cache outside the waste chamber. As a result, fungus garden workers do not have to enter the waste chamber with its associated higher levels of *Escovopsis* and other harmful microorganisms, nor do waste workers need to enter the garden (which would be the other alternative). This organisation ensures both that workers in regular contact with the fungus do not become contaminated with waste, and that contaminated waste chamber workers do not have to enter the fungus gardens to collect waste. However, task partitioning alone is not sufficient to isolate the waste chamber. Full isolation is achieved by adding division of labour between waste transporters and waste chamber workers. Since waste chamber workers rarely, if ever, leave the chamber, contamination is kept within the chamber and away from the sensitive fungus gardens.

Task partitioning in the external waste heaps of *Atta colombica*

The organisation of external waste heaps, characteristic of *A. colombica* (Weber 1972), but also known in *A. cephalotes*, *A. mexicana*, *Acromyrmex lundi pubescens*, and *A. landolti* (Haines 1971; Weber 1956, 1972; Fowler 1985; Deloya 1988; Marquez-Luna and Navarette-Heredia 1994), follows a similar pattern to internal waste chambers, with task partitioning and division of labour acting in concert, although without aggression directed to waste-contaminated workers (Hart and Ratnieks 2002). Waste transporters carry particles to the external waste heap where they are dropped, often from an elevated position such as a tree branch. Waste heap workers then collect the particles and spread them around the heap surface. Task partitioning appears to occur early on in the transport of waste with excavation of small nests revealing waste caches in tunnels just outside the fungus garden (Hart and Ratnieks 2002). This is, therefore, an example of three-stage task partitioning with fungus garden workers depositing waste outside the garden, where transporters collect it and carry it to the heap. Once at the heap, dedicated waste heap workers take over and move the waste particles around the heap. Task partitioning may also occur on the trail leading to the waste heap with a single intermediate cache present on the waste trails of 3 of 50 heaps (A.G.H., unpublished data). Multistage partitioning can also occur on waste trails with one *A. colombica* colony having three intermediate caches on the waste trail (C.A., unpublished data). Collecting the loose yellow-brown plant and fungal refuse from a cache is more difficult than collecting leaves; the ants must first compress the material into a compact ball, which they do using their head and their front four legs. This

Table 1 Examples of task partitioning in leafcutting ants

Behaviour and species	Reference
Leaf collection and transportation	
Leaf dropping from source	
Acromyrmex versicolor versicolor	Gamboa 1975
Atta cephalotes	Lund 1831a, b; Hubbell et al. 1980[a]
A. colombica	A.G.H., personal observation[a]
A. laevigata	Vasconcelos and Cherrett 1996
A. saltensis	Daguerre 1945
A. sexdens rubropilosa	Fowler and Robinson 1979
A. texana	McCook 1909[a]
Two-stage partitioning of leaves at base of source tree[b]	
A. cephalotes	Hubbell et al. 1980 (both direct and indirect)
A. colombica	C.A., unpublished data (both direct and indirect)
A. laevigata	Vasconcelos and Cherrett 1996 (indirect)
A. saltensis	Daguerre 1945
Three-stage partitioning of leaves on trails	
A. cephalotes	Hubbell et al. 1980
A. sexdens rubropilosa	Fowler and Robinson 1979
Collecting leaves from caches on trails (i.e. indirect transfer)[c]	
A. cephalotes	Hubbell et al. 1980; Hart and Ratnieks 2000
A. colombica	Hart and Ratnieks 2001a; C.A., personal observation
A. sexdens	Fowler and Robinson 1979; A.G.H., personal observation
A. texana	Wheeler 1907
Direct transfer of material on trails	
Acromyrmex octospinosus	Sumner 2000; A.G.H., personal observation (see Fig. 1)[a]
Atta colombica	Anderson and Jadin 2001
A. cephalotes	Rudolph and Loudon 1986; Hubbell et al. 1980
Caching at nest entrance	
Acromyrmex versicolor	Wheeler 1907: Fig. 18[a]
Atta cephalotes	Hart and Ratnieks 2000
A. colombica	Hart and Ratnieks 2000; C.A., personal observation
A. sexdens	A.G.H., personal observation
A. texana	U.G. Mueller and F.L.W.R., personal observations[a]
Caching inside nest entrance	
Acromyrmex spp. and *Atta* spp.	A.N.M. Bot, personal communication[a]
Trachymyrmex septentrionalis	Wheeler 1907[a]
T. turrifex	Wheeler 1907[a]
Leaf processing in the nest	
Acromyrmex echinator	A.G.H., in preparation
Atta cephalotes	Wilson 1980
Waste management	
Task partitioning at internal waste chambers	
A. cephalotes	Hart and Ratnieks 2001b
Task partitioning at external waste chambers	
A. colombica	Hart and Ratnieks 2002; C.A., unpublished data
Other	
Task partitioning in emigration	
Atta sp.	Belt 1928[a]

[a] Anecdotal observations. More detailed observational and quantitative data are needed
[b] This is specifically observed collection from a cache. There are several other anecdotal observations of caches on trails (see text)
[c] Both direct and indirect transfer have been reported at the base of the source tree. Where the nature of the transfer is known it has been included

takes an average of 22.7±14.93 s (*n*=77). However, on an average of 0.53±1.08 times per trip (*n*=97), the ball would fall apart and the ant would have to start again. All told, an ant collecting material from a refuse pile takes 43.39±42.99 s (*n*=88; C.A., unpublished data), a surprisingly large cost for a waste material.

Suggestions for further study

Effective waste management is almost certainly an important factor in colony success. Task partitioning plays a key role in separating waste from the fungus gardens in at least one species with internal waste chambers (*A. cephalotes*) and one with external waste heaps (*A. colombica*). Furthermore, the combination of task partitioning and division of labour (which often co-occur as in *Oecophylla longinoda*) has particular significance in waste management because it enables colonies to isolate hazardous waste from the vulnerable fungus gardens. It is likely that the patterns of waste management observed in the two species studied are general patterns of organisation representative of all leafcutting ant colonies that generate much waste. Further study of different species and small colonies may, however, reveal additional refinements or simpler situations, for example, partitioned corpse removal. Studies that interfere with the organisation of the waste system and document a cost in terms of increased ant mortality or *Escovopsis* presence would directly demonstrate the importance of task partitioning for maintaining colony hygiene (e.g., Hart et al. 2002).

Task partitioning in colony emigration

Colony emigrations have been observed in *Atta cephalotes* and *Acromyrmex histrix* following strong physical disturbance (Weber 1972), in *Atta rugosus* (Fowler 1981) and in *A. colombica*, where severe infection with *Escovopsis* may have been the cause of nest abandonment (Hart 2002). Belt (1928, pp. 60–61) observed task partitioning during an emigration of *Atta* sp. that he initiated by pouring carbolic acid into the colony entrance.

Next day I found them busily employed bringing up the ant-food [fungus garden] from the old burrows, and carrying it to a new one a few yards distant; and here I first noticed a wonderful instance of their reasoning powers. Between the old burrows and the new one was a steep slope. Instead of descending this with their burdens, they cast them down on the top of the slope, whence they rolled them to the bottom, where another relay of labourers picked them up and carried them to the new burrow. It was amusing to watch the ants hurrying out with bundles of food, dropping them over the slope, and rushing back immediately for more.

The dropping of material from the upper to the lower group of workers is analogous to arboreal cutters dropping leaves to ground-based carriers (Anderson and Ratnieks 2000), thereby presumably saving time and effort in transportation. This behaviour, however, potentially has a large cost – that is, contamination of the fungus (e.g., Weber 1972, p. 69)– that could prove fatal for the colony. As such this behaviour is likely very unusual, expressed only in times of crisis, and Belt was, in a word, lucky.

Discussion

In their review of task partitioning, Ratnieks and Anderson (1999b) called for more 'alpha' studies, that is, studies reporting the existence of task partitioning, to assess its importance in social insects. Additionally, they emphasised the need for studies of task partitioning outside of foraging and for quantitative studies of the various (and variable) costs and benefits of task-partitioned systems. Leafcutting ants have proved to be an excellent group to study all these aspects of task partitioning (Table 1). They have shown task partitioning outside of foraging, have shown the first example of within-nest task partitioning, and have shown a clear situation of a novel (presumably) adaptive benefit-enhanced hygiene. They have filled many of the gaps in our knowledge and understanding to the extent that they may now be considered a model system for studying task partitioning.

Task partitioning occurs in nearly every material-handling task performed by *Atta* (Table 1). Leaf collection and leaf transportation are subject, at various times, to multi-stage task partitioning with direct and indirect transfer variously occurring at the leaf source, on the foraging trails, and at the nest entrance (Fig. 2). In combination with a size-based division of labour, task partitioning is central to the production of the leaf mulch used to nourish the fungus garden. Similarly, task partitioning combines with division of labour in waste management, both inside and outside the nest, to isolate potentially hazardous waste and waste-contaminated workers from the fungus gardens. Perhaps the biggest single bulk transport task faced by a colony is emigration. Here again we find that task partitioning has a role, this time reducing the time and effort involved in fungus garden relocation by partitioning transport between two (or possibly more) groups connected with a gravity-mediated indirect transfer. The only material-handling task in leafcutting ants where we have been unable to confirm that task partitioning occurs is nest excavation. However, it has been documented in other ant species (Todd 1885; Hingston 1929; Anderson and Ratnieks 2000) and there is no reason to think that it does not occur in leafcutting ants. For example, *A. texana* has been observed dropping excavated soil down slopes in a fashion similar to that employed by emigrating colonies (U.G. Mueller and F.L.W.R., personal observations). However, task partitioning did not occur because the soil was not retrieved from the base of the slope. Nest excavation, particularly
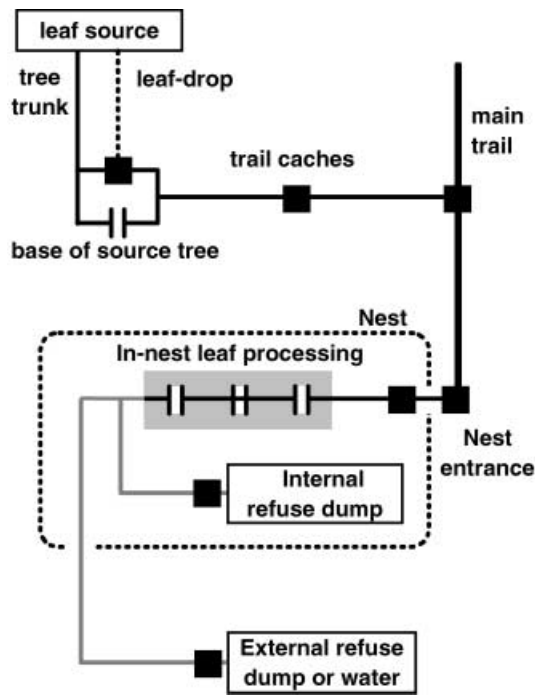
Fig. 2 Overall pattern of task partitioning in leaf cutting ants. *Black squares* represent caches (indirect transfers) and *parallel lines* direct transfers. This is not to say that any particular species or colony exhibits all of these transfer locations (although some *Atta* spp. might), or indeed that more transfer points may not occur, or that a particular leaf fragment will be transferred at all these locations. Direct transfers may also occur on trails but further quantification is needed. *Black lines* indicate material movement into the nest; *grey lines* represent the flow of waste material out of the nest

observations of what occurs underground, is likely to be a fruitful area to explore for further task-partitioning examples.

One generalisation arising from this review is the contrast between obligate and facultative task partitioning. Waste disposal tasks are always partitioned. This appears to make adaptive sense since task partitioning is probably essential to nest hygiene (although the adaptive nature of the organisation has not been shown). Task partitioning in foraging, regardless of the system of partitioning employed, is much more variable. Leaf caching is sometimes stimulated by trail blockages, may or may not occur when exploratory trails join main trails, and occasionally occurs at the leaf source when cutters drop leaves to carriers waiting below. Despite all these refinements, and their apparent advantages, the majority of forage is probably conveyed to the nest without task partitioning. Although some headway in understanding facultative task partitioning has been made by studying caching on trails and at the nest entrance (Vasconcelos and Cherrett 1996; Hart and Ratnieks 2000, 2001a; Anderson and Jadin 2001), further work is needed to examine the occurrence of partitioned foraging in other species, the circumstances that cause the switch to partitioned foraging, and the associated costs and benefits.

Studies of leaf dropping in both *A. sexdens* and *A. laevigata* have revealed that task partitioning is combined with division of labour, perhaps allowing a more efficient use of labour. However, the two species are a contrast, with *A. sexdens* having smaller arboreal cutters and *A. laevigata* having larger arboreal cutters (Fowler and Robinson 1979; Vasconcelos and Cherrett 1996). No data are available for other species known to use leaf dropping, providing another area worthy of further attention.

Leafcutting ants also reveal an interesting combination of task partitioning and gravity. In both foraging, where arboreal 'cutters' drop leaves from trees, and colony emigration, where workers drop fungus garden pieces down slopes to other workers, task partitioning reduces transport costs by using gravity to connect two groups of workers. In nest emigration this is likely to be facultative and dependent on the topography through which the colony must move. However, despite the fact that many species generally forage in trees and that the advantages that gravity offers are always present, leaf dropping is infrequently used. A thorough investigation of which trees and other plant types are harvested using leaf dropping, when leaf dropping occurs, and an analysis of the costs and benefits of this harvesting technique will greatly increase our understanding of facultative work organisation and organisational switching.

Anderson and Ratnieks (1999a, b; see also Anderson and McShea 2001) hypothesize that colony size is important in the evolution and maintenance of task partitioning. One cost of partitioning is that direct transfers inevitably cause delays as donor and recipient workers arrive at a transfer point stochastically. Simulations show that these delays are disproportionately longer in smaller colonies. Direct transfer of forage in leafcutting ants provides an excellent opportunity to test this hypothesis. Leafcutting ant colonies are generally founded by a single queen who carries a small piece of fungus in her infrabuccal pouch (although multiple founding does occur; e.g., *Acromyrmex versicolor*, Rissing et al. 1986). She rears the first brood of workers who then take over all colony tasks, the queen assuming her role as egg layer. Consequently, a leafcutting ant colony generally develops from a single individual into a large mature colony through all colony sizes in between (Weber 1972). Linking task partitioning with colony size and worker size distribution will enable us to quantify and more fully understand Anderson and Ratnieks' colony size hypothesis. For example, it would also be possible to perform a 'sociogenesis' (Wilson 1985) study of the emergence of task partitioning in waste disposal as colonies increase in size. A comparison of *Atta* (with many documented examples of task partitioning) with *Acromyrmex* (with small colonies and few fully documented examples of task partitioning) is another project of relevance here. We predict that *Acromyrmex* will have a similar system of task partitioning for leaf processing in the nest but that task partitioning will be less prevalent in foraging because of their less-developed foraging trail network and because *Acromyrmex* has smaller colonies than *Atta*.

Waste management behaviour is not well studied in *Acromyrmex*, but hygiene issues similar to *Atta* must exist and so task-partitioned waste disposal (probably linked with division of labour) is likely. The cross-genera comparison of work organisation could be extended to include the lower attines, with processing of fungal substrate being an obvious candidate for attention. In fact, the organisation of work in general in lower attines has yet to be studied in any detail.

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