ORIGINAL ARTICLE

Jerome J. Howard

Costs of trail construction and maintenance in the leaf-cutting ant *Atta columbica*

Abstract Leaf-cutting ants of the genus *Atta* use trunk trails during foraging which may persist for months or years. The time and energy costs of trail construction and maintenance were estimated for colonies of *Atta columbica* on Barro Colorado Island, Panama, to determine if these costs are likely to constrain new trail construction and promote persistence of existing trails. Large workers 2.2–2.9 mm in headwidth participated in trail-clearing significantly more frequently than typical leaf-carriers, indicating that they may form a distinctive task group within the foraging force. Small litter items were carried off trails, while large ones were cut up before removal, greatly increasing the costs of removing large litter items. The average time cost of removing a kilogram of litter was estimated at 3,359 ant-hours, and energy costs at 4.6 kJ. Colonies maintained trail systems 267 m in length and 16.5 m^2 in area, and built an estimated 2.7 km of trail with an area of 134 m^2 during a year. Based on litter standing crop and estimates of litter-fall rates, total costs to colonies averaged 11,000 ant-days of work and the energy equivalent of 8,000 leaf burdens. These costs are small relative to the number of available workers and rates of mass harvest, suggesting that costs do not significantly constrain trail construction. Instead, trails may persist because they provide access to high-quality resources or because only a few trails are required to fully exploit the foraging territory.

Keywords *Atta columbica* · Energy costs · Foraging · Time costs · Trunk trails

J.J. Howard (✉)
Program in Conservation Biology,
Department of Biological Sciences, University of New Orleans,
New Orleans, LA 70148, USA
e-mail: jjhoward@uno.edu
Tel.: +1-504-2805441, Fax: +1-504-2806121

Introduction

The use of recruitment trails is a ubiquitous feature of foraging by ants (Hölldobler and Wilson 1990). In most cases, recruitment trails are temporary, and are abandoned when the specific food resource to which recruitment is taking place is exhausted. However, in a few genera such as *Pogonomyrmex* (Hölldobler 1976), *Formica* (Rosengren 1971), and *Atta* (Weber 1972), trails may last for months or years, and may be partially or completely cleared to facilitate locomotion (Rockwood and Hubbell 1987). In some cases these "trunk" trails are long-lasting because they serve high-quality, long-lasting resources such as aphid colonies (Rosengren and Sundström 1987), but for other species the reasons for trail longevity remain unclear.

The case of *Atta* is particularly interesting because these ants maintain long-lasting trunk trails despite foraging on leaf resources that are patchy and highly ephemeral (Rockwood 1975; Fowler and Stiles 1980; Sheperd 1985). A typical adult colony may simultaneously maintain three–ten large trails, each as much as 30 cm wide and cleared of leaf litter to the bare ground (Weber 1972; Fowler and Robinson 1979). These long-lasting trunk trails give access to numerous partially cleared, temporary trails that connect specific resources to the colony. Single trunk trails may exceed 200 m in length (Lewis et al. 1974) and appear to represent a significant investment in time and energy by the colony (Lugo et al. 1973; Shepherd 1982). This investment is repaid with a four- to tenfold reduction in travel costs for ants using the trail system versus those traveling over uncleared ground (Rockwood and Hubbell 1987). In addition, the application of trail pheromone to cleared and relatively smooth substrates may greatly increase the strength and persistence of major trails, allowing ants to rapidly relocate and exploit favorable resources after periods of inactivity.

Despite their striking appearance and importance for foraging, little research has been undertaken on the construction and maintenance of trail systems in *Atta*.

Wilson's (1980) detailed analyses of caste optimization took place in the laboratory and so excluded the tasks involved in trail construction and maintenance under natural conditions. Much work has focused on the performance of workers utilizing trails (Lutz 1929; Hubbell et al. 1980; Rudolph and Loudon 1986; Lighton et al. 1987; Waller 1989; Shutler and Mullie 1991; Wetterer 1994; Burd 1995, 1996) and the use of trail systems by colonies in exploiting resources (Fowler and Robinson 1979; Fowler and Stiles 1980; Shepherd 1982; Rockwood and Hubbell 1987). However, our understanding of foraging economics in leaf-cutting ant colonies will remain incomplete until the costs of trail construction and maintenance are included in colony time and energy budgets.

In particular, the striking persistence of a few major trails in each colony begs an explanation. Trails may represent such a large investment of time and energy that, once established, it is uneconomical to continually abandon existing trails and clear entirely new ones. Lugo et al. (1973) provided some evidence to support the idea that trail construction and maintenance is costly. They estimated that up to 75% of ants on trails at any given time do not carry leaves, and suggested that many if not most of these ants might be involved in trail construction or maintenance. If most ants on trails are so engaged, then the rate of energy input into ant colonies may frequently be limited by allocation of aboveground workers to trail maintenance rather than to foraging. Additionally, access to high-quality resources may frequently be limited by allocation of workers to maintenance of existing trails rather than to construction of new ones. In the extreme case, foraging may be limited to areas along major trails initially laid out years before when colonies were young, and leaf-cutters may have only limited ability to exploit the resources available in their territories.

Alternatively, if costs of trail construction and maintenance are substantially lower than suggested by Lugo et al. (1973), the persistence of trails might be due to benefits accruing to colonies from their placement rather than to time and energy constraints. Trails might persist because they afford consistent access to areas within the foraging territory that contain numerous high-quality (though individually ephemeral) resources, or because only a few major trails are required to bring the entire territory within easy reach of foraging ants. However, if most aboveground workers not carrying leaves are not engaged in trail maintenance, their exact role in ant colonies would remain to be determined.

This study quantified the costs of trail construction and maintenance by colonies of *Atta columbica* on Barro Colorado Island (BCI), Panama. I estimated the number of ants in the aboveground worker force engaged in trail-clearing activities, and measured the time and energy required to handle litter items of varying types and sizes. I used this information to estimate total costs to colonies of clearing and maintaining trail systems during the course of a year, and relate these costs to overall time and energy budgets during foraging.

Methods

The study was conducted on BCI, Panama, on adult ant colonies in the Allee Creek drainage near the laboratory clearing. The vegetation, geology, and physical environment in this area are described in detail elsewhere (Leigh et al. 1982). Five adult colonies in this drainage were studied: one below the Kodak House laboratory (hereafter referred to as KH), one at the water tower (WT), one at the junction of the Barbour-Lathrop and Wheeler trails (BLW), one near the edge of the Lutz Creek drainage (LC), and one north of the dormitory complex (DOR). The KH colony died in late June 1996, and was excluded from some studies of trail dynamics, and the LC colony was used only for studies of caste differentiation due to the inaccessible terrain traversed by its trails. Studies related to ant behavior and litter-handling efficiency were primarily conducted during May–June 1995; those addressing trail and litter dynamics were primarily conducted during May–June 1996 and 1997. Voucher specimens taken from colonies used in this study are deposited in the Louisiana State Arthropod Museum.

I studied task-specificity of workers and estimated the size of forager populations by marking workers with enamel paint. Permanent marking of *Atta* workers is difficult due to their spiny thoraces and reduced abdomens, the efficiency of allogrooming, and the toxic effects of some solvents (personal observation). The loss of marked individuals from these sources can introduce significant error into population estimates derived from mark-release-recapture (MRR) studies (Southwood 1978). To maximize the efficiency of paint marking and to minimize mortality due to paint application, I practiced using an insect pin to apply enamel paints (Testor's) to the thoraces of workers in laboratory colonies prior to the studies reported here. In the laboratory, mortality from paint marking was concentrated in smaller size classes, and in this study I marked only workers larger than 1.8 mm headwidth. After considerable practice on laboratory colonies, 85% of paint-marked workers were consistently recovered after 24 h. The loss of individuals was mainly attributable to removal of paint marks, since the corpses of only about a third of the missing individuals were recovered from colony dumps. In this study, worker populations were estimated only on the basis of 24-h MRR studies and estimates were adjusted to reflect a loss of 15% of marked individuals due to loss of paint marks and mortality.

Size and task specificity of trail-clearers

Atta workers divide tasks performed on trails according to size (Stradling 1978; Wilson 1980). Preliminary observations suggested that ants clearing trails were comparable to or larger in size than those carrying leaves. To determine whether trail-clearers were physically distinct from leaf-carriers, I collected samples of at least 50 leaf-carrying ants and 50 ants clearing obstructions placed on trails from each of three colonies (KH, WT, and LC). Ants were stored in 70% ethanol until measured in the laboratory. The maximum width of the head capsule was measured using a dissecting microscope with a micrometer scale.

I used the KH colony to study the specificity of trail-clearing behavior, marking 300 ants carrying leaves with one color and 100 ants clearing obstructions placed on trails with a different color. During the mid-afternoon peak in foraging activity on the following day (2:00–4:00 p.m.), I counted the number of color-marked ants that carried leaves or recruited to debris placed on trails. I then used a χ^2-test to compare the ratio of ants marked with different colors that were observed performing these two tasks to the expected ratio of 3:1 derived from the original number of marked leaf-carriers and trail-clearers.

Estimation of worker populations

The total number of ants engaged in foraging, and the number participating in trail-clearing activities, was estimated by paint-mark-

ing ants engaged in each task and tallying the proportion of marked ants observed performing these same tasks 24 h later. To estimate the total number of foragers, ants were picked up using forceps, quickly marked with a spot of paint on the thorax using an insect pin, and then returned to the trail edge. Between 300 and 500 ants were marked in each colony save BLW, in which 150 ants were marked. Paint marks placed on the thorax elicited little response from the ants; many leaf-carriers held on to their burdens during marking and immediately resumed travel toward the colony when replaced on the trail.

I then determined the proportion of marked ants at the peak of foraging on the next day. I counted the number of ants passing a fixed point during 3 min on each active trail, and used the Lincoln index (Southwood 1978) to estimate total size of the foraging force from the proportion of marked ants on trails. Due to the effort involved in marking large numbers of ants, I obtained a single estimate of forager number for each colony via this method, based on the summed activities of all trails 24 h after initial marking.

To check the accuracy of estimates based on paint-marking, I compared forager numbers calculated from MRR to those estimated from direct counts using the method of Lewis et al. (1974). I counted the average number of ants passing a fixed point on each active trail during three 1-min samples, and estimated the forager population from the average running speed and the total length of the trails. A total of five estimates of forager numbers were made for each colony using this method.

To estimate the number of ants specifically engaged in trail-clearing activity, I marked ants attempting to cut or move obstructions, and tallied the proportion of marked ants performing the same task after 24 h. I attempted at least two separate MRR estimates of the number of trail-clearers in each colony, each based on a sample of 50 marked ants, using different colors for each estimate.

Time and energetic cost of litter handling

I determined the effort required to remove a given quantity of litter by placing obstructions of different types and sizes on trails. I then counted the number of ants attempting to cut or move the obstruction at 1-min intervals and calculated the total number of ant-minutes required to clear the trail as an estimate of the time costs of removal. Since ants continued to work on obstructions even when they were no longer blocking the trail, I continued the observations until all ants abandoned each item. I used two types of obstacles to block trails: haphazardly collected leaves of varied species taken from litter in various stages of decomposition, and twigs varying in diameter and mass.

Energetic costs of litter handling were estimated from published models of laden transport (Lighton et al. 1987) and cutting (Roces and Lighton 1995). Ants lift and carry small litter pieces in the same way that burdens are carried, and the energetic cost of carrying or pulling litter off trails was estimated from the number of ant-minutes required to handle the obstruction, at the metabolic rate of laden transport (Lighton et al. 1987). Energy calculations were made with the assumption that all ants working on leaves were the median mass for trail-clearers (9.55 mg in this study). The measured aerobic scope of 11.2 is considered the minimum cost of laden transport (Lighton et al. 1987) and estimates derived from these data should be considered the minimum energetic costs of moving litter.

Large litter pieces are often cut before being moved, and the energy cost of handling these pieces was estimated by separately calculating, and then summing, the energy expended during the time spent cutting and the time spent carrying each piece. I first determined the maximum mass of a litter fragment that could be moved without cutting, and estimated the handling time of this mass by regressing observed handling times on litter mass. I assumed that all large litter pieces were cut until they reached this size, and were then moved off the trail without further cutting. Energy expenditure for moving these residual fragments was calculated from the cost of laden transport (Lighton et al. 1987) as

outlined above. I then estimated the time spent cutting each piece of litter by subtracting the carrying time from the total number of ant-minutes required to handle the litter pieces. I calculated energy expenditure during cutting using the metabolic rate of cutting ants measured by Roces and Lighton (1995), again assuming that all ants were the median mass for trail-clearers. The energy costs of cutting and moving litter were then summed to estimate the total energetic cost of handling large litter pieces.

Litter biomass and construction of trail systems

Time and energy costs of clearing a kilogram of litter were determined by calculating the cost of moving or cutting each individual piece of litter in three samples. The costs of handling an individual item vary with its mass, which may be greatly affected by moisture content. I used a standard protocol for all litter collections in this study to reduce variability in moisture content due to extrinsic factors such as rainfall. All litter samples were collected from a 0.25-m^2 quadrat between 9:00 a.m. and noon, and from 24 to 36 h after the last rainfall. Because large pieces of litter often partially overlapped quadrat boundaries, I used a knife to cut around the perimeter of all quadrats before harvesting litter within the designated area. Each sample was placed in a plastic bag and individual litter items removed one at a time for weighing. Items were grasped with forceps and removed from the bag exactly as they would have been encountered by ants; e.g., if several small litter fragments were held together by fungal hyphae, they were weighed as a single litter item. The bag was kept sealed when not removing litter to avoid dessication of the sample in the laboratory.

To estimate the cost of constructing the active trail system of each colony, I determined the amount of litter removed from trails and calculated the time and energy costs of this task. I compared the average standing crop of leaf litter in the vicinity of active trails to the amount of residual litter remaining on trails, and calculated the time and energy required to remove the missing litter. I measured the length of each active trail, and measured trail width at 10-m intervals to estimate total area cleared in trail construction. Although many authors dichotomize trail structure into large, persistent, mostly cleared "trunk" trails serving numerous small, temporary, relatively uncleared "branch" trails, this dichotomy proved difficult to apply objectively to the study colonies because trails varied continuously in both width and degree of clearing. Instead, trail segments first marked in 1996 and reused in 1997 were classified as persistent trails; those used in only 1 year of the study were classified as ephemeral trails.

To estimate litter standing crop, litter was collected from 0.25-m^2 quadrats placed approximately 50 cm from the edge of active trails, at 10-m intervals, using the standard protocol described above. Litter was bagged and weighed within 0.5 h of collection to obtain wet mass. The mass of residual litter remaining on trails was measured by collecting all litter present on a segment of trail 20–50 cm in length, adjacent to each quadrat used for measuring litter standing crop. The residual mass of litter left on a trail segment was subtracted from the litter standing crop estimated from the adjacent 0.25-m^2 quadrat to calculate the amount of litter actually cleared from trails.

The costs of constructing the trail system active at any given time are only a portion of the total yearly cost to an ant colony. Colony trail systems are dynamic, with trails continually being abandoned or constructed as colonies switch from old to new resources. In addition, litter falling upon active trails must be removed as it falls. To estimate the yearly cost of trail construction, I measured the rate of new trail construction and the amount of litter cleared from newly constructed trails during the study, and estimated the yearly cost of this activity. Estimates of litter standing crop and residual litter remaining on newly constructed trails were obtained as described above for existing trail systems. The yearly cost of clearing litter falling on trail surfaces was calculated from published measurements of litterfall on BCI (Leigh and Windsor 1982). Previously published measurements of litterfall were ex-

pressed as dry mass, whereas ants must cut and move wet litter. To obtain estimates of wet litter mass from published measurements of dry mass, I dried litter samples used for standing crop estimates at 70°C for 48 h, and assumed that litter samples collected by Leigh and Windsor (1982) contained the same percent water as the ones in this study.

Results

### Worker size and task specificity

Two-way analysis of variance revealed that colonies KH, WT, and LC differed significantly in mean size of workers found on trails (F-ratio=15.5, df=2,344, $P<0.001$), and that ants clearing trails were significantly larger than those carrying leaves (F-ratio=86.4, df=1,344, $P<0.001$). The difference in mean size of ants performing the two tasks was mainly attributable to an excess of workers between 2.2–2.9 mm headwidth clearing debris, and not to extensive participation by soldiers (headwidth ≥3.0 mm; Wilson 1980) in trail-clearing (Fig. 1). Although soldiers were occasionally observed both carrying burdens and clearing debris, only 5.8% (9 of 156) of workers collected while clearing debris had headwidths of 3.0 mm or more.

Ants marked while attempting to handle trail obstructions or while carrying leaves exhibited different degrees of task fidelity. Both groups of workers were equally likely to be observed carrying leaves 24 h later (Table 1). However, workers originally marked while clearing trails were significantly more likely to recruit to debris experimentally placed on trails 24 h later than were those originally marked while carrying leaves (Table 1).

Estimation of worker populations

MRR estimates of forager populations for four colonies ranged from 20,000 to 70,000 (Table 2). In general, forager population estimates using the method of Lewis

et al. (1974) were consistent with those obtained from MRR, differing by an average of only 11% (Table 2), suggesting that MRR could be used with confidence for estimating populations of foragers and trail-clearers. Although the two methods gave estimates differing by over 25% for one colony (BLW), for consistency, the MRR
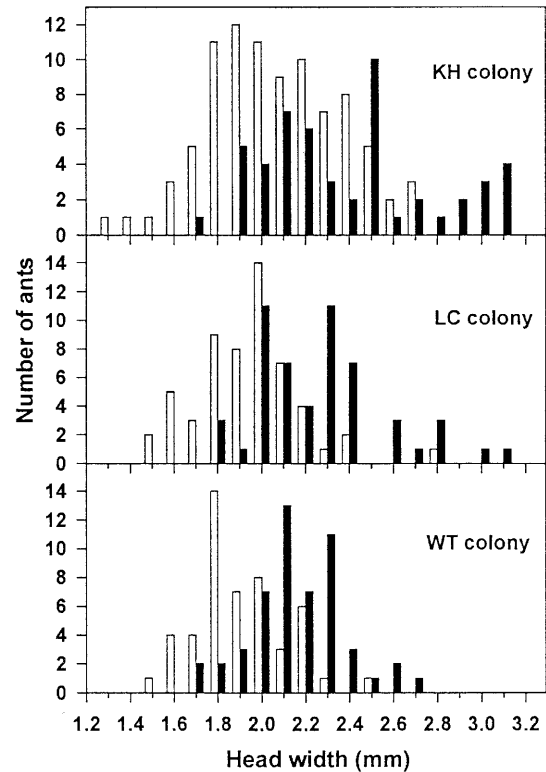
Fig. 1 Distribution of ants carrying leaves (*open bars*) and clearing trails (*shaded bars*) in three *Atta columbica* colonies on Barro Colorado Island, Panama. Size distributions differ significantly among colonies (two-way ANOVA: F=15.5, df=2,344, $P<0.001$), and among tasks (F=86.4, df=1,344. $P<0.001$)

Table 1 Task fidelity of ants originally marked while carrying leaves (n=300) or clearing obstructions from trails (n=100)

Subsequent task	Original task		Expected 3:1 ratio	χ^2	df	P
	Carrying leaves	Clearing trails				
Carrying leaves	51	10	45.75:15.25	3.3	1	>0.05
Clearing trails	5	10	11.25:3.75	13.7	1	<0.001

Table 2 Estimates of total foraging force and number of ants participating in trail construction and maintenance in four colonies of *Atta columbica*. Trail count estimates are based on the method of Lewis et al. (1974). Mark-release-recapture (*MRR*) estimates are based on 24-h MRR studies of painted ants, adjusted to reflect losses of 15% due to mortality and loss of paint marks

Colony	Estimated foraging force		Estimated trail-clearers	
	Trail counts	MRR	Number (MRR)	Percent foragers
KH	52,513±2,580	52,727	2,483±550	4.7±1.0
WT	70,186±2,463	69,003	–	–
BLW	60,103±2,632	46,604	1,117	2.4
DOR	17,279±2,504	19,826	1,128±149	5.7±0.8
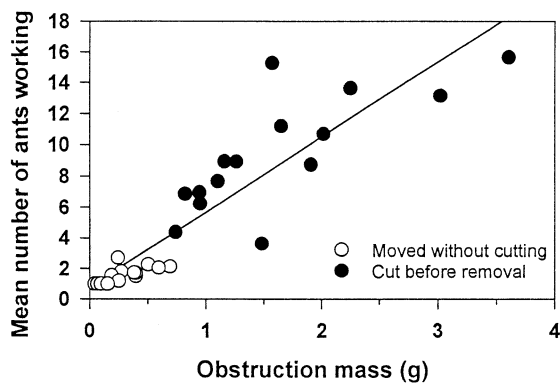
Fig. 2 Mean number of ants recruiting to obstacles placed on trails ($Y=5.24X+0.6$; $r^2=0.82$) (*open circles* obstacles removed by pulling them off the trail without cutting, *filled circles* obstacles that were cut prior to being pulled off the trail)
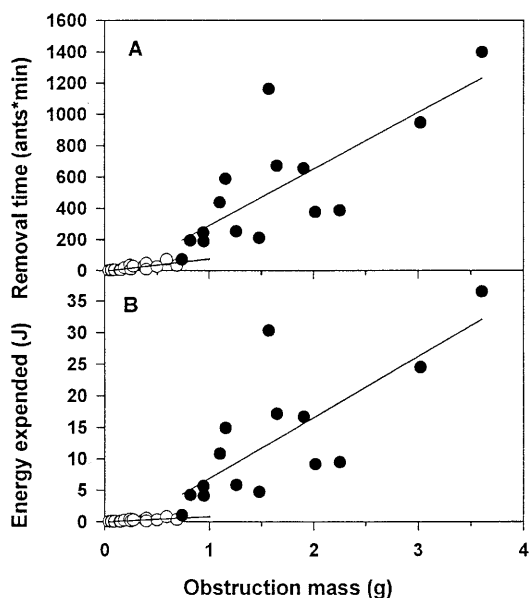

Fig. 3A,B Time and energy costs of removing obstructions from trails (*open circles* obstacles removed by pulling them off the trail without cutting, *filled circles* obstacles that were cut prior to being pulled off the trail). **A** Time costs of clearing obstructions. Obstacles removed without cutting: $Y=79.7X-3.8$; $r^2=0.76$. Obstacles cut prior to removal: $Y=360.5X-70.8$; $r^2=0.58$. **B** Energy costs (J) of clearing obstructions. Obstacles removed without cutting: $Y=0.83X-0.38$; $r^2=0.75$. Obstacles cut prior to removal: $Y=9.67X-2.81$; $r^2=0.58$

estimate was used in calculating the percentage of trail-clearers in all colonies.

MRR estimates of trail-clearers were obtained for three of the four colonies, and ranged from 1,000 to 2,500 (Table 2). Only one estimate was obtained from the BLW colony, and none from the WT colony, due to heavy rains on the day following marking. These estimates suggest that 1,574±641 ants per colony, or 4.2±1.4% of the foraging force, participated in trail-clearing.

Efficiency and energetic cost of litter handling

Most ants encountering obstructions placed on trails simply ignored them, and attempted to walk around or over them. This was true for both laden and unladen ants. Obstacles less than 0.02 g did not generally impede ants and were never removed. Masses of workers quickly accumulated on either side of larger obstructions, milled about and disrupted trail activity. The first workers to attempt to move obstructions arrived 123±75 s (*n*=9) after the object had been placed on the trail, and invariably attempted to move the obstruction off the trail by seizing it in the mandibles and pulling to one side. If initially unable to move an obstruction, the ants attempted to cut and remove it piece by piece.

Small pieces of leaf litter (less than 0.7 g) attracted only one or two ants, which moved the item rapidly and without cutting (Fig. 2). Larger pieces at times attracted as many as 30 ants, each pulling on the edge of the object in a different direction. The resulting stasis required the ants to cut large objects until they were small enough to be pulled off the trail. Small twigs of up to 0.5 g were rapidly cleared by one or two ants. Heavier twigs either became wedged in debris at the trail edge or were too large in diameter for ants to grasp with their mandibles, and ants gave up without removing these obstacles from trails. Workers appeared to spend more time than necessary in clearing trails of obstructions, often continuing to

cut and pull objects away from the trail long after the trail itself was clear.

The differing treatment of large and small litter items greatly affected the amount of time required to clear obstructions from trails. The rate at which twigs and leaf litter weighing 0.5 g or less were cleared from trails did not differ significantly (analysis of covariance: litter type×mass interaction, *P*=0.627), and all litter items 0.7 g or less were combined for subsequent analyses. The time required to clear obstacles from trails increased linearly with obstacle mass, but the rate of increase for large litter pieces (>0.7 g) that were cut before being removed was 4.5 times greater than that for small litter pieces removed by pulling alone (≤0.7 g; Fig. 3A). Because litter was cut only beyond a distinct threshold mass, the distributions of cut and uncut litter pieces did not overlap, and no statistical comparison of slopes was made.

Estimated energy expenditures during trail-clearing also differed among litter items that were moved without cutting, versus those that were cut before moving. The longer handling times of large litter pieces, combined with the greater metabolic cost of cutting (aerobic scope of 30.7 vs 11.2), produced an 11.6-fold greater rate of increase for energy expended in removing obstructions greater than 0.7 g than for removing those less than 0.7 g (Fig. 3B). Again, the distributions of cut and uncut litter pieces did not overlap and statistical comparisons were not made.

Table 3 Mean costs of trail construction and maintenance for four *A. columbica* colonies on Barro Colorado Island

	Clearing standing litter (existing trails)	New trail construction	Clearing litterfall (existing trails)[a]
Trail length (m)	267±74	2,730±460	267±74[b]
Trail area (m^2)	16.5±5.8	134±54	16.5±5.8
Litter cleared (kg)	14.4±7.9	40.7±16.4	23.8±7.9
Time costs (ant-days)	2,012±1109	5,697±2293	3,328±1,109
Energy costs (kJ)	66.3±7.9	187.6±75.5	109.5±33.2

[a] Estimated annual litterfall/m^2 taken from Leigh and Windsor (1982)
[b] Average length of trail systems during the study assumed to be representative of yearly averages
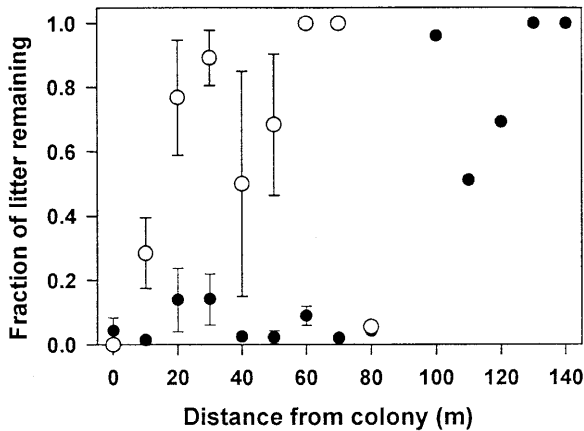
Fig. 4 Fraction of litter standing crop remaining on trails at varying distances from ant colonies (*Open circles* ephemeral trails, *closed circles* persistent trails)

Litter biomass and construction of trail systems

A total of 1,138 individual litter items were weighed in the three samples. An average of 26±2.5% of the total litter mass occurred in pieces either too small (<0.02 g) or too large (i.e., twigs>0.5 g) to be handled by leafcutter ants, and these items were excluded from calculations of time and energy cost. The estimated time cost of removing a kilogram of material from trails was 3,359±460 ant-hours, and the energy cost was estimated at 4,608±795 J.

Litter standing crop (capable of being moved by ants) in the study area averaged 1,226±478 g/m^2 wet mass (*n*=69). Litter dry mass averaged 525±204 g/m^2, or 42.7% of wet weight. Colonies maintained trail systems averaging 267 m in length and 16.5 m^2 in area (Table 3). Colonies cleared large amounts of litter from persistent trails up to 80 m from the colony center (Fig. 4). In contrast, large amounts of residual litter were left on ephemeral trails, even those occurring within 20 m of the colony (Fig. 4). Trail systems utilized logs, lianas, and branches for 9.3% of their total length, and these accumulated essentially no litter at all. Colonies removed an estimated 14.4±7.9 kg of wet litter to establish active trail systems, at a cost of 2,012±1,109 ant-days of effort and 66.3±36.5 kJ (Table 3).

During May–June 1997, colonies established 7.47± 1.25 m of new trail, with a total area of 0.37±.015 m^2,

per day. This rate of trail building would suggest that colonies establish 2.73±0.46 km of trail during the course of a year, with an area of 134±54 m^2. A small amount of new trail construction was cleared to bare ground, but substantial amounts of litter were left on most such trails. On average, only 0.3 kg/m^2 of litter was removed from newly constructed trails, approximately 25% of litter standing crop in the study area. This yields an estimate of 40.7±16.4 kg of litter removed from all trails cleared during the course of a year, at a cost of 5,697±2,293 ant days of effort, and an energy expenditure of 187.6±75.5 kJ.

Previous studies of litterfall in the adjacent Lutz ravine between 1974 and 1979 estimated annual leaf fall, which matches well with litter items actually removed by ants, at 615±49 g/m^2 dry mass (Leigh and Windsor 1982). Based on moisture content measured in this study, this is equivalent to 1,441±115 g/m^2 of wet litterfall. If active trail systems measured in this study are representative of yearly averages, then 23.8±8.4 kg of wet leaf litter would fall on active trail systems during the course of the year. If all falling litter is removed, the time cost would be 3,328±466 ant-days of effort, and the energy cost would be 109.5±39.2 kJ.

Discussion

Cost and the persistence of colony trail systems

The trail systems of leaf-cutting ant colonies are large and impressive feats of construction, but the subjective impression that they represent a large cost of time and energy to colonies is not borne out by the results of this study. The total time cost of constructing an average active trail system, all temporary trails for a year, and clearing annual litterfall amount to approximately 11,000 days of work by trail-clearers. If a typical adult colony has 1,000–2,000 workers engaged in trail-clearing, the entire task can be accomplished in a matter of days. The energy costs are even less limiting, a pattern consistent with previous studies (Fewell 1988; Howard 1991). If colonies gain an average of 45 J per burden harvested (Howard 1991), then the cost of active trail construction, clearing of temporary trails for a year, and removing annual litterfall could be met by harvesting 1,473, 4,169, and 2,434 average-sized burdens, respectively. The total

of approximately 8,000 burdens is easily exceeded in a single day of foraging by adult colonies (Lugo et al. 1973).

The results of this study suggest that the persistence of major "trunk" trails in *Atta* colonies is not due to high costs of trail construction. This is despite the fact that the study took place at the interface between dry and wet seasons in Panama, when litter standing crop is at a yearly maximum (Wieder and Wright 1995). Litter particle sizes also decrease during decomposition, and trail construction costs should steadily decline during the early wet season from levels calculated in this study as litter size distributions shift toward smaller items that can be removed from trails without cutting. Ant colonies in this study thus proved capable of clearing new trails rapidly and relatively inexpensively, even at maximum time and energy costs. This suggests that trails may persist because colonies benefit from their location, perhaps by obtaining consistent access to high-quality resources. Alternatively, trails might persist because a few main trails, regardless of their location, permit temporary branches to penetrate the entire foraging area. Further work will be required to distinguish among these, and perhaps other, alternative explanations.

Trail-clearing and the behavior of individual foragers

The size and task specificity of trail-clearers indicates that they form a physically and behaviorally distinctive task group, comprising 4–5% of foragers. Workers with headwidths in the range of 2.2–2.9 mm were particularly common among those recruiting to trail obstructions, suggesting that these workers, somewhat larger than typical leaf-cutters and carriers but smaller than soldiers, have the primary responsibility for clearing trails. Given the relatively low costs of trail construction and maintenance, the number of clearers per colony might seem to be larger than necessary. However, even with this number of clearers, large obstructions placed on the trail in this study blocked major trails for 20–30 min, caused most leaf-carriers on the trail to drop their loads, and reduced mass flow into the colony by over a thousand burdens. Large amounts of debris from treefalls or branchfalls could cause major disruptions in foraging, and the ability to respond rapidly to obstructions falling across trails appears to be essential to maintaining the high rates of mass flow required to sustain fungus gardens.

Individual workers appeared to work largely independently of one another when removing obstacles from trails, and as a result, the process of trail-clearing was relatively inefficient. Items weighing over 0.7 g were cut up prior to removal, but this was only necessary because workers tended to interfere with each other by pulling in different directions. When I allowed single workers to pull on obstacles without interference from other ants, they proved capable of moving litter fragments up to 1.5 g in mass. Ants also continued to work on litter fragments long after they were moved off the trail, work which accounted for as much as 30% of the handling time for some items. Much of the time and energy expended in litter handling was thus not strictly necessary, but was required because of poor coordination among trail-clearing workers. Despite the inefficiency of individuals, trail-clearing at the colony level appears to be a highly efficient and low-cost activity, and I suggest that inefficient individual behavior persists because the overall cost of this activity is so low that it is largely invisible to selection on colonies.

Contrary to the suggestions of Lugo et al. (1973), this study reveals that relatively few of the unladen workers on leaf-cutting ant trails are likely to be engaged in trail construction and maintenance. The question remains: what is the role of these workers in foraging? One possibility is that these ants may serve as a reserve force of leaf-cutters, permitting rapid exploitation of newly discovered resources. Recruitment in *Atta* occurs largely from existing trails rather than from the nest (Jaffe and Howse 1979), and this requires that some ants on trails be uncommitted to cutting existing resources and available to follow scouts. Some of these ants may also be scouts, either traveling from the colony in search of new resources or returning to the colony after an unsuccessful search. Finally, unladen ants may distribute information about resource identity, location, or quality to foragers leaving the colony. Many workers recruited to a resource return to the colony without cutting, either because they arrive early in the recruitment process and reinforce recruitment rather than cutting (Jaffe and Howse 1979) or because they are unable to find a location to cut (Sheperd 1982). These unladen returning workers frequently contact outgoing foragers, and at times these contacts may last for several seconds (personal observation). Such worker-worker contacts regulate the likelihood that workers will assume a particular task in *Pogonomyrmex* harvester ants (Gordon and Mehdiabadi 1999). The significance of contacts between outgoing and incoming workers in *Atta* is not yet clear, but the high frequency of such contacts on trails clearly represents a mechanism by which information may potentially be exchanged and foragers allocated among resources.

Trail construction and maintenance by *Atta* colonies

The colonies in this study maintained trail systems of between 200–300 m in length, a rather modest amount given that some colonies may have single trails of over 200 m (Lewis et al. 1974). The number of foragers ranged from 20,000 to 70,000, suggesting an overall colony size of 400,000–1.4 million workers for the colonies studied, assuming that foragers represent an average of 5% of the worker force (Lewis et al. 1974; Martin et al. 1967). *Atta* colonies are capable of reaching much larger sizes; some studies place the typical population of adult colonies at between 1 and 7 million workers (Martin et al. 1967; Pereira-da-Silva 1975). While the study colonies may have been at the low end of the adult size

range, the results of this study should be broadly applicable to larger colonies so long as investment in trail-clearers relative to the total number of foragers is consistent from colony to colony. Larger colonies may construct and maintain larger trail systems, but the costs relative to total time and energy budgets should be no more limiting than for the colonies in this study.

Finally, a comparison of the results of this study with other estimates of litter standing crop and litterfall from throughout the Neotropics suggests that trail building by *Atta* is unlikely to be limited by either litterfall or standing litter crop anywhere in their range. A survey of published estimates of litter standing crop at several Neotropical sites yields an average of 592 ± 208 g/m^2 (range: 355–1,020) (Golley et al. 1975; Anderson and Swift 1983; Scott et al. 1992; Sampaio et al. 1993; Wieder and Wright 1995), which is quite comparable to the estimate of 525 ± 204 g/m^2 obtained in this study. Although estimates of total litterfall may be over twice those reported by Leigh and Windsor (1982) for the study area, total litterfall includes many items that ants would ignore. Estimates of annual rates of leaf fall alone at several sites average 677 ± 196 g/m^2 (range: 441–1,050) (Golley et al. 1975; Klinge and Rodrigues 1968; Haines and Foster 1977; Leigh and Wright 1990; Sampaio et al. 1993), which is again very comparable to the estimate of 615 ± 49 g/m^2 derived from Leigh and Windsor (1982). These results provide an interesting contrast to Fewell's (1988) study of *Pogonomyrmex occidentalis*, which indicated that foragers preferentially established trunk trails in areas of low vegetation cover. The amount and type of litter and living plants encountered by *Atta* during trail-building in tropical forests differ greatly from those encountered by other *Atta* species in the grasslands of South America, *Pogonomyrmex* in deserts, and *Formica* in boreal forests, and it would be of great interest to determine whether time or energy costs do influence trail placement and persistence in these species.

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