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Central-place foraging continues beyond the nest entrance: the underground performance of leaf-cutting ants

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Leaf-cutting ants (*Atta* spp.) are central-place foragers that use fragments of leaf tissue as substrate for symbiotic fungal gardens. A standard hypothesis of central-place foraging theory is that foragers will select load sizes that optimize their performance, but previous study has shown that *Atta* workers carry loads well below the size needed to maximize either the rate or the energetic efficiency of leaf tissue delivery to the nest. We propose that the underground processing of leaf fragments following delivery restricts the overall rate of resource acquisition in a way that should favour the collection of small loads. We used laboratory colonies of *Atta colombica* housed in transparent nests to study tissue transfer between chambers, and hoisting, cleaning and shredding of fragments on the fungal gardens. Leaf fragment size had strong effects on all these processes except hoisting fragment on to the garden. The time needed for these underground activities would often be greater than the time used to retrieve it from a vegetation source. Thus, maximization of the delivery rate may not maximize the overall rate of resource acquisition. Load selection by foragers outside the nest may have evolved to optimize the processing activities below ground in which they do not take part.

Leaf-cutting ants (*Atta* spp.) of the neotropics are easily observed in the field and often used as model organisms in the study of central-place foraging (Jaffe & Howse 1979; Hubbell et al. 1980; Howard 1987, 1988, 1990; Rockwood & Hubbell 1987; Kacelnik 1993; Wirth et al. 2003). A common hypothesis of foraging theory is that central-place foragers will behave in a way that maximizes either the rate of delivery of food to the nest (mass or energy per unit time), or the energetic efficiency of the delivery (energetic gain per unit of energetic expenditure). Load selection is one of the principal decision variables that should affect these measures of performance. An early interpretation of field data suggested that *Atta* workers carried loads that maximized their delivery rate (Rudolph & Loudon 1986), but this conclusion has not held up to closer scrutiny (Burd 1996a, 2000a, 2001). Alternative explanations for load selection in leaf-cutting ants (Roces & Nuñéz 1993; Burd 1996b) have also found little support in studies of field colonies (Burd 2000b). The only thing that seems clear is that *Atta* foragers in the field regularly fail to maximize either the delivery rate or energetic efficiency of their activity (Howard 1991; Burd 1996a). It is surprising that the underlying strategy of foraging behaviour has been so hard to elucidate, because the relations between load size and cutting time, locomotion speed and travel time have been well characterized for *Atta* ants (Lighton et al. 1987; Burd 1996a, 2000a, b). Despite the accessibility of this model system and the apparent simplicity of their activity, we lack a convincing theoretical explanation for the foraging behaviour of leaf-cutting ants.

However, an important feature has been overlooked in previous efforts to measure foraging performance by *Atta*: unlike most central-place foragers, leaf-cutting ants do not return to their nests with food. Instead, an elaborate routine of tissue processing and fungal culture within the nest is required to transform plant material into a nutritional resource. Fragments delivered to the nest are taken over by smaller workers that distribute them throughout the nest chambers (Wilson 1980). A fragment is eventually hoisted on to the face of the garden where it is received and held in the mandibles of one or two workers. These holders slowly ascend the garden while other workers clean the leaf surfaces with their

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mouthparts (Stahel 1943). Workers then shred the fragment by removing small morsels from the perimeter and implanting them among the hyphae at the top of the garden. Further tending of the fungus (Bass & Cherrett 1994, 1996) eventually yields specialized hyphal structures called gongylidia that are harvested as food.

Two other examples of central-place foraging by social insects in which foragers pass their loads to other workers for additional handling on or in the nest have been carefully studied. Jeanne (1986) has shown that the rate of nest construction by paper wasps, *Polybia occidentalis*, depends on the dynamics of load transfer between water and pulp foragers arriving at the nest and the workers that accept these loads. Larger *Polybia* colonies have not only higher rates of nest construction, but also higher rates per worker, because laden foragers in larger colonies experience shorter average delays between arrival and unloading. Stochasticity poses a greater hindrance to the dynamics of worker transactions in smaller workforces, and the handling efficiency of materials is impaired (Jeanne 1999). Seeley (1989; Seeley & Tovey 1994) documented a similar effect in honeybees, *Apis mellifera*. The lag between arrival of a pollen or nectar forager at the nest and unloading to a storage worker reveals the relative abundance of pollen and nectar reserves in the colony. This information affects task allocation between pollen and nectar foraging.

The dynamics of sequential handling tasks may play an even larger role in the activity of leaf-cutting ants than in bees and wasps because the size of a leaf fragment should have an especially long effect on the pace of postdelivery handling within the nest. There has been no previous attempt to quantify the rates of leaf fragment processing in *Atta* nests or how these rates are affected by fragment size. An impediment to such studies in field colonies is the difficulty of observing events in underground nests. Hence, in this study we measured these activities in laboratory colonies.

METHODS

Experiments

We used three laboratory colonies of *Atta colombica* (numbered 29, 41 and 54) that were obtained from Gamboa, Republic of Panama, in 1998 and kept at ambient temperature and daylength in a quarantine laboratory at the University of New Orleans. Export and import permits were issued by the Instituto de Recursos Naturales y Renovables (now the Autoridad Nacional del Ambiente), Republic of Panama, and Animal and Plant Health Inspection Service, U.S. Department of Agriculture, respectively. Colonies were maintained on an ad libitum supply of leaves of a variety of local woody plants, including the species used for our experiments. Each nest was constructed of three closed 2.5-litre, transparent, plastic boxes connected by 100-mm lengths of tubing with an internal diameter of 20 mm (commensurate with the diameter of 20–30 mm reported by Weber 1972 for tunnels in field nests of *Atta*). The floor of each box held a plaster base about 5 mm thick that was moistened as needed to maintain internal humidity. In each colony, the most 'upstream' nestbox (chamber 1) did not contain a fungal garden and was connected to an open 10-litre foraging arena where fresh leaves were supplied. Two nestboxes (chambers 2 and 3) were serially connected 'downstream' to chamber 1. Both these chambers held fungal gardens in colonies 41 and 54, whereas only chamber 2 held a garden in colony 29. Chamber 3 was connected to an open refuse dump in all colonies.

To examine the effect of fragment size on processing rates in the nest, we introduced discs of leaf tissue of known size directly into chamber 1 of the three colonies. We used the area, a, of one face of the disc as the measure of fragment size. We cut discs in 10 different sizes from 11 to 246 mm^2, from two species that formed part of the maintenance diet. Colony 29 received discs of white mulberry, *Morus alba*, leaves with an area-specific density of 0.12 mg/mm^2, and colonies 41 and 54 received discs of Chinese tallow, *Sapium sebiferum*, leaves with an area-specific density of 0.14 mg/mm^2. Discs were punched with circular cutting tools from throughout the lamina (avoiding the midrib) of freshly gathered leaves.

We conducted 27 trials in March and April 2003. Colonies were deprived of leaf tissue for 12–16 h before each trial, sufficient time to clear previously harvested tissue and for colony demand to build. We then introduced discs of a single size per trial into the most upstream nest chamber, forming an aggregation that resembled the caches of leaf fragments that form naturally when the influx of plant material exceeds the processing capacity (Hart & Ratnieks 2000; personal observation). The amount of leaf material initially introduced varied with disc size, but usually fell between 2500 and 3600 mm^2. We added more discs of the same size when the original cache was reduced to fewer than five discs. The additional material kept the workers on the fungal garden occupied for several hours while we carried out observations of handling.

We monitored the rate of transport of discs within the nest in each of the trials by recording the elapsed time between the introduction of the cache and the appearance of the first 10–22 fragments in the downstream chambers. This measurement represents the rate obtained immediately after introduction of the cache when downstream fungal gardens were idle and demand for leaf tissue was, presumably, at a peak.

For 82 discs of varying size processed in colonies 29 and 54, we measured the time required for a fragment to be (1) hoisted on to a garden once it had been carried to the base of the garden, (2) cleaned and (3) shredded and planted in the garden. We defined the hoisting phase as the period from first contact of a laden ant or its fragment with a garden until it was held on the garden face and the first worker made contact with its mouthparts to begin cleaning. This phase was typically very short. Cleaning lasted from the first contact of a cleaner until the first shred was cut from the fragment. Shredding lasted from this first cut until all the tissue was planted among the hyphal threads of the garden. All times were measured (± 1 s) with a hand-held event recorder.

Data Analysis

Transport between chambers

In a given trial, we plotted the lag time for transfer (i.e. time between introduction of the cache into chamber 1 and transfer of a disc to a downstream chamber) versus the ordinal number of arrival of a disc (first disc, second disc, etc.). Linearity in such a plot implies that discs are transferred downstream at regular intervals, and the linear regression slope of this relation represents the average time for transfer of a disc in that trial. We took the reciprocal of this slope to express the transport rate in average number of discs moved per unit time. Natural logarithms of the transport rates calculated in this manner for each trial were plotted as a function of the disc sizes involved. For each colony and chamber, these relations were approximately linear, and we analysed them by ANCOVA with colony and chamber as a categorical factor. The ANCOVA accounts for differences in transport rates between colonies resulting from different worker populations, garden sizes, or other factors such as colony demand for food; our interest is then in the common regression slope, which describes the effect of load size on transport rate. The regression equations we found in this manner were back transformed from the logarithms and algebraically manipulated to give a transport rate in units of area of tissue per unit time, as explained further in the Results.

Handling on the fungal gardens

Hoisting, cleaning and shredding times showed no apparent differences between the two colonies in which observations were made, and we pooled data across colonies for analysis. Hoisting and cleaning times as a function of disc size were analysed by linear regression. Shredding time was analysed with respect to the following model. We expected the instantaneous loss of tissue during shredding to be proportional to a fragment's current perimeter, because workers remove shreds from the perimeter. Since the perimeter should be proportional to the square root of area, this decay process is described by the differential equation $da/dt = -ka^{1/2}$ in which k is an arbitrary proportionality constant. The total time required to reduce a fragment from area a to zero is given by the solution $t = 2a^{1/2}/k$. Log transformation linearizes this solution to $\ln t = \ln(2/k) + 1/2 \ln a$. We tested this shredding model by least-squares linear regression of ln-transformed data. The slope was tested against the null hypothesis that it would equal 0.5. The regression equation was then back transformed.

Although we measured the duration of cleaning and shredding phases by distinct events, some workers would often continue cleaning a disk after others had begun removing the first shreds. Because of this overlap the phases of fragment handling may be ill defined. We therefore analysed the total handling time on the garden (hoisting, cleaning and shredding) in relation to disc size. Regression was used to find the linear relation between ln-transformed variables; the regression equation was then back transformed to the original variables.

To carry out back transformations from logarithms in these analyses we used the correction factor $\exp(s^2_{y|x})$, in which $s_{y|x}$ is the standard error of estimate of the regression, as recommended by LaBarbera (1989). These back-transformed equations describe the total time used in a processing step as a function of the disc area, i.e. $t(a)$. Often, the processing rate is more informative than total time. If a fragment of a mm^2 is processed in $t(a)$ s, then the mean processing rate is $a/t(a)$ mm^2/s. We used this manipulation to describe the total handling rate for discs of different size.

RESULTS

Transport between Chambers

Very small discs presented no difficulties for lifting, carriage or transport through tunnels, but little tissue was moved by this effort. With increasing disc size, workers had greater difficulty carrying the loads through the tunnels between chambers. In addition to their own slow movement under heavy burdens, workers with large discs noticeably hindered the flow of other workers through the tunnels. Fragments delivered to chamber 3 were sometimes carried there directly from the cache, but more often were first deposited in chamber 2 and subsequently removed further downstream.

Plots of elapsed time to transfer a disc and the sequential order of that disc yield approximately linear relations. Figure 1 shows representative plots for transfer from the cache to chamber 2 (plots for transfer of discs to chamber 3 were similar, but the elapsed times tended to be longer). For each colony, the trial with the poorest linear fit (judging by the regression coefficient of determination, r^2) is included in Fig. 1. The salient feature of each graph is the difference in regression slope (representing average patterns of disc transfer) with changing disc size. The reciprocal of the regression slope for a trial gives the average rate of internal transport in discs/s.

Upon log transformation, these transport rates were linear functions of disc size in all three colonies (Fig. 2a, b). A preliminary test showed no significant chamber × disc size interaction effect on log transport rate ($F_{4,35} = 0.476$, $P = 0.75$), indicating that the ANCOVA assumption of homogeneous regression slopes was not violated. The ANCOVA results are given in Table 1. Increasing disc size had the expected effect of reducing transfer rates ($F_{1,39} = 140.6$, $P < 0.0001$). Covariate-adjusted rates differed significantly between colonies and chambers ($F_{4,39} = 35.3$, $P < 0.0001$). In particular, a post hoc contrast showed that discs of a given size were transferred more slowly to chamber 3 than to chamber 2 in the colonies that had two fungal gardens, suggesting that the most interior gardens in the nest may have the greatest difficulty obtaining substrate.

The common ANCOVA regression slope was −0.017. That is, the data for each colony and chamber can be described by an equation of the form $\ln y = b_i - 0.017a$, in which the rate y has the units discs/s, a is measured in mm^2, and the b_i are intercepts for each colony and chamber combination. The intercepts in Fig. 2a, b indicate strong differences between colonies in the distribution

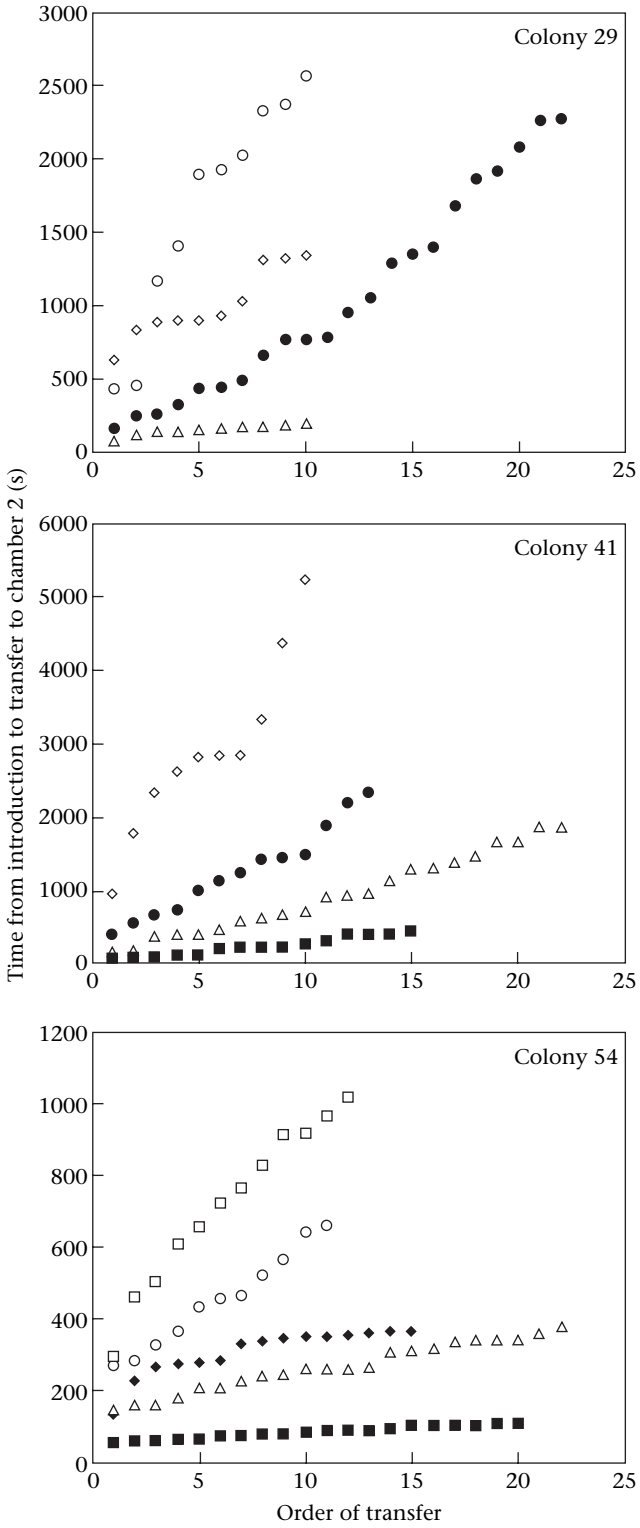

Figure 1. Downstream transfer of discs in representative individual trials for the three colonies 29, 41 and 54. The vertical axis represents elapsed time from the introduction of a cache into chamber 1 until the delivery of a fragment to chamber 2. The horizontal axis indicates the ordinal sequence of discs. Symbols represent trials with different disc sizes (in mm^2): ■: 11; △: 34; ●: 77; ♦: 100; ◇: 133; ○: 167; □: 209. Range of regression r^2 among trials: 0.89–0.97 (colony 29); 0.81–0.98 (colony 41); 0.79–0.99 (colony 54). The trial with the lowest r^2 for each colony is included in this figure.

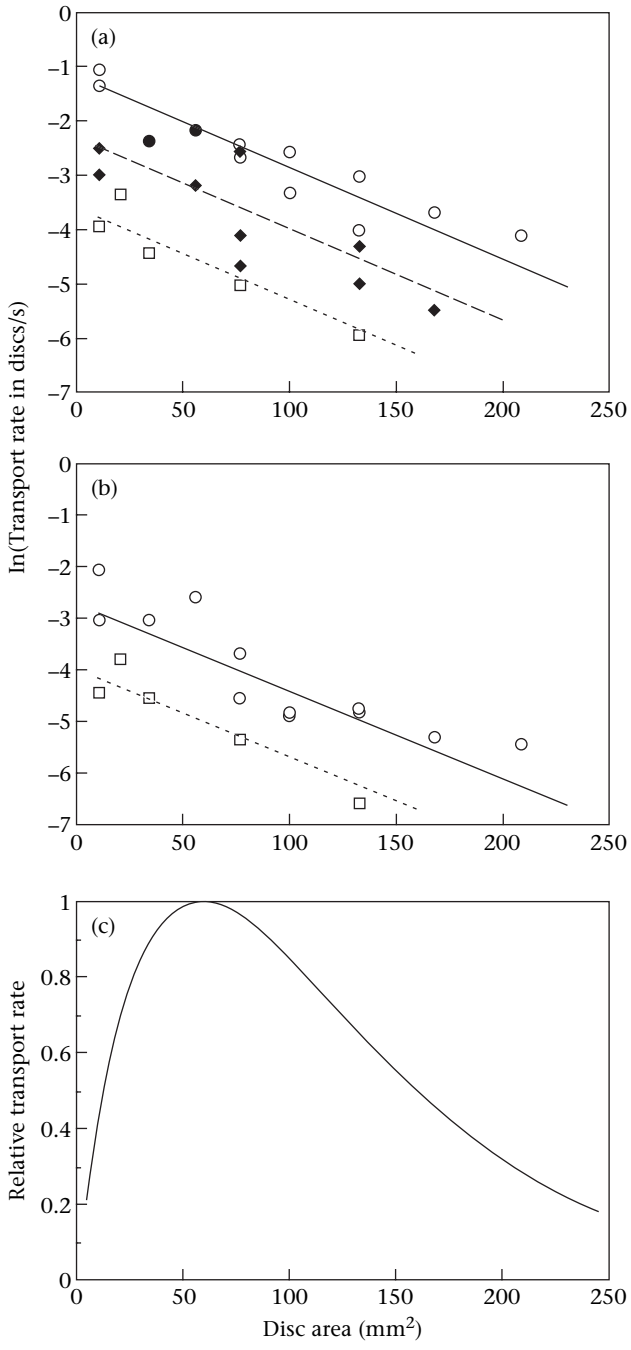

Figure 2. Transport rate in relation to disc size. (a) From the cache to chamber 2. (b) From the cache to chamber 3. Each symbol represents the mean transport rate in discs/s for a single trial (e.g. the reciprocal of the regression slope for a single disc size in Fig. 1). Symbols for different colonies: □: colony 29; ♦: colony 41; ○: colony 54. Regression lines for each colony and chamber are based on adjusted means and common slope from ANCOVA; see Table 1 for statistical results. (c) Transport rate in area per unit time corresponding to the regressions in (a) and (b), scaled to a maximum of unity for all chambers and colonies.

rate, reflecting colony size differences, but perhaps also garden condition, nutritional demand of the colony, or other unknown factors. Within the context of fast or slow distribution in different colonies, fragment size had

Table 1. ANCOVA results for internal transport rate

Effect	Sum of squares	*df*	Mean square	*F*	*P*
Disc size	36.82	1	36.82	140.6	<0.0001
Chamber and colony	36.97	4	9.24	35.3	<0.0001
Residual	10.21	39	0.26		

Raw data for the ANCOVA are shown in Fig. 2.

a statistically identical relative effect on the rate, as reflected in the uniformity of slopes. Back transformation from the logarithms yields equations of the form $y = ke^{-0.017a}$. The units of y, discs/s, do not account for the amount of tissue in a disc. To correct this, we multiplied the back-transformed equation by a (the area per disc, in mm^2), which expresses the rate as $ake^{-0.017a}$ with units of mm^2/s. The magnitude of this transport rate depends on the value of k, which varied between chambers and colonies. However, scaling the maximum rate to unity produced an identical relation for all cases (Fig. 2c). Whatever the value of the proportionality constant, k, the expression $ake^{-0.017a}$ attains a maximum at a fragment size of 59 mm^2. Tissue transport was slow for smaller discs because each disc contained little tissue, and slow for larger discs because few of them were moved per unit time. Given the area-specific density of the mulberry and Chinese tallow leaves used in the experiment, fragments of 59 mm^2 would have a mass of 7.1–8.3 mg.

Handling on the Fungal Gardens

Once a disc had been carried to a fungal garden, it took little time to transfer possession to workers on the garden. Hoisting time was less than 3 min for three-quarters of the 82 fragments observed, and had no relation to fragment size (Fig. 3a; linear regression, $F_{1,79} = 0.30$, $P = 0.58$, $r^2 = 0.004$).

Cleaning time was linearly, albeit loosely, related to the fragment area (Fig. 3b). Linear regression describes this pattern as $t = 2072 + 3.5a$ (cleaning time in s and disc area in mm^2; $F_{1,79} = 13.0$, $P = 0.0006$, $r^2 = 0.14$). An interesting feature of this equation is the large value of the regression intercept: 2072 s or 34.5 min. Intuition suggests that the regression line would pass through the origin, that is, cleaning time would tend towards zero as the area of the disc to be cleaned declined towards zero.

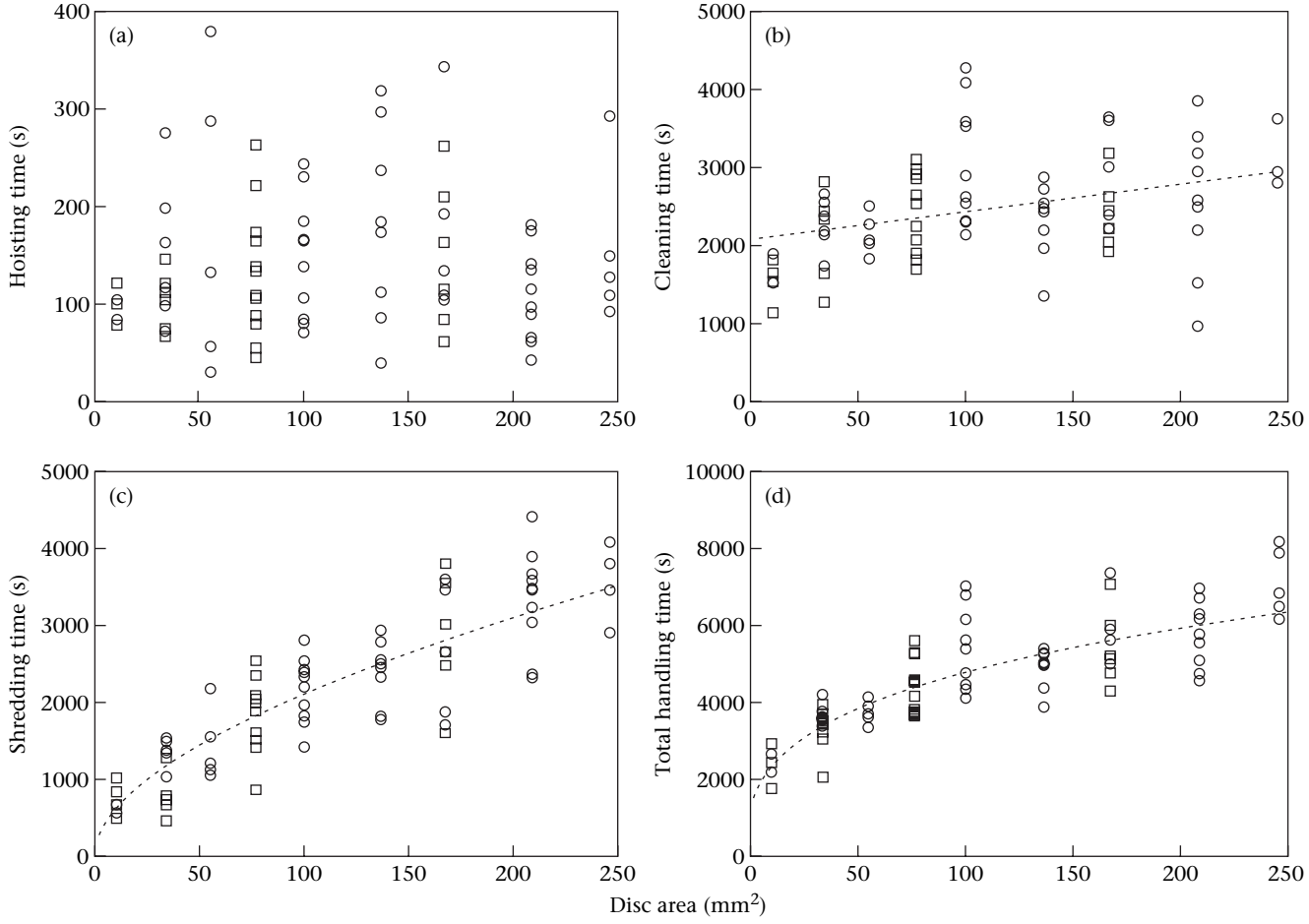

Figure 3. (a) Hoisting time, (b) cleaning time, (c) shredding time and (d) total handling time in relation to disc size. (a) Symbols for colonies are as in Fig. 2. Regression lines: (b) $t = 2072 + 3.5a$; (c) $t = 159.0\ a^{0.56}$; (d) $t = 1088\ a^{0.32}$. See text for further explanation and statistical results.

Instead, there was a substantial minimum cleaning time that each fragment received regardless of its size.

Shredding time was linearly related to disc area after log transformation of both variables. Regression analysis yielded the equation $\ln t = 5.03 + 0.56 \ln a$ (shredding time in s and disc area in mm^2; $F_{1,79} = 237.0$, $P < 0.0001$, $s_{y|x} = 0.28$, $r^2 = 0.75$). The 95% confidence interval for the regression slope was (0.49, 0.63). Thus, the null hypothesis from our shredding model that the slope equals 0.5 could not be rejected. Back transformation from the regression equation with the correction factor yields $t = 159.0\ a^{0.56}$ (Fig. 3c).

Total disc handling time (hoisting, cleaning and shredding) was linearly related to disc area after log transformation of both variables. The regression relation was $\ln t = 6.98 + 0.32 \ln a$ (handling time in s and disc area in mm^2; $F_{1,79} = 242.1$, $P < 0.0001$, $s_{y|x} = 0.16$, $r^2 = 0.75$). Back transformation with correction yields $t = 1088\ a^{0.32}$ (Fig. 3d). This formula for total handling time implies the following mean handling rate: a disc of a mm^2 handled in $1088\ a^{0.32}$ s implies a rate of $a/(1088\ a^{0.32}) = a^{0.68}/1088$ mm^2/s. Thus, handling rate rises as leaf fragments become larger, but the marginal improvement in handling rate does not keep pace with the marginal increase in size, as indicated by the exponent of 0.68.

The time a leaf fragment is handled on a fungal garden can be usefully compared to the time needed in the field to carry it from the vegetation source back to the nest. Hoisting, cleaning and shredding 50–200-mm^2 discs required an average of 3805–5930 s (Fig. 3d), that is, 63–99 min. Leaf-cutting ants generally move at 1–2 m/s on foraging trails, depending on their size and load (Howard 1991). A worker would then need 25–50 min to return 50 m to the nest (the modal foraging distance found by Shepherd 1982 for two Costa Rican *A. cephalotes* colonies). Thus, underground processing of a fragment may often consume as much time as delivery of the fragment to the nest entrance, or even more.

DISCUSSION

Load selection is one of the principal behaviours affecting the performance of central-place foragers (Stephens & Krebs 1986). Although it is not always easy to determine the ecologically and evolutionarily relevant criterion of foraging performance for a particular species, the hypothesis of rate maximization is commonly used in studies of *Atta* (Rudolph & Loudon 1986; Howard 1991; Wetterer 1991, 1994; Roces & Nuñéz 1993; Burd 1996a, 2000a, b) and many other species (Stephens & Krebs 1986). We have shown that the size of leaf fragments delivered to the nest by *Atta* foragers affects the underground distribution and handling of the material. These postdelivery steps are so essential for a colony's acquisition of nutrition that they should be included in any measurement of foraging rate by *Atta* colonies. Previous studies of *Atta* foraging, including our own, which have not taken the underground components into account, are incomplete and offer an unreliable guide to behavioural evolution in these ants.

Our results suggest that underground processing, distribution of leaf fragments among garden chambers, in particular, may often be a bottleneck in the sequence of events from cutting a fragment to planting shredded tissue among fungal hyphae. There is evidence that such bottlenecks do arise in field colonies. If the influx of fragments exceeds the rate at which they can be received in the nest, foragers begin to deposit their loads at nest entrances, forming caches of leaf fragments that may be retrieved later (Hart & Ratnieks 2000). These caches represent a temporarily lost opportunity to process harvested leaf material, and the overall foraging rate of the colony should be reduced as a consequence. Thus, the leaf-cutting behaviour of foragers may have evolved so that 'downstream' work can proceed faster, even if the resulting loads are not optimal for delivery rate.

Nests of mature *Atta* colonies may contain hundreds of chambers with fungal gardens (Weber 1972), and a few hundred kilograms of leaf material may be distributed among these chambers each year (Wirth et al. 1997). It is not immediately apparent why *Atta* colonies divide their gardening effort among so many chambers, since the division only exacerbates the problem of internal tissue distribution. Small chambers do not seem to be required by architectural constraints: fungal chambers are typically small (less than 30 cm across), but refuse chambers can have diameters five or six times greater (thus volumes over 100 times larger; Weber 1972). A growing fungal mass may be limited in size by the need to dissipate carbon dioxide, or for other metabolic reasons. Carbon dioxide concentrations may be an especially important consideration because the colony's brood develop within the gardens (Kleineidam & Roces 2000). Functional constraints might, therefore, limit garden size and force the division into numerous small chambers, creating, in turn, a distribution problem.

Internal transport of leaf material in our laboratory nests would be fastest if the material were delivered in fragments of about 59 mm^2 (Fig. 2c), or 7.1–8.3 mg given the density of leaves we used. The 20-mm diameter of tunnels in the laboratory nests (which appeared to pose the main obstacle to transporting larger fragments) is similar to the width of tunnels in the field (Weber 1972), so field colonies might also distribute leaf tissue most rapidly if it were delivered in fragments of about 59 mm^2. However, leaves of the tropical trees harvested by leaf-cutting ants typically have a higher area-specific density than our experimental discs: values of 0.15–0.25 mg/mm^2 for naturally harvested fragments were common in Wetterer's (1994) study of Costa Rican *A. cephalotes*. For these denser tropical species, a fragment area of 59 mm^2 corresponds to a mass of approximately 9–15 mg. This value is well within the range of fragment sizes normally delivered by foragers in the field (Rudolph & Loudon 1986; Howard 1991; Wetterer 1991, 1994; Shutler & Mullie 1991; Burd 1996a, 2001).

Once a fragment reaches a fungal garden, hoisting it on to the garden seems to pose little difficulty for the garden workers regardless of fragment size (Fig. 3a). This activity is unlikely to affect processing rates to any great extent.

Fragment cleaning is an essential hygiene measure to prevent infection of the gardens (Quinlan & Cherrett

1977). The time devoted to cleaning seems to be regulated by the worker holding the fragment. The holder slowly drags the fragment upwards over the garden while other workers scour the fragment surface with their mouthparts. The fragment attracts workers that begin shredding only when it nears the top of the garden. Cleaning time may be a simple consequence of the way a holding ant responds to fragment mass, using more time to ascend with a larger, heavier fragment. Nevertheless, holders seem to ascend slowly even when holding a trivially small mass, so that small discs in our trials were cleaned for up to half an hour before shredding began (Fig. 3b). Cleaning is less efficient for smaller fragments because of this minimum time investment.

Total shredding time was proportional to $a^{0.56}$, approximately the relation expected under the perimeter-dependent process modelled by $da/dt = -ka^{1/2}$ (Fig. 3c). If the perimeter limits the shredding rate, larger fragments have the disadvantage of initially presenting less perimeter relative to area than small fragments. This effect would partially offset the efficiency advantage of larger fragments for cleaning. The net effect is seen in the complete sequence of hoisting, cleaning and shredding. Total handling time was proportional to $a^{0.32}$, which implies a mean rate proportional to $a^{0.68}$. Thus, as fragment size increases, the overall handling rate rises but not as fast as the increase in tissue to be processed.

We can summarize the effect of fragment size on the underground components of foraging as follows. (1) Distribution within the nest favours fragments of intermediate size (estimated to be about 9–15 mg under field conditions), because very small fragments are distributed swiftly but inefficiently, whereas large fragments are moved very slowly. (2) Handling rate increases with fragment size, but with diminishing marginal gains, so there would be less and less advantage from harvesting fragments further and further above the size most conducive to internal transport.

Intuition suggests that the optimal fragment size for the entire sequence of resource capture from tree to fungal garden will involve some compromise between underground processing and above-ground delivery. Rate maximization for delivery alone requires foragers to carry large loads, about 35 mg (175 mm^2 if leaf tissue density is 0.20 mg/mm^2) for the average worker size in *A. colombica* and *A. cephalotes* foraging parties (Burd 1996a). Actual loads tend to be smaller: mean fragment size was 93 mm^2 for 11 colonies of *A. cephalotes* in Costa Rica (Wetterer 1994), and 86.3 mm^2 for 49 colonies of *A. colombica* in Panama (Wirth et al. 2003). These means are closer to our estimate of 59 mm^2 for maximizing the internal distribution rate than they are to the delivery-maximizing size, suggesting that the more time-consuming steps of underground processing have the greater effect on load selection.

The results presented here indicate how overall rate maximization could be achieved despite the apparent suboptimal performance of out-of-nest foragers. If *Atta* colonies are indeed selected to maximize their rate of incorporation of tissue into fungal gardens, the long-standing inability of researchers to explain load selection by leaf-cutting ants would be caused not by any shortcoming in central-place foraging theory per se, but by the omission of the activities most difficult to observe.

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