

Waste management in the leaf-cutting ant *Atta colombica*

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Unlike most leaf-cutting ants, which have underground waste dumps, the leaf-cutting ant *Atta colombica* dumps waste in a heap outside the nest. Waste is hazardous, as it is contaminated with pathogens. We investigated the organization of the workforce involved in outside-nest tasks (foraging, waste disposal) and quantified task switching and heap location to test hypotheses that these tasks are organized to minimize contact between the heap and foraging entrances and trails. Waste management is an important task: 11% of externally working ants were either transporting waste or manipulating waste on the heap, and the other 89% were foragers. There is strict division of labor between foragers and waste workers, with no task switching. Waste management also has division of labor and is undertaken by transporters that carry waste to the heap margins and heap workers that manage the heap. Waste heaps are always located downhill from nest entrances. The distance to the waste heap is positively related to colony size and negatively related to slope. Foraging trails avoid the heap, with 92% of trails going away from the heap. This avoidance behavior is costly, increasing foraging trail length by at least 6%. Waste management in *A. colombica* is a sophisticated system that encompasses both work and spatial organization. This organization is probably adaptive in reducing disease transmission. Division of labor separates waste management from foraging, reducing the likelihood of foragers becoming contaminated with waste. The downhill location of heaps reduces waste entering entrances during rain. The orientation of foraging trails reduces the possibility of foragers becoming accidentally contaminated with waste. *Key words:* *Atta colombica*, disease transmission, division of labor, leaf-cutting ants, waste management, work organization. [*Behav Ecol* 13:224–231 (2002)]

A general trend in both human and insect societies is that the larger the society, the greater the challenge faced in waste disposal (e.g., Meadows, 1972). Not only does waste get in the way, but it can also be hazardous by serving as a reservoir for disease (Visscher, 1983; Weber, 1972). Leaf-cutting ants (*Atta* and *Acromyrmex*) face particular problems with waste and disease. These exclusively New World ants live in large colonies (10^3 – 10^6 workers; Wilson, 1971) and use collected vegetable matter to grow a symbiotic basidiomycete fungus in underground chambers. The fungus is used for food (Hölldobler and Wilson, 1990; Chapela et al., 1994; Mueller et al., 1998). The combination of large colony size and fungus growing results in formidable quantities of waste, including old fungus garden, culture medium, and dead workers (Weber, 1972). In addition, the symbiotic fungus is parasitized by a specialized pathogenic fungus, *Escovopsis*, which, if left unchecked, can kill a colony (Currie et al., 1999a,b). *Escovopsis* is known to be present in *Atta* waste (Bot et al., 2001). Thus, there is an explicit link between waste and disease.

Despite the importance of leaf-cutting ants in natural ecosystems (Haines, 1975, 1978; Wheeler, 1907), as pests in agricultural systems (Walter et al., 1938), and as a model system in studies of symbiosis (Herre et al., 1999; North et al., 1997) and work organization (Wilson, 1980a,b, 1983a,b; Wetterer, 1999), waste management has received little attention. Most species dig special underground chambers for waste disposal (Weber, 1972), but at least two, *Atta colombica* and *A. mexicana* (Deloya, 1988; Marquez-Luna and Navarette-Heredia, 1994; Weber, 1972) have external dumps. Hart and Ratnieks (2001) studied the organization of waste management in *A. cephalo-*

tes, which has internal waste chambers. This species combines nest structure, division of labor, task partitioning, and aggression into a sophisticated system that effectively isolates waste from the vulnerable fungus gardens. Bot et al. (2001) showed that active management of waste heaps occurs in *A. cephalotes*, which have specialized heap workers that rearrange and move waste on the heap, presumably to increase its decomposition rate. Bot et al. also showed that in *Acromyrmex echinator* (formerly *Ac. octospinosus echinator*), waste is potentially harmful to the fungus garden because it concentrates *Escovopsis*, and waste buildup increases ant mortality.

This study provides the first quantitative field study of waste management in leaf-cutting ants. We investigated waste management in *Atta colombica*, a species that forms waste heaps outside the nest. This provides an opportunity to compare waste management in an external dumper with *A. cephalotes*, an internal dumper. It also gives the opportunity to investigate the impact that colony organization has on the internal transmission of disease. We were able to demonstrate how colony organization at many levels may defend against parasites, and therefore provide a novel approach to an important but currently understudied aspect of eusociality (Schmid-Hempel, 1998).

Our study had two main aims. The first was to characterize quantitatively the main features of waste disposal. Specifically, we described and quantified the work involved in waste transportation and management and compared the workload and labor demand of waste-related tasks with those of foraging. We also investigated the divisions of labor that occur both within waste-related tasks and between waste handling and foraging. We tested the hypotheses that foraging and waste management tasks are mutually exclusive tasks for ants working outside the nest and that limited task switching (i.e., workers switching from waste management to foraging or vice versa) occurs between the two tasks.

The second aim was to test specific hypotheses concerning the adaptive location of waste heaps and foraging trails with

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Received 14 November 2000; revised 18 May 2001; accepted 22 May 2001.

respect to improved colony hygiene, specifically that (1) waste heaps are situated downhill from foraging entrances, (2) distance to the heap will decrease as the slope to the heap increases, and (3) foraging trails avoid waste heaps to prevent foragers from becoming contaminated with waste.

Our results show that waste disposal accounts for approximately 10% of work performed outside the nest. We show that there is a strict division of labor between foraging and waste work and that this organization is adaptive in improving colony hygiene. Further, the placement of waste heaps and the positioning of foraging trails is probably adaptive in reducing contact between waste and foragers.

METHODS

We studied *Atta colombica* waste heaps in 50 colonies of a wide size range, from small colonies less than a year old ($\sim 10^3$ – 10^4 workers) to established colonies ($\sim 10^5$ – 10^6 workers). The work was carried out around Gamboa, Panama, during March–May 2000.

Heap workload

To determine the tempo of outside-nest activities, we observed a large nest (nest 5) for 24 h. Forage input and waste output rates were determined hourly by three 1-min counts of laden workers entering with forage or leaving with waste. Ten forage and waste loads were taken hourly and weighed. The mean fresh weights were used to determine the total weights of forage collected and waste removed per hour. A further 11 nests were observed for one 10-min period at 0200 h and 1400 h on 6 occasions per nest over 2 months.

Number of workers involved in waste disposal

Six study nests were selected across the natural size range. Two tasks, transporting waste and heap working, were studied in detail. Waste transport was quantified by counting the number of waste loads per minute at 30-min intervals over 6 h during the day, between 1000 h and 1600 h. To determine the number of waste transporters, we used mark–release–recapture. Fifty (nests 2, 3, and 4), 100 (nest 1), 150 (nest 5), or 200 (nest 6) waste transporters were marked with a pen containing blue water-soluble poster paint as they were walking. Marking did not affect their behavior; marked workers continued with their task without interruption. Thirty minutes after the last worker was marked, the number of marked workers in the first 150 (nest 1), 100 (nests 2, 3, and 4), and 150 transporters (nests 5 and 6) leaving the nest were counted every 30 min for 6 h. To determine the number of heap workers (workers entirely confined to the heap surface) in each nest, three scan counts were taken in the morning and evening across 3 days (giving a total of six counts per nest, per day). For comparison, we determined the number of foragers for three nests (nests 1, 5, and 6). We also measured the total length of foraging trails. The number of foragers present (both laden and unladen) was counted three times in three 50-cm sections along each trail during a foraging activity peak. We determined the mean number of foragers per 50-cm section per trail and multiplied this number by the total trail length to estimate the total number of foragers. This is likely to be an underestimate of total forager number, as it only counts foragers on main trails. The number of laden foragers entering the nest was counted for 3 min hourly for 5 h during a foraging-activity peak.

Division of labor

Nest 5 was selected to test the hypothesis that waste management is an alternative endpoint to foraging for workers outside the nest and that waste workers do not become foragers or vice versa. Such a division of labor would prevent waste workers from contaminating leaf fragments entering the nest, which would occur if they became foragers. The methods used also allowed us to investigate the division of labor between waste transporters and heap workers. In particular, we tested whether waste transporters become heap workers and vice versa.

Do foragers ever become transporters or heap workers?

Two groups of 2200 and 3000 foragers were paint-marked over a 3-day period on the pronotal spines of the thorax using car-body paint applied with a seeker. Group 2 workers (3000) were marked 6 weeks after group 1 and were also used in the recruitment experiment (see below). The heap was observed for two 20-min periods each morning and evening for a total of 20 days between 15 March and 3 April (giving 40 observation periods). Marked ants working as either transporters or heap workers were noted. Marked heap workers were removed. We also observed foraging trails to ensure that marked foragers were still alive.

Do transporters become heap workers?

Two groups of 500 and 2200 transporters were marked as above but with a second color. The heap was observed for two 20-min periods each morning and evening for the following 20 days (giving 40 observation periods). Any marked heap workers were removed. As above, we also observed the transporters to ensure that marked individuals were still alive.

Do heap workers become transporters?

Seventy-six heap workers were marked over 4 days with a third color, and their presence or absence on the heap or transporting trails was observed daily for two 20-min periods.

Weights of workers

To determine whether there was a size-based division of labor among foragers, waste transporters, and waste heap workers, we took 50 foragers, 50 transporters, and as many heap workers as could be collected from each of 13 nests and weighed them.

Transporter recruitment

The group of 3000 marked foragers was also used to investigate whether foragers are recruited to waste management if the number of waste transporters is drastically reduced. We counted the number of waste transporters per minute for 3 min every 30 min for 60 min as they emerged from the waste exit. Then approximately 4000 transporters were removed over 60 min. These ants represented approximately 75% of transporters. We recorded the waste output rate and the presence of marked foragers among transporters over the next 3.5 h. The number of heap workers was also recorded.

Waste-directed aggression

Hart and Ratnieks (2001) showed that in laboratory colonies of *Atta cephalotes*, both foragers artificially contaminated with waste and waste heap workers were subject to heightened aggression from nest mates. They proposed that this aggressive response to waste-contaminated ants helps prevent waste workers from leaving the heap and thereby contaminating the

fungus gardens (Hart and Ratnieks, 2001). We investigated whether similar aggression occurred in *A. colombica*. First, we determined whether ants working with waste (transporters and heap workers) were subject to heightened aggression from nest mates. From a single nest we collected stocks of three categories of ants (foragers, transporters, and heap workers), from which 9 groups of 25 ants (3 categories \times 3 replicates) were housed separately in Fluon-lined bowls 30 cm square. Taking the three forager groups, 25 foragers from the remaining forager stock were individually introduced to forager group 1. Twenty-five workers from the transporter stock were similarly introduced to forager group 2. Finally, 25 workers from the heap worker stock were introduced to forager group 3. We performed similar introductions for the three transporter and three heap worker groups, giving all possible combinations of resident worker group and introduced workers. For each introduction, any aggression, defined as resident ants biting the focal ant, was noted, and the focal ant was removed before the next introduction. This was repeated for five colonies. Second, to investigate the effect of waste contamination, a separate group of 25 foragers was housed for 3 h in a petri dish half-filled with waste and introduced, following the same procedure as above, to a group of 25 foragers. This was repeated for five colonies.

Waste heap location

We tested two hypotheses concerning how the juxtaposition of the waste heap and foraging trails can be adaptive in terms of colony hygiene. First, we hypothesized that heaps would be located downhill from forage entrances to prevent rain from washing waste back into the nest and that heaps could be closer to forage entrances when the colony was situated on a steep slope. Second, we hypothesized that foraging trails do not pass close to heaps, to prevent foragers from becoming contaminated with waste.

For colonies with a single forage entrance, we measured the shortest distance along the ground between the hole and the heap. This line is henceforth referred to as the "heap-entrance line." For colonies with more than one forage entrance, the distance was measured from the point midway between all the forage entrances. The slope of the ground to the heap was measured using a clinometer. The orientation of foraging trails as they left the foraging entrances was measured with a compass relative to the heap-entrance line. Any unusual additional features of waste heap location were also documented.

RESULTS

General features of waste heaps

All 50 colonies had external waste heaps. Heaps were up to 11.7 m from the foraging entrances (mean = 3.81 m, SD = 3.00, $n = 50$ colonies) and varied in size from virtually flat deposits less than 10 cm diam to heaps > 2 m diam in larger colonies (mean diam = 0.97 m, SD = 0.81, $n = 50$). Three colonies were depositing waste into ponds. Twenty-two colonies had waste heaps around the bases of trees, and two colonies were depositing waste along the length of a fallen tree trunk, forming linear heaps, both approximately 5 m long. The remaining 23 colonies were depositing waste onto heaps on areas of the forest floor with no obvious features.

General features of waste disposal

Typically, ants carried waste from an exit hole located between the foraging entrances and the heap on a well-maintained

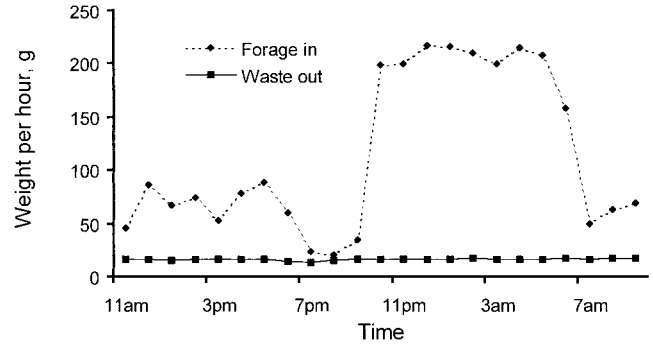


Figure 1

Daily tempo of foraging and waste removal activity in nest 5. The weight of waste removed per hour remains constant throughout the day. Foraging activity peaks between 2200 h and 0600 h.

trail. In very small nests the same hole served as both a forage entrance and a waste exit ($n = 7$ nests); otherwise, the exit hole was located anywhere between 0.35 m and 7.8 m from the heap and was always farther than 1.8 m from the nearest forage entrance. Waste loads were primarily pieces of dead fungus garden (mean fresh weight = 2.24 mg, $n = 60$ pieces weighed together) but also some dead ants, including reproductive (0.24%, 0.13%, and 0.09% of loads in 3 colonies, $n = 1200$ loads per colony). The loads were either placed directly onto the heap or dropped onto the heap from an elevated position, such as a tree branch or trunk if the heap was around a tree base (observed in all 22 tree-base heaps and 4 forest floor heaps near overhanging rocks). Workers were continuously present on the heaps of all but seven of the smallest nests. These workers moved waste around the heap. Tunnels were sometimes present within the heap (observed in 8 of 50 colonies). In addition, heap workers carried dead ants to the heap margins (observed in 12 of 50 colonies).

Heap workload

Waste disposal was constant throughout the day and night, both with respect to number of loads and weight per hour. In contrast, foraging showed a strong increase in both numbers of foragers and weight of forage between 2200 h and 0600 h (Figure 1). Waste removal occurred at all observation times for the 11 other study nests. Indeed, the only time any colony ceased removing waste was during extremely heavy rain, although heap workers were still present on the heap ($n = 4$ colonies). The total estimated number of waste loads exiting the nest in 24 h was 173,818 compared to 135,990 forage items entering. However, although waste loads had a mean fresh mass of 2.40 mg (60 loads = 144 mg), forage loads had a mean fresh mass of 19.75 mg (SD = 8 mg, $n = 150$). Therefore, the total mass of forage brought in was 2687 g, compared to 390 g of waste removed. This nest had 5300 waste workers (see below), so each waste worker made, on average, 33 trips in 24 h.

Number of workers involved in waste disposal

The six focal nests had 260–5300 transporters and 4000–32,000 foragers (Figure 2). The number of heap workers ranged from 1 to 77 (mean = 27 workers, SD = 27, $n = 6$). Pooling results across all colonies, 11.2% of the workers working outside the nest were waste workers (98.6% transporters, 1.4% heap workers) and 88.8% were foragers.

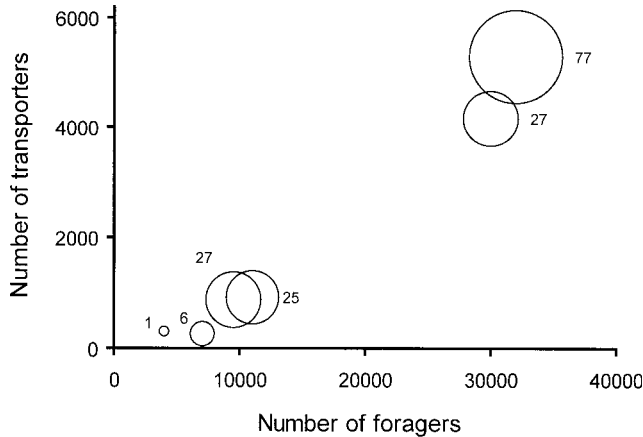


Figure 2
Numbers of foragers, waste transporters, and heap workers in six nests. The diameter of each circle is proportional to the number of heap workers in that colony, which is also given beside each circle.

Division of labor

200 of the 2700 (7.4%) marked waste transporters became heap workers, 89 (44.5%) within 3 days of being marked. None became foragers. Only two of the 5200 marked foragers later worked at waste disposal, both becoming heap workers. None of the 76 marked heap workers switched tasks to transporting, and 21 were dead on the heap within two days (Figure 3).

Weights of workers

The pattern of forager, transporter, and heap worker weights across the 13 colonies was variable. Worker task and nest had a significant effect on worker weight, with significant interaction (two-way ANOVA; worker task, $F_{2,992} = 28.2, p < .001$; nest, $F_{12,992} = 11.4, p < .001$; worker task \times nest, $F_{24,992} = 10.8, p < .001, n = 1031$). Pooling data across all colonies, heap

workers were significantly heavier than foragers, which were significantly heavier than transporters (heap workers, mean = 11.4 mg, SD = 0.7; foragers, mean = 9.2 mg, SD = 3.0; transporters, mean = 7.7 mg, SD = 2.0; one-way ANOVA, $F = 20.87, df = 2, p < .001$). However, the weight of waste transporters and heap workers considered together was not significantly different from that of foragers (mean waste workers = 9.2 mg, $n = 637$; mean foragers = 9.2 mg, $n = 384, t = 0.295, df = 635, p >> .05$).

Transporter recruitment

Removal of transporters resulted in a decrease in waste output rate from 150 to 21 loads/min. It took 80 min for the output rate to recover. None of the 3000 marked foragers was recruited to waste transporting. The number of heap workers remained constant (Figure 4).

Waste-directed aggression

No aggressive responses were recorded from any of the introductions ($n = 225$ introductions for each of five colonies to investigate whether ants working with garbage were subject to heightened aggression; $n = 25$ introductions per colony for each of five colonies to investigate the effect of waste contamination on aggression).

Waste heap location

Heaps were generally placed downhill from the foraging entrances. Small nests were an exception to this. Of the seven incipient nests lacking a separate waste hole, three had heaps on level ground and four on slopes 5° or less. The distance to the heap in these nests was between 0.4 m and 1.3 m (mean = 1.0 m, SD = 0.29, $n = 7$). The 43 nests with a separate waste hole were categorized according to the number of active foraging entrances (1 hole, $n = 8$; 2 holes, $n = 19$; 3 holes, $n = 14$; 4 holes, $n = 12$). Slopes were categorized into bins of 0–14°, 15–29°, and so on for a two-way ANOVA. There was a significant positive effect of nest size and a significant neg-

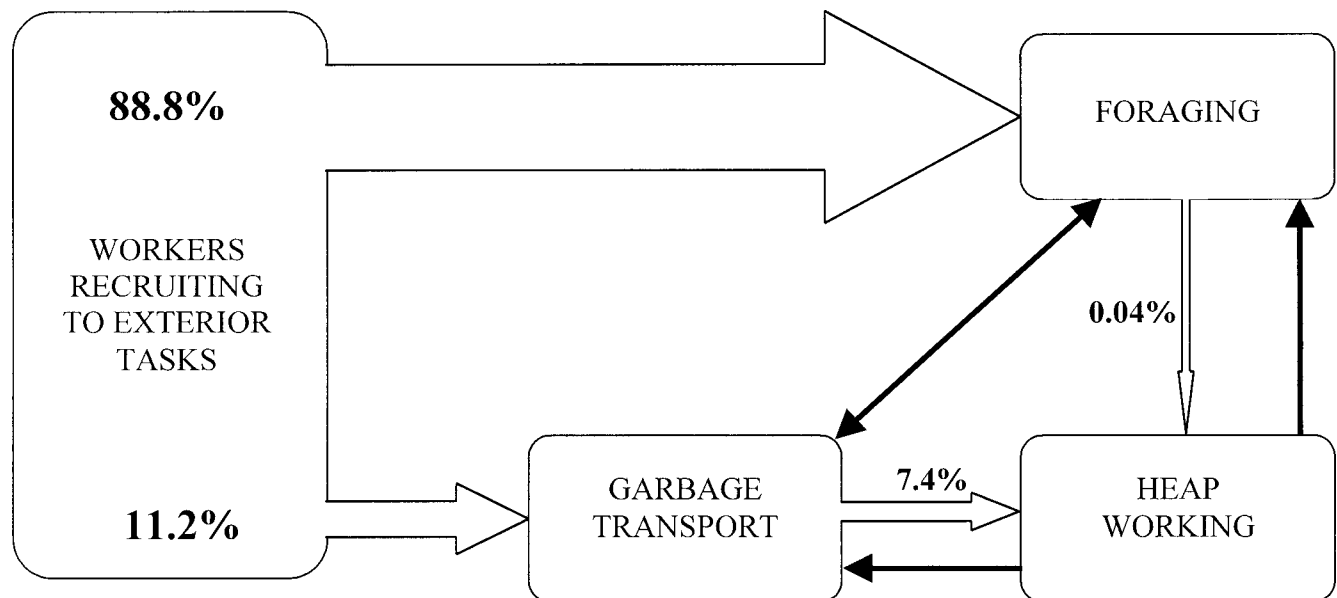


Figure 3
Transitions of workers between foraging and waste work. Waste work consists of two subtasks, transporting waste loads to the heap and working with waste on the heap. Together with foraging, these are the main tasks performed outside the nest. Black arrows mean that a transition was not observed.

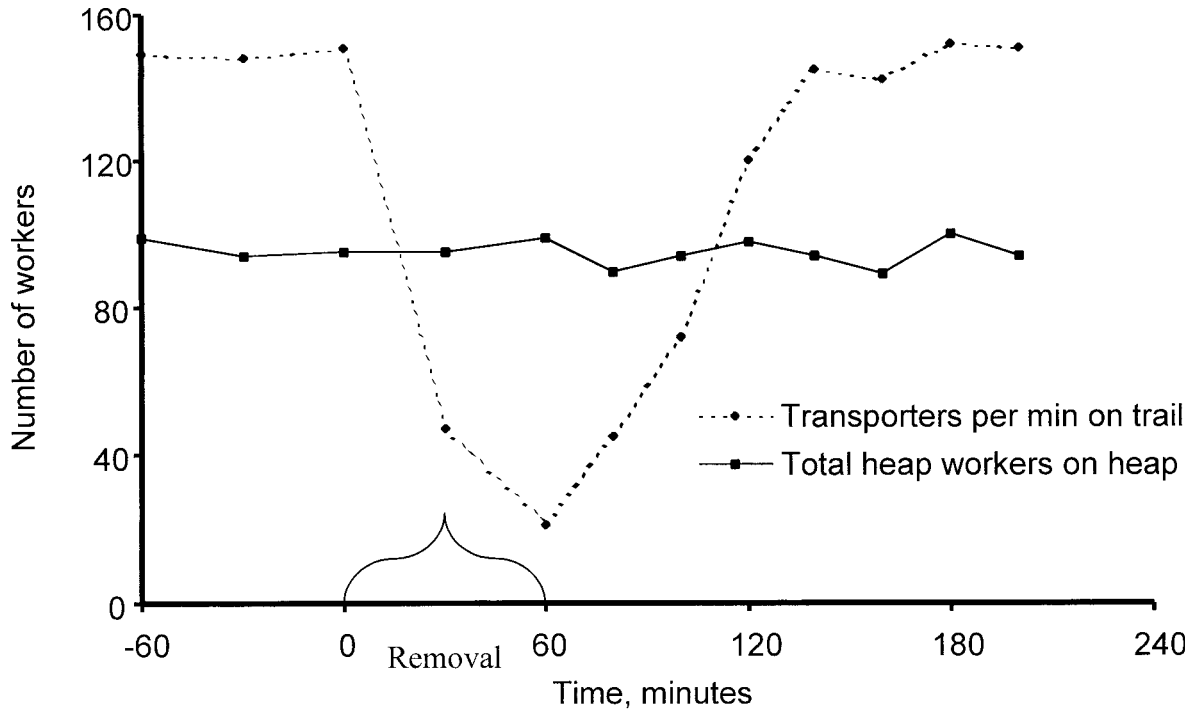


Figure 4
Removal of waste transporters and subsequent recruitment. Removal began at time 0 and continued for 60 min.

ative effect of slope on the distance of the heap from the foraging entrances, but no significant interaction (two-way ANOVA; nest size, $F_{2,31} = 10.4$, $p = .0003$; slope, $F_{3,31} = 3.9$, $p = .02$; nest size \times slope, $F_{6,31} = 0.45$, $p = .84$). There was a highly significant positive relationship between distance to the heap and colony size ($r = .58$, $n = 43$, $t = 4.6$, $df = 41$, $p < .0001$; Figure 5). There was no significant relationship between distance to the heap and slope to the heap for one-hole nests ($r = .44$, $n = 8$, $t = 1.2$, $df = 6$, $p > .05$). There were significant relationships for two-hole nests ($r = .47$, $n = 19$, $t = 2.2$, $df = 17$, $p = .02$) and for three-or-more-hole nests ($r = .69$, $n = 19$, $t = 3.6$, $df = 14$, $p = .001$; Figure 6).

Trail orientation was measured for 88 trails for 36 colonies,

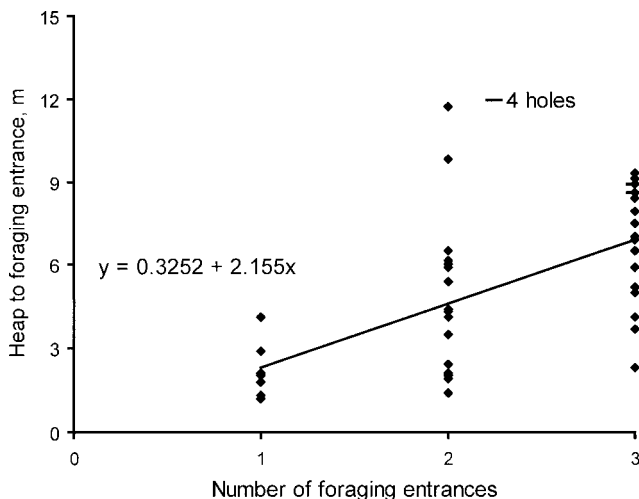


Figure 5
Relationship between distance to the waste heap and nest size (measured by the number of foraging entrances) for 43 nests with a separate waste hole.

chosen randomly from the study set of 50 colonies. Eighty-one trails (92%) were in the opposite direction of the waste heap, and only seven trails (8%) were within 90° of the heap (Figure 7). Taking equal numbers of trails going toward the heap and away from the heap as the null hypothesis, this was a highly significant difference ($\chi^2 = 37.8$, $df = 1$, $p < .001$). The closest approach of any trail to a heap in this sample was 1.5 m.

Additional heap features

Dumping into water

Three colonies were dumping waste into water, two into a pond and one into a slow-moving stream. However, only five of the 50 nests were within 12 m of water (measured as the distance from a water body to the nearest foraging entrance). The remaining two of the five colonies close to water had waste heaps farther from the foraging entrances than the nearest water body (6.7 m compared to 4.9 m to water, and 3.2 m compared to 2.3 m to water).

Dumping from positions elevated above the waste heap

Twenty-six colonies (52%) were dumping waste onto the heap from an elevated position. Nineteen of those colonies were dumping waste around the base of a tree, and waste transporters were dumping from sites on the trunk between 10 cm and 120 cm above the heap surface. Three colonies dumping around the base of a tree were not dumping from the trunk but rather were dumping waste onto the edges of the heap. Two colonies with linear heaps along fallen trees were dumping from the fallen trunk 5–15 cm above the heap. Three colonies were dumping from tree roots exposed on the slope above the heap, and two colonies were dumping from rocks positioned above the heap. Dumping from elevated positions was not observed in colonies with no separate waste hole and was only observed in one of eight of colonies (12.5%) with one foraging entrance. Dumping from an elevated position occurred in 13 of 19 colonies (68%) with two foraging en-

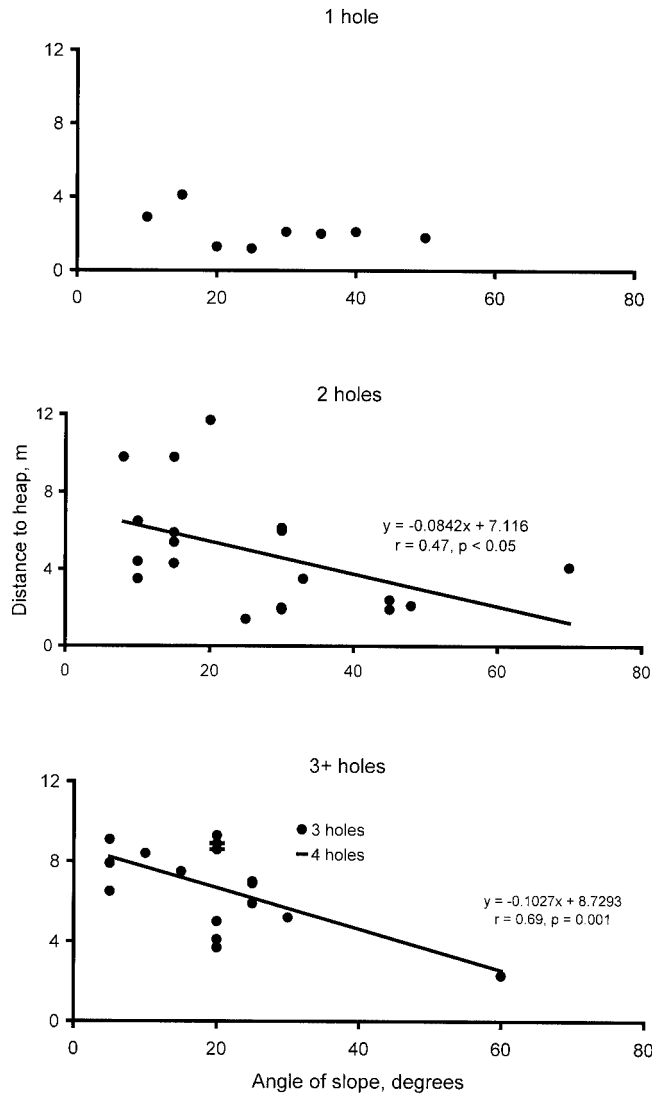


Figure 6 Relationship between distance to the heap and angle of slope between the foraging entrances and the waste heap in nests of 1, 2, and > 3 foraging entrances. There is no significant relationship for one-hole nests. Overall, both nest size and angle of slope are significant predictors of the distance to the waste heap, but there is no significant interaction.

trances and in 12 of 16 colonies (75%) of colonies with three or four entrances.

DISCUSSION

Waste dumping in *Atta colombica* is organized in a sophisticated way. This organization encompasses the work itself, the workers that carry it out, and the location of the heap.

As in *A. cephalotes*, there is division of labor in waste disposal. Transporters convey waste to the heap, where heap workers take over, distributing the waste around the heap surface. Waste disposal is a partitioned task, with transporters and heap workers connected through indirect material transfer (Anderson and Ratnieks, 2000; Ratnieks and Anderson, 1999). It is possible that waste removal is further partitioned within the nest. The entrance tunnels of three incipient colonies were excavated, and we found evidence of an underground waste cache just outside the fungus garden in two colonies.

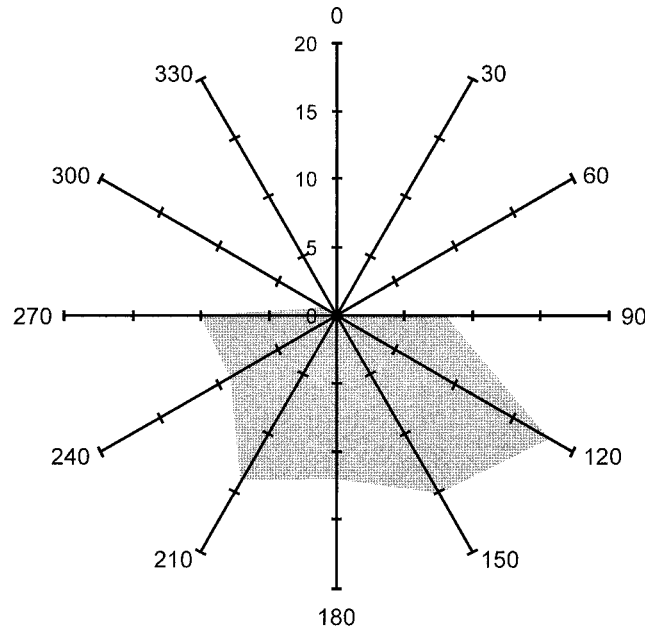


Figure 7 Direction of foraging trails in relation to the waste heap for 88 trails in 36 nests. The 0 axis represents the line from the waste heap to the foraging entrance, which is represented by the center of the web plot.

This suggests that workers move waste to just outside of the fungus garden, ready for collection by waste transporters. This is similar to what occurs in *A. cephalotes*, where one group of workers caches waste outside the heap, while others transport waste from the cache to the heap. Unlike *A. cephalotes*, however, waste-contaminated *A. colombica* workers were not subject to aggression from nest mates. This may be because *A. colombica* has external heaps that are likely to be farther from the fungus gardens than the internal heaps of *A. cephalotes*. Consequently, *A. colombica* heap workers are less likely to travel back into the nest and contaminate the fungus gardens with waste.

Unlike foraging, which has a daily peak, waste removal occurs constantly throughout the day and night, only ceasing during heavy rain. Heap workers work continuously, even during rain. It has been suggested that nocturnal foraging in *Atta* is influenced by diurnal parasitic phorids (Braganca et al., 1998; Feener and Brown, 1993; Orr, 1992). Assuming that waste transporters are equally vulnerable to phorid attack, our results suggest that phorids may have less of a role in influencing foraging rhythms than previously supposed. Further work is needed to determine the threat posed by phorids to waste workers. Of all workers outside the nest, 11.2% are engaged in waste work and 88.8% are foragers. Waste transporters remove 28% more loads from the nest over 24 h than foragers bring in, although this waste is only 14.5% of the weight of forage. Using data from nest 5, each forager makes 4.25 trips in 24 h. Each trip is approximately 96 m (the average trail length being 48 m in this nest), with a mean of 20 mg of forage collected per trip. Waste transporters can make 32.8 trips in 24 h, covering a smaller round-trip distance than foragers (approximately 10 m), with a mean of 2.4 mg of waste disposed. Therefore, per day, a forager covers 212 m unladen and 212 m laden with 85 mg of forage in 4.25 loads, and a waste transporter covers 164 m unladen and 164 m laden with 80 mg of waste in 33 loads. Although waste is much lighter than forage, the increased number of waste disposal trips means that individuals of both worker classes have approxi-

mately equal daily workloads. Because there are fewer waste transporters than foragers, waste activity accounts for about an eighth of a colony's exterior work.

There is strict division of labor between foragers and waste workers, with negligible task switching. Only 0.04% of foragers become heap workers, and switching from waste work to foraging does not occur. Waste work and foraging are, therefore, alternative tasks for outside-nest workers. Task switching does occur from waste transporting to heap work, but workers never make the switch back. Given that virtually all heap workers are recruited from transporters, then presumably transporters are able to respond to local cues (e.g., stridulation cues; Roces and Hölldobler, 1995, 1996) and switch to being heap workers when the need arises. Further research is needed to determine the mechanism of heap worker recruitment.

Waste transporters and heap workers, taken as a group, do not differ significantly from foragers with respect to fresh weight, so the foraging/waste-work division of labor is not size dependent. However, heap workers are significantly heavier than foragers, and transporters are significantly lighter than foragers. Because waste loads are light with respect to forage (2.24 mg compared with 20 mg), it is arguably more labor efficient to have smaller ants as transporters and larger ants as heap workers. Larger workers are able to gather larger pieces of waste, which, being crumbly, can only be moved small distances across the heap. The division of labor here appears to be adjusted for small, fast-moving transporters and large "bulldozers."

The data strongly support adaptive hypotheses of waste heap placement that reduce nest and forager contamination. Except in very small colonies, heaps are always placed downhill of foraging entrances. Small colonies do not separate waste and foraging entrances, suggesting that at this stage of colony development waste has little cost or that there is a high cost of having a second entrance. Presumably the benefit of separating waste output from forage input is to reduce contamination of incoming forage with waste, but the costs are not clear, and this area of colony organization requires further research. Disregarding these nests, there is a significant negative regression between the distance of the heap from the nest entrances and the slope of the ground to the heap; this regression increases in gradient, intercept, and significance as nests increase in size. Certainly larger nests have a greater area in which heaps can be efficiently sited, with both the distance and the distribution of distances to the heap increasing with colony size. The most likely explanation for downhill placement is that during rain, the flow of material from the heap (which can be considerable; Hart, personal observation) will be away from the nest entrances.

The waste heap profoundly affects the placement of foraging trails. Foraging trails predominately go away from the heap, with only 8% of trails initially heading toward the heap. The closest approach of a foraging trail to the waste heap was 1.5 m. Thus, the heap creates an exclusion zone of at least 5 m diam (assuming a 2-m diam heap at the center) through which foraging trails do not pass. Zeh et al. (1999) found a similar effect in *A. cephalotes*, where waste acts as a short-term repellent to foragers when placed on trails. Although this exclusion zone certainly reduces the risk of foragers and forage items being contaminated with waste-borne pathogens, it may impose a foraging cost. Trails may pass around the exclusion zone to exploit sources beyond the waste heap, but this increases the length of foraging trips. Idealizing the path around the heap as a semicircle of radius 2.5 m centered on the heap (assuming that the closest approach of the trail to the heap is 1.5 m and that the heap is 2 m diam), then the foraging path around the heap is 8 m compared with 5 m across the heap. For a 100-m foraging journey (50 m each

way), this adds 6 m (6%) onto the travel time. Because 1.5 m was the closest a foraging trail came to a heap, 6% is the minimum cost imposed by heap avoidance behavior when trails pass in the direction of the waste heap.

Waste heaps may be in water, but this occurred in only 6% of colonies. However, with 90% of colonies >12 m from water, a water-sited heap is not an option in most cases. Three out of five nests with water within 12 m were dumping waste into the water, and colonies dumping in water have no heap workers, reducing the demographic cost of the waste heap. Further study is needed to determine if dumping in water is an adaptive feature of waste management.

Waste transporters frequently dump from sites elevated above the heap. The tree trunk around which 38% of nests had positioned their waste heap provides the most common site. However, features around the heap, including rocks, roots, and fallen trees, are used if available. This behavior reduces transporter contact with the waste heap. Although transporters contact waste with every piece they carry, it is likely that such pieces are less contaminated with *Escovopsis* spores than is the heap, where *Escovopsis* sometimes produces large quantities of mycelium and spore-bearing bodies (Hart, personal observation). Thus, we propose that elevated-dumping behavior reduces the spread of *Escovopsis* from the heap to the fungus gardens via transporters. Sometimes transporters dump on the heap even when elevated sites are available, such as the trunk of a tree, leading to the testable hypothesis that *Escovopsis* presence influences dumping behavior.

The unchecked buildup of waste in a society can have disastrous consequences (e.g., Burnstein, 1990; *New York Times*, 2000). Leaf-cutting ants have a number of strategies that ameliorate the hazard that waste presents. A species with internal waste heaps, *A. cephalotes*, demonstrates sophisticated waste management as might be expected a priori given the proximity of waste chambers to fungus gardens. We have shown that *A. colombica*, which dumps waste outside the nest, demonstrates a similar level of sophistication, incorporating the organization of work and workers, worker behavior, and heap placement. External dumping removes the costs associated with excavating dump chambers. But, as we have shown, external dumping at least imposes a foraging cost. Why closely related, sympatric species have different solutions to the problem of waste is unclear, but we hypothesize that as-yet-undetermined, interspecific differences in disease susceptibility, particularly to *Escovopsis*, could be important.

This work was carried out with the assistance of a short-term fellowship awarded by the Smithsonian Tropical Research Institute (to A.G.H.). We thank Bill Wcislo and Ulrich Mueller for their assistance both before and during field work and Andy Gregson and Stephen Martin for their advice on the manuscript. We thank Koos Boomsma, Steven van Borm, Jeanette Bot, Mark Brown, and Serian Sumner for their assistance and company. A.G.H. also thanks Cris Thompson, Vanessa Bull, Hermogenes Fernandez, and all at Gamboa Field Station, Panama.

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