Behav Ecol Sociobiol (2001) 49:387–392
DOI 10.1007/s002650000312

ORIGINAL ARTICLE

Adam G. Hart · Francis L.W. Ratnieks

Task partitioning, division of labour and nest compartmentalisation collectively isolate hazardous waste in the leafcutting ant *Atta cephalotes*

Received: 21 July 2000 / Revised: 8 November 2000 / Accepted: 2 December 2000 / Published online: 23 February 2001

Abstract We studied the organisation of garbage disposal and management in the leafcutting ant *Atta cephalotes*. The nest of this species has an internal garbage heap to which waste from the fungus garden is taken. The transport of waste from the fungus gardens to the garbage heaps is an example of task partitioning. Ninety-four percent of the garbage loads transferred from the fungus garden to the garbage heap were transferred indirectly via a caching site just outside the garbage heap entrance. A further 3% were transferred directly from a fungus garden worker to a garbage heap worker, again just outside the heap entrance. Only 3% were taken directly to the garbage heap without task partitioning. This is the first described example of task partitioning in insect societies for work other than foraging and the first example of task partitioning occurring entirely within the nest. Furthermore, there is a strong division of labour between the fungus garden workers and the garbage heap workers, with garbage workers hardly ever leaving the heap. Division of labour is reinforced by aggressive behaviour directed towards workers contaminated with garbage. This pattern of work organisation minimises contact between garbage heap workers, who are probably contaminated with pathogens hazardous to both the ants and their symbiotic fungus, and both fungus garden workers and the fungus garden. Task partitioning, division of labour (reinforced by aggression) and nest compartmentalisation act synergistically to isolate the hazardous garbage heap from the fungus gardens.

Keywords Task partitioning · Division of labour · *Atta cephalotes* · Waste management

Communicated by J. Heinze

A.G. Hart114-2760159) (✉) · F.L.W. Ratnieks
Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK
e-mail: bop98agh@sheffield.ac.uk
Tel.: +44-114-2220149, Fax: +44-144-2760159

Introduction

Insect societies are notable for the sophisticated organisation of their workforce (e.g. Oster and Wilson 1978; Hölldobler and Wilson 1990; Seeley 1995). One important aspect of work organisation is task partitioning, a term coined by Jeanne (1986) to describe situations when two or more workers contribute sequentially to a piece of work. A clear example is nectar foraging in the honey-bee *Apis mellifera*. Forager bees return to the nest where they transfer nectar to receiver bees who store it in cells (Seeley 1995). Task partitioning occurs because each nectar load is transferred between two or more bees as it is brought from the field to the cell. Ratnieks and Anderson (1999) raise several issues regarding the current state of knowledge of task partitioning in insect societies and highlight areas for further study. One need is for studies that describe novel situations of task partitioning, for example for work other than foraging. Currently, all published examples of task partitioning concern the collection of food and other materials, such as wood pulp for nest building. However, task partitioning does occur in other situations that require material handling, for example nest excavation (reported in Anderson and Ratnieks 2000).

Leafcutting ants, *Atta*, use task partitioning in foraging with the occurrence of both direct and indirect transfer (reviewed in Ratnieks and Anderson 1999). *Atta cephalotes* has garbage heaps within the nest (Stahel and Geijskes 1939) and casual observations have suggested that task partitioning occurs in the transfer of waste from the fungus garden to the garbage heap (A.N.M. Bot, personal communication). Workers removing garbage from the fungus garden generally drop their loads near the garbage heap from where it is collected by other workers which take it into the heap.

The garbage heaps of leafcutting ants are known to harbour micro-organisms harmful to both the ants and their symbiotic fungus (Fisher et al. 1996; A.N.M. Bot, C.R. Currie, A.G. Hart, J.J. Boomsma, unpublished data). If ants working within the heap are contaminated

or infected with pathogens, the risk of these microorganisms spreading within the nest is increased. However, in garbage processing, task partitioning combined with a division of labour between garbage transporters and garbage heap workers could actually decrease parasite spread by reinforcing segregation between contaminated and uncontaminated areas of the nest and the ants that work there.

In this study, we investigated the organisation of garbage disposal in laboratory colonies of *A. cephalotes*. Our results show that task partitioning and division of labour both occur in the transport and processing of waste material and that garbage-contaminated workers are subject to significantly more aggression by nestmates than are non-contaminated workers.

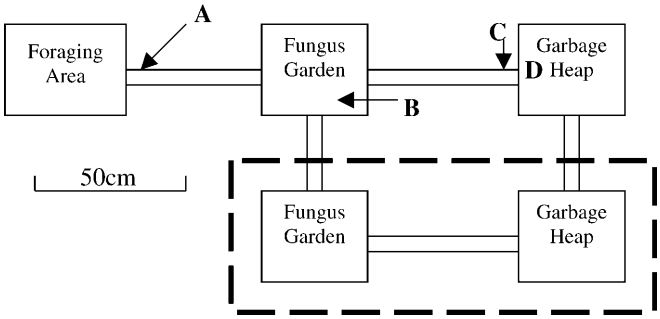

Fig. 1 Schematic diagram of the experimental nests. The second fungus garden and garbage heap (inside the *dashed box*) were present only in colony 1. Caches formed at *C* in colony 1, at *D* in colony 2. Foragers were collected for the garbage contamination experiments at point *A* and put into the nest at point *B*

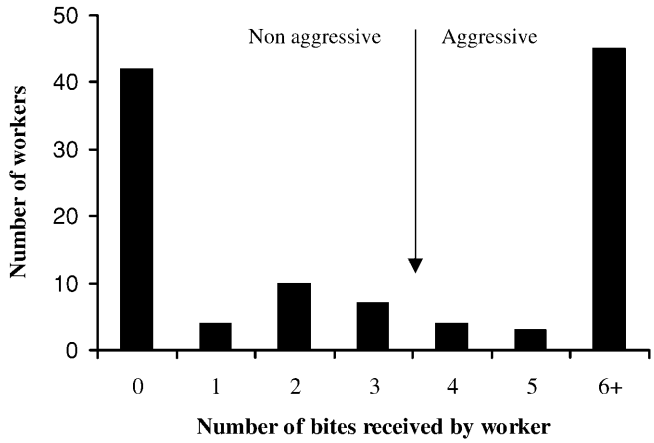

Fig. 2 Number of bites from nestmates received by workers contaminated with garbage (experiment 1). The bimodal distribution shows that the classification into aggression and non-aggression used follows the actual pattern, with the threshold in the trough between the two modes

Methods

Study organism

We studied two colonies of *A. cephalotes* collected in El Liano, Panama, during January 1996, housed in climate rooms at Aarhus University, Denmark and Sheffield University, UK (25°C, 70% relative humidity). Colony 1 (Aarhus) had approximately 30,000 workers with two 2-l fungus garden chambers (predominately filled with fungus garden) and two 2-l garbage heaps. A horizontal tube connected fungus gardens and garbage heaps (Fig. 1). Colony 2 (Sheffield) had approximately 15,000 workers and occupied a nest of 2 l (with one fungus garden and one garbage heap; Fig. 1). The ants were fed with fresh leaves, predominantly bramble (*Rubus*, Aarhus), and lime (*Tilia*, Sheffield), at least three times a week, and appeared to be thriving.

Description and quantification of task partitioning

Garbage loads being carried by workers out of the fungus garden and towards the waste heap along the tubing (Fig. 1, location C) were observed. Task partitioning occurs when a garbage load taken from the fungus garden by one worker is transferred to a worker either directly, or indirectly via a cache (Ratnieks and Anderson 1999). Alternatively, no task partitioning occurs if the load is taken to the heap by the same ant that carried it from the fungus garden. These were the only alternatives that occurred and enabled the fate of each garbage load to be categorised unambiguously as either task partitioning with indirect transfer or task partitioning with direct transfer, or no task partitioning. Multiple transfers, where three or more workers sequentially handle one piece of material, were never seen.

Division of labour

We were specifically interested in knowing whether heap workers ever leave the heap. Therefore, rather than performing a comprehensive study of the division of labour occurring in the heap we marked heap workers with nail polish and determined their location for 10 min every hour for 8 h a day for 10 days. In addition, individual workers in the garbage heap were observed for 3-min periods to determine if they left they the heap.

Aggressive-behaviour study

Forager contamination experiment 1

Samples of ten foraging workers were collected from the foraging trail (point A, Fig. 1) using forceps and randomly subjected to one of two treatments. Experimental-group ants were housed for 2.5 h in a small box containing nest garbage. The control treatment was identical but without the garbage. During this time, the experimental ants began to manipulate the garbage and frequently built tunnels through it, ensuring that they were contaminated. Ants were then individually removed with forceps, placed into an area under the fungus chamber where foragers were abundant (location B in Fig. 1), and observed for 2 min. Interactions with nestmates were classified as “aggressive” if they involved the experimental worker receiving four or more bites from her nestmates. Otherwise, they were classified as “non-aggressive”. This classification follows the actual bimodal distribution of the number of bites observed (Fig. 2) so that the dichotomy between “aggressive” and “non-aggressive” responses reflects a real difference. In practice, aggressive interactions frequently escalated beyond six bites, making it easy to categorise them as aggressive but difficult to count the exact number of bites. In extreme cases, the target worker was dismembered by nestmates after a protracted struggle. Trials (i.e. ten garbage treated and ten controls) were performed no more than once in any 12-h period to minimise the possibility of the research itself altering the aggressive response.

Forager contamination experiment 2

This experiment was an extension of experiment 1, using workers displaced directly from the garbage heap and from the foraging

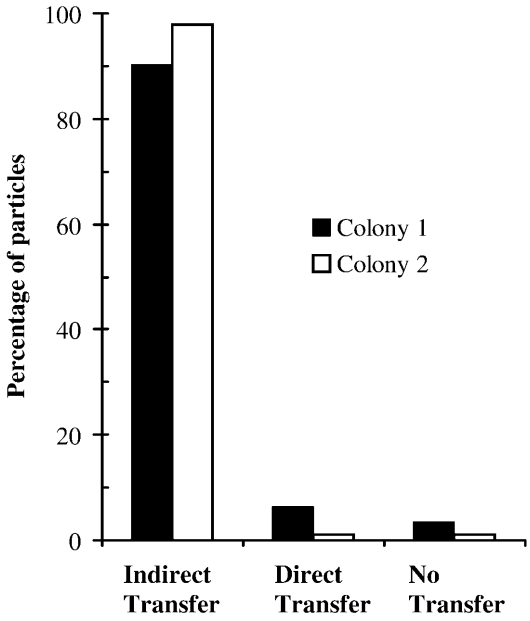

Fig. 3 Fates of garbage particles taken from the fungus garden to the garbage heap. Task partitioning occurs when the worker carrying a particle from the fungus garden transfers it to another worker who takes it to the heap. This transfer may be either direct (from worker to worker) or indirect (via a cache at the garbage heap entrance)

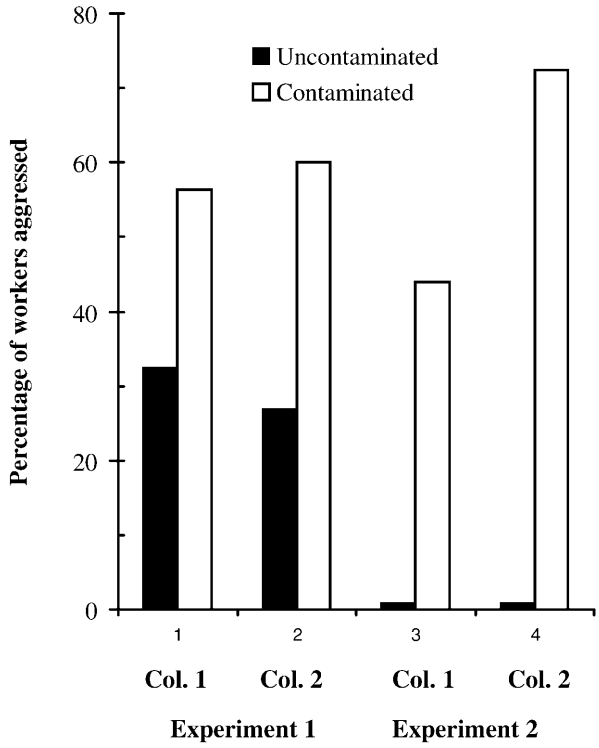

Fig. 4 Effect of garbage contamination on aggression. In experiment 1, workers were either contaminated with garbage or isolated for 2.5 h prior to reintroduction into the nest. In experiment 2, workers from the garbage heap and from the foraging trail were placed into the nest. In both experiments, garbage-contaminated workers were subject to more aggression than were non-contaminated workers (experiment 1, $P<0.005$, experiment 2, $P<0.001$)

trail. The latter were a control group for the possible effects of handling. Interactions with nestmates were observed for 2 min (at point B in Fig. 1) and classified as aggressive or non-aggressive using the criterion above. Trials were carried out with no more than ten ants per 12-h period.

Results

Description and quantification of task partitioning

Five hundred and eighty-four of the 600 garbage loads (97.3%) followed were subject to task partitioning: 565 (94.2%) were transferred indirectly and 22 (3.7%) directly (Fig. 3). This pattern of organisation was similar in both colonies, although there was a small significant difference between the two, colony 2 having a higher level of task partitioning than colony 1 (99% vs 96.7%; $\chi^2=5.44$, $df=1$, $P<0.05$). In colony 1, the worker typically deposited her load of garbage on a garbage cache just outside the entrance to the heap from where it was recovered by a worker from within the heap. In colony 2, the caching point was just inside the box containing the heap but formed a distinct transfer area where no working or storage of garbage was ever observed. In both colonies, the caches were generally of less than 20 loads and formed a small pile. In direct transfer, the load of garbage was transferred from the mandibles of the transit worker to the mandibles of a heap worker. In rare cases (13 out 600, 2.2%) the worker entered the heap and deposited the load directly onto the heap surface herself, with no task partitioning. Workers doing this always left the heap immediately ($n=13$, mean stay=14.6 s, $SD=9.2$, maximum observed stay=32 s) after depositing their garbage and were not subject to any aggression from nestmates on leaving the heap area.

Division of labour

Of the workers marked in the garbage heap (40 in colony 1, 80 in colony 2), none were ever seen outside the garbage heap but they were observed working within the heap. Four of 40 (colony 1) and 12 of 80 (colony 2) had died (their corpses were visible on the heap surface) within 2 days of marking, and only 1, a soldier (a large worker caste with prominent mandibles and an enlarged head), was still alive after 10 days (colony 1).

Of 612 workers observed at the garbage heap (312 from colony 1, 300 from colony 2), during 1,836 min, only 3 were seen to successfully leave the heap (1 from colony 1, 2 from colony 2). An additional 4 workers from colony 1 were observed attempting to leave the heap but these were harried back by the workers in the tube connecting the heap to the garden. Three workers from colony 1 died during the observations. Workers in the heap have a varied repertoire of behaviours, including moving fresh garbage into the heap, rearranging the

garbage within the heap and digging tunnels. The low incidence (0.49%) of workers leaving the heap suggests that garbage processing is strongly divided between fungus garden workers who transport garbage loads from the garden to the cache and garbage heap workers who remain on the garbage heap.

Aggressive-behaviour study

Forager contamination experiment 1

Foragers contaminated with garbage received significantly more aggression than non-contaminated workers in both colonies (colony 1: contaminated, n=190, 56% aggressed; non-contaminated, n=187, 33% aggressed; χ^2=21.42, df=1, P<0.001; colony 2: contaminated, n=120, 38% aggressed; non-contaminated, n=127, 21% aggressed; χ^2=7.88, df=1, P<0.005; Fig. 4).

Forager contamination experiment 2

Workers from the garbage heap were subject to significantly more aggressive interactions than workers from the foraging trail in both colonies (colony 1: garbage heap workers, n=40, 73% aggressed; foraging workers, n=200, 0% aggressed; χ^2=165, df=1, P<0.001; colony 2: garbage heap workers, n=72, 31% aggressed; foraging workers, n=200, 0% aggressed; χ^2=66.49, df=1; P<0.001).

Although the same general pattern, with greater aggression directed towards garbage-contaminated workers, occurred in both colonies, colony 1 was significantly more aggressive than colony 2 in both experiments [experiment 1 (aggression against contaminated workers): colony 1, n=190, 106 aggressed; colony 2, n=120, 45 aggressed; χ^2=9.85, df=1, P<0.005; experiment 1 (aggression against non-contaminated workers): colony 1, n=187, 62 aggressed; colony 2, n=127, 27 aggressed; χ^2=5.27, df=1, P<0.05; experiment 2 (aggression against heap workers): colony 1, n=40, 29 aggressed; colony 2, n=72, 22 aggressed; χ^2=18.24, df=1, P<0.001].

Discussion

Task partitioning occurs in the transport of waste from the fungus garden to the garbage heap in *A. cephalotes*. Ninety-seven percent of waste loads transferred from the garden to the heap were subject to task partitioning. Of these, 97% were transferred indirectly via a cache just outside the garbage heap and 3% directly to a heap worker. Anderson and Ratnieks (2000) briefly describe three examples of task-partitioned nest excavation, but this is the first fully described example of task partitioning occurring entirely within the nest in insect societies, and the first described example outside of foraging. (Ratnieks and Anderson 1999; Anderson and Ratnieks 2000).

In addition to task partitioning there is also division of labour between ants working in the heap and ants working in the rest of the nest. In particular, ants working in the heap seldom try to leave. If they do, they are frequently prevented from doing so by the aggressive behaviour of nestmates. The results of the aggression experiments strongly support the hypothesis that significantly increased levels of aggression are directed towards garbage-contaminated workers by nestmates working in the fungus garden, and that this helps reinforce the division of labour. Furthermore, workers in the heap appear to have a low life expectancy, suggesting that these are old workers performing heap tasks at the end of their lives. However, this hypothesis cannot be tested without additional research.

Numerous potential pathogens and competitors, of both ants and fungus, are present in the nests of leafcutting ants. Fisher et al. (1996) isolated 18 potentially competitive fungal taxa and a number of sterile mycelia and yeasts from *A. cephalotes* fungus gardens, most of which were the endophytic and epiphytic flora of food plants. Currie et al. (1999a) showed that seven genera of leafcutting ants use antibiotic-producing *Streptomyces* bacteria to suppress the growth of the fungus *Escovopsis*. Importantly, *Escovopsis* has also been identified in the garbage heaps of *A. cephalotes* (A.N.M. Bot, C.R. Currie, A.G. Hart, J.J. Boomsma, unpublished data) It represents a serious threat to the colony because it is a virulent parasite that can kill fungus gardens (Currie et al. 1999b).

Schmid-Hempel (1998) has suggested that the organisation of insect colonies has important implications for the internal transmission of disease, and has outlined the need for further study of how colony organisation may defend against parasites. Both task partitioning and division of labour can serve to reinforce colony compartmentalisation, which in turn can act to reduce the spread of pathogens (reviewed in Schmid-Hempel 1998). However, under some circumstances, task partitioning could also increase the spread of pathogens because of the additional inter-individual contact that occurs, especially with direct transfer (Ratnieks and Anderson 1999). Whether task partitioning increases or decreases the spread of disease depends upon the occurrence of compartmentalisation and division of labour. In garbage management in *A. cephalotes*, task partitioning is combined with a strong division of labour, which together with nest compartmentalisation and aggressive behaviour, form a multi-faceted, and synergistic, isolation mechanism. This mechanism achieves near complete separation of the garbage heap from the rest of the nest.

Division of labour between fungus garden workers and heap workers complements task partitioning in garbage management. Consequently, the garbage heap is a physically separated chamber with a dedicated workforce that has practically no contact with other nestmates (Fig. 5). This pattern of work organisation is mirrored in the spatial organisation of the nest into two types of chamber, either for fungus cultivation or waste disposal

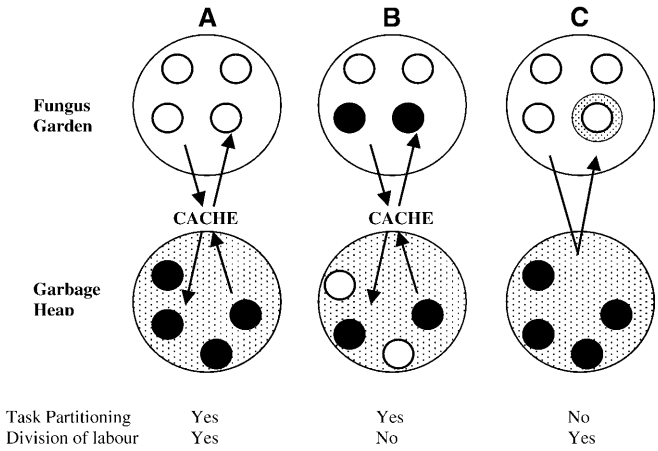

Fig. 5A–C How task partitioning and division of labour, in a situation with nest compartmentalisation, are both needed to prevent the spread of pathogens between contaminated and uncontaminated chambers. **A** Division of labour between ants working in the garbage heap and those working in the fungus garden prevents contaminated workers (*filled circles*) from entering the uncontaminated area of the nest (i.e. the fungus garden), and task partitioning with indirect transfer via a cache prevents uncontaminated workers (*open circles*) entering the contaminated area of the nest (i.e. the garbage heap). **B** If division of labour is absent, contaminated workers move freely between the two nest compartments and pathogens can be spread. **C** If task partitioning is absent, uncontaminated workers have to enter the contaminated compartment and may become contaminated themselves

(Stahel and Geijskes 1939; Moser 1963 shows a similar structure in *Atta texana* nests). Ants may have spatial preferences, which reinforce this compartmentalisation. Stradling et al. (1998) state that *A. cephalotes* foragers and garbage workers exhibit strong chamber fidelity and they suggest that this serves to reduce the distribution of contaminants throughout the nest.

Aggressive behaviour directed towards workers contaminated with garbage reinforces division of labour. Our results show that garbage contamination releases aggressive behaviour in nestmates and that garbage heap workers are subject to aggression when they are placed in other areas of the nest. Few workers attempted to leave the heap and four of the seven that did met aggression from nestmates and re-entered the heap. It is well known that workers can identify chemical cues on other workers in various recognition contexts, for example in distinguishing between nestmates and non-nestmates (e.g. honey-bees, reviewed by Breed 1998). Recognition of dead nestmates and the disposal of corpses, or necrophoric behaviour (Wilson et al. 1958), have also been studied in ants (e.g. McCook 1879, 1882; Weber 1972; Howard and Tschinkel 1976). However, in these cases, chemical cues release non-aggressive necrophoric behaviour, rather than aggression. Since the control ants in experiment 1 were subject to aggression (although at a significantly lower level than garbage-contaminated ants), such aggression might be the result of workers losing the colony odour through reduced contact with nestmates and the fungus garden. However, the elevated aggression experienced by garbage-contaminated workers indicates that the presence of an odour associated with garbage may release such behaviour. Whatever the cause, the rapidity of the effect warrants further work.

Garbage management in *A. cephalotes* shows a synergism among two simultaneously acting processes (division of labour and task partitioning) that collectively should reduce pathogen spread from the garbage heap to the fungus garden. If only one is occurring, then the isolation of the heap and the fungus garden is not complete. A multi-faceted approach is also seen in other social insects. For example, the honey-bee (*A. mellifera*) combats microbial spoiling of honey by three systems: acidity (pH range 3.2–4.5; White 1975), high osmotic pressure, and the release of hydrogen peroxide when the honey is diluted (White et al. 1963). However, unlike *A. cephalotes*, these three systems do not act simultaneously. Acidity and high osmotic pressure are simultaneous but the peroxide system acts sequentially, only being activated when the honey is diluted, as occurs when it is fed to larvae. The honey-bee also has a broad array of generalised physiological, behavioural and organisational adaptations, which protect the colony from harmful micro-organisms. Parasites that are ingested may be removed by the proventriculus, which forms a filtering device between the crop and midgut (Seeley 1985). In addition, the honey-bee displays "hygienic" behaviours such as removing dead larvae from cells (Rothenbuhler 1964a, 1964b), removing dead nestmates (Visscher 1983) and defecating outside the nest (Seeley 1985). These adaptations by the honey-bee act individually rather than synergistically, and provide a general defence against numerous pathogens.

How could such a multi-faceted system of adaptations, embracing nest structure, work organisation and behaviour evolve? The presence of internal garbage heaps is likely a derived characteristic in fungus-growing ants (Attini), with *Atta* generally having internal heaps, and the lower attines (including *Acromyrmex* and *Trachymyrmex*), external heaps (A.G. Hart, personal observations). However, *Atta colombica*, which occurs sympatrically with *A. cephalotes*, also has external garbage heaps and at least two of the lower attines (*Mycetophylax conformis* and *Myrmicocrypta ednaella*) show evidence for some internal garbage dumping (U.G. Mueller, personal communication). These dumps are in the same chamber as the fungus garden, consist of very compacted clumps of moist vegetable material, and may not be homologous with internal garbage heaps in *Atta*. The presence of internal compartmentalisation, though providing a physically distinct environment for garbage storage, is not an essential feature for the isolation of garbage. The critical factor is the co-occurrence of task partitioning and division of labour (as shown in Fig. 5), with spatial separation adding an extra level of refinement. With task partitioning and division of labour both in place, reinforced by aggressive behaviour, the heap becomes an entity separated from the fungus garden, whether inside or outside the nest. The higher attines tend to have larger colonies (up to millions of workers;

Hölldobler and Wilson 1990) and, therefore, produce a lot of garbage. An *A. cephalotes* colony has been estimated to harvest as much as 276 kg of leaves per year compared to 0.94 kg/year per colony for *Acromyrmex octospinosus* (for an overview of leafcutting harvests, see Fowler et al. 1990). This may have been important in the evolution of internal garbage chambers where waste can be actively managed and its decomposition accelerated, e.g. by the building of tunnels and the turning over of surface loads. This is supported by observation of internal heaps in larger colonies of *A. octospinosus* during the dry season but not during the wet season (A.N.M. Bot, personal communication). Decomposition rates are likely to be high in the wet season, while in the dry season, with lower decomposition rates, garbage can build up in large colonies and internal garbage heaps appear. Whether external garbage heaps have the same risk of disease as internal heaps, and whether task partitioning and division of labour are used in their management are questions that field studies may help to resolve. Such studies may also throw light on the value of retaining waste in nest compartments. A comparison between *A. cephalotes* and *A. colombica* and an investigation into the relationship between internal heaps and colony size in *Acromyrmex* are likely to be particularly fruitful. Containing potentially harmful waste and managing it through the strategy of isolation may be a more cost-effective and hygienic strategy than dispersing the waste outside where returning foragers may become contaminated or transfer material back into the nest. Leafcutting ants are among the most advanced of all the social insects, with sophisticated systems of agriculture and pest control (Hölldobler and Wilson 1990), foraging and leaf processing (Wilson 1980, 1983). Studies such as ours show that garbage management is another sophisticated aspect of colony life.

Acknowledgements This study was funded by a Hossain Farmy Studentship of the University of Sheffield (A.G.H.) and in part by the European Union Training and Mobility of Researchers (T.M.R.) Social Evolution Network. We thank Koos Boosma and Jeanette Bot for their expertise and knowledge and for providing both the colonies used in this study.The experiments performed comply with the current laws of the United Kingdom.

References

Anderson C, Ratnieks FLW (2000) Task partitioning in insect societies: novel situations. Insectes Soc 47:198–199

Breed MD (1998) Recognition pheromones of the honey bee. Bioscience 48:463–470

Currie CR, Scott JA, Summerbell RC, Malloch D (1999a) Fungus growing ants use antibiotic-producing bacteria to control garden parasites. Nature 398:701–704

Currie CR, Mueller UG, Malloch D (1999b) The agricultural pathology of ant fungus gardens. Proc Natl Acad Sci USA 96: 7998–8002

Fisher PJ, Stradling DJ, Sutton BC, Petrini LE (1996) Microfungi in the fungus gardens of the leaf-cutting ant *Atta cephalotes*: a preliminary study. Mycol Res 100:541–546

Fowler HG, Forti LC, Romagnano LFTD (1990) Methods for the evaluation of leaf-cutting ant harvest. In: VanderMeer LK, Jaffe K, Cedeno A (eds) Applied myrmecology: a world perspective. Westview, Boulder, Colo, pp 228–241

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, Mass

Howard DF, Tschinkel WR (1976) Aspects of necrophoric behavior in the red imported fire ant, *Solenopsis invicta*. Behaviour 56: 158–180

Jeanne RL (1986) The evolution of the organisation of work in social insects. Mon Zool Ital 20:119–133

McCook HC (1879) The natural history of the agricultural ant of Texas: a monograph of the habits, architecture, and structure of *Pogonomyrmex barbatus*. Academy of Natural Sciences, Philadelphia

McCook HC (1882) The honey ants of the garden of the gods, and the occident ants of the American plains. Lippincott, Philadelphia

Moser JC (1963) Contents and structure of *Atta texana* nests in summer. Ann Entomol Soc Am 56:286–291

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton, NJ

Ratnieks FLW, Anderson C (1999) Task partitioning in insect societies. Insectes Soc 46:95–108

Rothenbuhler WC (1964a) Behavior genetics of nest cleaning honeybees. I. Responses of 4 inbred lines to disease-killed brood. Anim Behav 112:578–583

Rothenbuhler WC (1964b) Behavior genetics of nest cleaning honeybees. IV. Responses of F1 and backcross generations to disease killed brood. Am Zool 4:111–123

Schmid-Hempel P (1998) Parasites in social insects. Princeton University Press, Princeton, NJ

Seeley TD (1985) Honeybee ecology: a study of adaptation in social life. Princeton University Press, Princeton, NJ

Seeley TD (1995) The wisdom of the hive. Harvard University Press, Cambridge, Mass

Stahel G, Geijskes DC (1939) Ueber den Bau der Nester von *Atta cephalotes* L. und *Atta sexdens* L. (Hym. Formicidae). Rev Entomol 10:27–7.

Stradling DJ, Edwards S, Tong CX, Calton S (1998) Worker autonomy, integration and team work in large colonies of the leafcutting ant *Atta cephalotes* L. Proceedings of the XIII international congress of IUSSI, Adelaide, Australia 1998–1999, pp 184

Visscher PK (1983) The honeybee way of death – necrophoric behavior in *Apis mellifera*. Anim Behav 31:1070–1076

Weber NA (1972) Gardening ants: the attines. Mem Am Phil Soc 92

White JW (1975) Physical characteristics of honey. In: Crane E (ed) Honey: a comprehensive survey. Heinemann, London pp 157–206

White JW, Subers MH, Schepartz AI (1963) The identification of inhibine, the antibacterial factor in honey, as hydrogen peroxide and its origin in a honey glucose oxidase system. Biochimic Biophys Acta 73:57–70

Wilson EO (1980) Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). II. The ergonomic optimisation of leaf cutting. Behav Ecol Sociobiol 7:157–165

Wilson EO (1983) Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). III. Ergonomic resiliency in foraging by *A. cephalotes*. Behav Ecol Sociobiol 14:47–54

Wilson EO, Durlach NI, Roth LM (1958) Chemical releasers of necrophoric behavior in ants. Psyche 65:154–161