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Global optimization from suboptimal parts: foraging *sensu lato* by leaf-cutting ants

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Abstract Central-place foraging theory has been unable to explain the load selection behavior of leaf-cutting ants (*Atta* spp., Attini: Formicidae). We suggest that this is due to incomplete consideration of the sequence of behaviors involved in resource acquisition by these ants. Unlike most central-place foragers, leaf-cutting ants do not return to their nests with food. Instead, the leaf fragments they gather must be processed within the nest to convert them to substrate for fungal gardens. We have shown previously that leaf fragment size affects the rate of distribution and processing of leaf tissue inside laboratory nests of *Atta colombica*. Including these tasks in the calculation of foraging rate may help explain load selection and other features of central-place foraging by *Atta* colonies. Here we develop a mathematical model of the complete sequence of external and internal tasks that lead to addition of substrate to fungal gardens. Using realistic parameter values, the leaf fragment sizes predicted to maximize a colony's rate of foraging in this broad sense correspond well with the mean fragment sizes actually collected by *Atta* colonies in the field. The optimal fragment size for global performance in the model is below the size that would maximize the delivery rate by above-ground foragers. The globally optimal size also fails to maximize the rate of either fragment distribution or fragment processing within the nest. Our results show how maximum collective performance of an ensemble of linked tasks may require behavior that would appear suboptimal in a piecemeal analysis of tasks.

Keywords Central-place foraging · Nest architecture · Rate-maximization · Social insects

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Introduction

Leaf-cutting ants (*Atta* spp.) of the neotropics are often studied as models of central-place foraging (Wilson 1980; Rudolph and Loudon 1986; Roces 1990; Howard 1991; Shutler and Mullie 1991; Wetterer 1991; Roces and Nuñez 1993; Kacelnik 1993; Burd 1996a, 2000a). They are nearly ideal for this purpose: their activity fits the basic central-place pattern of excursion, prey loading, and return to the central site, and individual *Atta* foragers are small, slow, numerous and apparent. But despite the seeming simplicity of the model system, much of the foraging behavior of *Atta*, and in particular their underlying strategy of load selection, has escaped explanation (Kacelnik 1993).

Atta workers clear and maintain trunk trails that convey foragers from their nest to a tree or other vegetation source where they take 'prey items' by cutting tissue from leaves, petals, or other plant parts. The fragments are then carried back to the nest to be used as substrate for the cultivation of a mutualist fungus (Mueller et al. 1998). The fungal gardens yield specialized hyphal structures (gongylidia) that are harvested and fed to the colony's larvae. Workers harvesting the leaf fragments can determine the mass of their loads by adjusting the size of the fragment they cut (van Breda and Stradling 1994) or by redistribution of loads among nest mates (Anderson and Jadin 2002). Load mass has a large influence on the return speed of a laden forager (e.g., Lutz 1929), and, therefore, on the rate at which substrate is delivered to the nest. The ability of foragers to regulate their loading should allow leaf-cutting ants to adhere closely to the predictions of central-place foraging theory (Roces 1990). Foragers are expected to carry loads that maximize their delivery rate—the amount of plant tissue delivered to the nest per unit of foraging time (Wetterer 1989).

An early interpretation of field data by Rudolph and Loudon (1986) appeared to confirm that *Atta cephalotes* foragers usually carried loads that maximized their individual performance (measured as the product of fragment mass and carriage speed). But this interpretation has not held up to closer scrutiny (Burd 2000b, 2001), and it now

seems clear that the average loads of leaf-cutting ants are well below the size needed to maximize their rate of leaf tissue delivery or the energetic efficiency of delivery (Burd 1996a).

Other hypotheses that appeal to the colony level effects of individual load selection have been proposed to explain load selection by *Atta* ants (Roces and Nuñez 1993; Burd 1996b), but field tests among five colonies at La Selva, Costa Rica, failed to support them (Burd 2000a). Thus, an appeal to colony-level effects of individual behaviors – although undoubtedly necessary – has not yet produced a convincing theoretical explanation for the foraging of leaf-cutting ants. But an important feature of the process has been overlooked: *Atta* ants do not return to their nests with food. The leaf fragments they harvest require further handling and processing underground to convert the plant tissue to fungal substrate, and ultimately to nutrients for the colony. This processing sequence is an example of task partitioning (Ratnieks and Anderson 1999a). Task partitioning may be ergonomically favorable if a single worker can supply sufficient material for multiple downstream workers (as with the leaf fragments of *Atta* foragers) or if teams of workers are required for material handling (as with fragment processing on fungal gardens). Under task partitioning, *foraging* requires a broader definition than the conventional one that considers only harvesting activity of workers outside the nest.

In an earlier investigation, we used laboratory colonies of *Atta colombica* in transparent nest boxes to examine the transfer of fragments among chambers and the handling of tissue on fungal gardens (Burd and Howard 2005). We found two simple but important patterns. Firstly, tissue was distributed within the nest most rapidly when fragments were of intermediate size (about 60 mm²). Smaller fragments were transported easily but contained little tissue, while larger fragments were more difficult to carry and often obstructed the flow of other workers through tunnels. Secondly, the rate of tissue processing at the fungal gardens increased with increasing fragment size, but the relation was one of diminishing marginal returns, i.e., successive increases in fragment size brought smaller and smaller improvements in rate. These two effects suggested to us that the underground activity of the colony might constrain the behavior of the above-ground foragers: there would be little colony-level advantage if foragers maximized their own performance but caused bottlenecks and poor performance within the nest. This supposition follows Howard's (1991) earlier suggestion that leaf fragment harvesting may be adjusted to match the demands created by fungal growth dynamics.

Jeanne (1986, 1999) has studied a similar case of task partitioning in social insect foraging. The rate of collective nest building by *Polybia occidentalis* wasps is dependent on the postdelivery handling of material at the nest. Larger colonies can build nest chambers at a higher rate per worker because there is less inefficiency in the transfer of pulp fibre and water from foragers to the workers that use these materials for construction. Thus, a large colony builds at a greater overall rate than a small colony not because the for-

agers retrieve larger loads or complete individual foraging excursions more quickly, but because the greater efficiency of activity at the nest allows them to make more foraging trips per unit time (Jeanne 1999).

Anderson and Ratnieks (1999) have begun developing a theoretical framework to consider the ergonomic value of task partitioning. When forage is transferred directly between workers, minimizing the average time cost of transfers for all workers maximizes the colony's rate of resource acquisition and use. But when foraging involves indirect transfers, as in caches of leaf fragments, individual and colony rate maximization may not coincide (Anderson and Ratnieks 1999).

To examine whether load selection by *Atta* is explicable when leaf harvesting and underground handling are considered as an integrated sequence, we develop here a simple mathematical model of foraging *sensu lato*. We first construct a basic representation of how the flux of leaf tissue is affected by the three processes of our broad-sense foraging: (1) delivery by above-ground workers, (2) transfer between chambers, and (3) incorporation into the fungal gardens. We then draw on published data to select realistic parameter values for this model, and analyze the effect of fragment size on individual performance and on the colony's total rate of resource acquisition.

Model

Colony architecture

The model nest is composed of three chambers connected in linear sequence. Leaf tissue is delivered by foragers via a single entrance to chamber 1. This chamber is connected by a tunnel to chamber 2, which leads in turn to the most interior chamber 3. Each chamber contains a fungal garden of equal size, staffed by sufficient workers to maintain the same maximum capacity for processing leaf fragments.

If we represent the total amount of leaf tissue in chamber i at any instant of time by the term A_i , then the derivative dA_i/dt represents the flux of tissue in that chamber. As noted above, there are three processes that determine this flux: let λ represent the delivery rate of tissue to the nest; T_{ij} represent the rate of tissue transfer from chamber i to j ; and P_i represent the rate of processing tissue into the fungal garden in chamber i . The entire central place foraging of a colony can then be described by the following system of equations:

$$\begin{aligned} dA_1/dt &= \lambda - P_1 - T_{12} \\ dA_2/dt &= T_{12} - P_2 - T_{23} \\ dA_3/dt &= T_{23} - P_3 \end{aligned} \quad (1)$$

We wish to draw attention to the simplicity of this model. Equation (1) describes conservation of mass: any leaf tissue brought into a chamber (e.g., T_{12} for chamber 2) must

either be used in the garden ($-P_2$) or transferred to another chamber ($-T_2$). (We ignore the possibility that a fragment might be discarded without being used. Our observations of lab colonies indicate that this occurs, but very rarely.) A system of equations like this could be made arbitrarily long to represent any pattern of connection among any number of chambers, but we restricted the model to three chambers for ease of comprehension and to allow comparison with results from laboratory colonies of similar size (Burd and Howard 2005).

Of course, we wish to examine the behaviors implicit in Eq. (1), so we must describe the way in which the processes designated by λ , T_{ij} , and P_i depend on fragment size, a . Such descriptions require the correct form (e.g., linear or nonlinear functions of fragment size) as well as the correct parameter values that reflect actual behavior of *Atta* ants. We develop expressions for these functions by drawing on previously published studies of *Atta*.

Delivery rate, λ

We use the area of one face of a fragment, a , as our metric of fragment size. Thus, rates in the model have the dimensions of *area per unit time*. *Atta* foragers are highly polymorphic (approximately an order of magnitude variation in body mass), and they cut and carry fragments that are correlated with their body size. Nonetheless, we simplify the model by supposing that fragments of a single size are collected by foragers of a single (mean) size.

An individual forager that delivers a fragment of size a after an excursion lasting t_f units of time has performed at the rate a/t_f . We merely need to know how long, t_f , such a trip will take. The velocity of leaf-cutting ants on foraging trails has been very well investigated (Lutz 1929; Rudolph and Loudon 1986; Lighton et al. 1987; Roces and Nuñez 1993; Burd 1996a, 2001). These studies show strong linear effects of load mass on velocity, which can be described by

$$v = v_0 - k\rho a = v_0 - k_v a \quad (2)$$

in which v_0 is the speed of an unladen ant, ρ is area-specific density, so that ρa is load mass, and k specifies the drop in speed when a unit of load mass is added. We combine k and ρ into a new constant, k_v , which specifies the effect of load *area* on velocity.

If, for simplicity, we ignore the time used to cut a fragment, then the foraging time, t_f , needed to travel a distance d from the nest to a vegetation source and a return with a fragment of size a is given by

$$t_f = \frac{d}{v_0} + \frac{d}{v_0 - k_v a}. \quad (3)$$

The right-hand expression in Eq. (3) can be substituted for t_f in the rate a/t_f , yielding an expression for individual foraging rate that depends only on fragment size and on the parameters d , v_0 , and k_v . Average values for each of these

parameters can be determined from published literature, as described below under *Parameter values*.

Although the model is far from fully developed, we can already determine an important benchmark: the fragment size that would maximize individual delivery rate. To do this, we use the standard technique of differentiating the rate a/t_f (having made the substitution from Eq. (3) for t_f) with respect to a , and setting the derivative equal to zero to find critical points. This yields a maximum attainable rate at the fragment size

$$\hat{a} = \left(2 - \sqrt{2}\right) \frac{v_0}{k_v}. \quad (4)$$

If there were no constraints at work, simple central-place foraging theory would predict that foragers select loads of this size.

If N workers are each foraging at the rate a/t_f and there is no interaction among them, the total delivery rate to the nest will be Na/t_f . But if the total amount of leaf tissue in the nest, $\sum A_i$, builds up (because it is delivered faster than workers in the nest can process it), we expect there to be some negative feedback control of foraging effort. That is, we suppose that leaf caches within the nest supply information about appropriate recruitment, in the same way that queuing delays for nectar transfer provide information about foraging effort relative to receiving capacity in honey bees (Seeley and Tovey 1994; Ratnieks and Anderson 1999b). Let the regulated delivery rate be given by

$$\lambda = \frac{Na}{t_f} - k_d \sum A_i \quad (5)$$

in which the parameter k_d specifies the strength of negative feedback from accumulated tissue. Such regulation of foraging effort has not been studied in *Atta*, to our knowledge, so there are no empirical measurements from which to determine k_d directly. We describe our method of estimating the value below.

Transfer among chambers

In earlier work, we timed the transfer of experimental leaf fragments of known size from an upstream cache to downstream chambers in three laboratory colonies (Burd and Howard 2005). From regression analysis, we determined that the transfer rate from one chamber to the next is described by the function $T = ak_T e^{-0.017a} \text{ mm}^2 \text{ s}^{-1}$ (the parameter k_T in this equation may reflect colony size, nutritional state, or other conditions).

We hesitate to insert this function directly into the model, because it does not account for the relative difference in ‘demand’ for leaf fragments between two chambers. Our measurements were made after colonies had been deprived of leaf tissue for 12–16 h, so that downstream fungal gardens were ‘empty’ and the upstream cache was ‘full’. If we assume that workers become less motivated to transfer

fragments as the difference in tissue accumulation between source and destination diminishes, we can scale our observed rate by the difference $A_i - A_j$ relative to some standard A_0 . Thus, we model transport rate from chamber i to j by

$$T_{ij} = \frac{A_i - A_j}{A_0} a k_T e^{-0.017a} \quad (6)$$

provided $A_i > A_j$, and $T_{ij} = 0$ otherwise.

Fragment handling

As with transfer rate, we have previously measured the time needed by workers on the fungal garden to process fragments of different size, from the moment they are hoisted onto the garden until all the tissue has been shredded and implanted among the hyphae (Burd and Howard 2005). We found the mean processing rate, p , for a single fragment of size a to be

$$p = a^{0.68} / 1088 \text{ mm}^2 \text{ s}^{-1}. \quad (7)$$

Equation (7) describes the handling of a single fragment, while the processing rates in Eq. (1) represent the total rate obtained within a chamber. The effective number of fragments in a chamber is A_i/a , and if each one is processed at the mean rate p , the total processing rate becomes pA_i/a at equilibrium. But we must also account for the finite capacity of a single garden to accommodate leaf material. Gardens in our laboratory colonies at the height of activity are completely draped with green fragments, such that standing room for workers as they hold, clean, shred, and implant the fragments seems to set the limit on processing capacity. Suppose that each fungal garden has a capacity, C , measured in area of leaf material that can undergo processing at a single time. At and above the critical amount C the total processing rate reaches a maximum of pC/a . Thus, the leaf processing rate in chamber i , P_i , is:

$$\begin{aligned} P_i &= pA_i/a, & \text{if } A_i < C; \\ \text{or} \\ P_i &= pC/a, & \text{if } A_i \geq C. \end{aligned} \quad (8)$$

Model solution

When the expanded expressions for λ , T_{ij} , and P_i are inserted with specific parameter values into the differential equations of (1), the system can be solved numerically using standard techniques. We used the Runge-Kutta method (implemented in Mathcad 8, Mathsoft Inc., Cambridge, Mass.) to obtain numerical solutions that simulated 24 h of activity. Harvesting and underground processing take place for 12 h, followed by 12 h of processing alone. This is a typical daily cycle for *Atta* colonies (Weber 1972; Wirth

Table 1 Terms and parameter values used in the model

Symbol	Meaning	Value and units
N	Number of foragers	1,000 ants
d	Distance to vegetation source	100 m
v_0	Speed of an unladen worker	53.7 mm s ⁻¹
k_v	Each mm ² of load reduces velocity by k_v , mm s ⁻¹	0.18 mm ⁻¹ s ⁻¹
k_d	Each mm ² in the nest reduces delivery by k_d mm ² s ⁻¹	0.0005 s ⁻¹
k_T	Constant in eq. (6)	0.2 s
A_0	Reference cache for weighting the difference $A_i - A_j$	3,000 mm ²
C	Capacity (maximum fragment area) of a fungal garden	10,000 mm ²

et al. 2003). All A_i values were set to zero at the start, and then updated every 5 s of simulated time in the numerical approximation. The processing rate of the system was calculated as the total area of tissue incorporated into the gardens divided by the 24 h of simulated time.

Parameter values

Table 1 lists the parameter values we used to evaluate the model. Modelers can employ two strategies with respect to parameters: choose realistic values based on actual measurements, or systematically vary the values to ‘explore parameter space’. We used a combination of these approaches. Some values are reasonably certain (at least as averages), based on published results. As a sensitivity analysis, we also examined a range of values for those parameters with the least empirical support or that are most likely to vary with colony size: number of foragers, N ; garden capacity, C ; regulation of fragment harvesting effort, k_d ; and k_T .

We derived values for v_0 and k_v from the regression equation for *A. colombica* locomotion reported in Burd (1996a, Table 2): $v = -7.83 - 0.92M + 16.41F$, for velocity, v , in mm s⁻¹, load mass, M , in mg, and femur length, F , in mm. Using the mean forager size of $F = 3.75$ mm in that study and assuming load density of $\rho = 0.20$ mg mm⁻², the regression equation above becomes $v = 53.7 - 0.18a$ (i.e., $v_0 = 53.7$ mm s⁻¹, and $k_v = 0.18$ mm⁻¹ s⁻¹).

The forager population of $N = 1000$ in Table 1 is well below the foraging traffic of large *Atta* colonies in the field, but approximately correct for our small lab colonies, and therefore appropriate to the simple 3-chamber nest modeled here. We model a trail distance of $d = 100$ m to provide round-trip travel times that are realistic for field conditions.

We can estimate the value of the parameter k_d that regulates fragment harvesting effort in Eq. (5) by reference to other processes in the model. The values for N , d , v_0 , and k_v in Table 1 allow a maximum delivery rate (Eq. (5)) of 31.3 mm² s⁻¹ if all N foragers are active and carry fragments of the optimal delivery size, \hat{a} . If the harvesting is then regulated by a value of $k_d = 0.0005$ s⁻¹, delivery would diminish to a realized

Table 2 Mean leaf fragment sizes harvested by *Atta* colonies in the field

Species	Mean fragment size(s)	Colonies and location	Reference
<i>A. cephalotes</i>	93 mm ²	11 colonies, Costa Rican forest	1
<i>A. cephalotes</i>	72, 93, 94, 97, 123 mm ²	5 colonies, Costa Rican forest	2
<i>A. colombica</i>	125, 153 mm ²	2 colonies, Costa Rican forest	3
<i>A. colombica</i>	86.3 mm ²	49 colonies, Panamanian forest	4
<i>A. colombica</i>	14, 19, 24 mg	1 colony at 3 trees, Panamanian forest	5
<i>A. colombica</i>	19.8 mg	1 colony, Venezuelan woodland	6
<i>A. vollenweideri</i>	18.9 mg	Grass-cutting colonies, Argentina	7

References: 1. Wetterer (1994a), 2. Burd (2000a), 3. Shutler and Mullie (1991), 4. Wirth et al. (2003), 5. Burd (1996a), 6. Burd and Aranwela (2003), 7. Röschar and Roces (2002)

rate (Eq. (5)) of zero when the accumulated tissue in the 3-chamber nest reaches $\sum A_i = 62600 \text{ mm}^2$, that is, an average of $20,900 \text{ m}^2$ per chamber. Since we employ a garden capacity of $C = 10,000 \text{ mm}^2$ (Table 1), this value of k_d allows each chamber to have a saturated garden and an equally large cache before foragers become completely inactive. At lower values of k_d (less negative feedback), delivery can be so great that the model colony is unable to process all harvested tissue in 24 h. At higher values of k_d , delivery becomes so strongly regulated that gardens in the model may operate below their capacity. We observe in freely foraging laboratory colonies that a large cache of unprocessed material does build up before foraging stops, but that all collected material is usually incorporated into the gardens by the next day. This suggests that $k_d = 0.0005 \text{ s}^{-1}$ is a reasonable estimate. However, we also examine the effect of values half and twice as great.

In our earlier work on tissue transfer between chambers, three colonies of different size yielded estimates of the fragment transfer parameter, k_T , from 0.032 to 0.265 (Burd and Howard 2005). Here we use an intermediate value of $k_T = 0.2$ as a touchstone, but we explore the effects of values from 0.05 to 1.0. We had measured fragment transfer after the introduction of caches totalling $2,600\text{--}3,500 \text{ mm}^2$; thus, for Eq. (6) we set $A_0 = 3,000 \text{ mm}^2$.

We observed during our previous experiments that a fungal garden in our laboratory colonies could accommodate a maximum of about $5,000 \text{ mm}^2$ of leaf material undergoing processing at the same time. These gardens were 12–17 cm in diameter, smaller than the common diameter of 20–30 cm reported by Weber (1966) for the gardens of *Atta* colonies in the field, although somewhat larger than the range of 10–12 cm diameter that he also reported as ‘frequent’ (Weber 1972). We set the garden capacity at $C = 10,000 \text{ mm}^2$ to reflect the likely field conditions with gardens of 20–30 cm diameter, but we also examine a range from $5,000\text{--}25,000 \text{ mm}^2$ to study the consequences of garden size.

Results

Model output

Although somewhat ‘stylized’, the full model behavior is realistic in several features (Fig. 1). The overall foraging rate represented in Fig. 1 is $12,259 \text{ mm}^2 \text{ h}^{-1}$, i.e., a mean of $4,086 \text{ mm}^2 \text{ h}^{-1}$ for each of the three gardens. The lab-

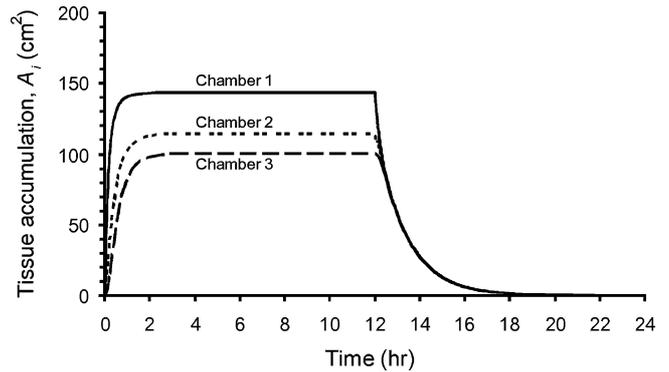


Fig. 1 Sample output from the model in Eq. (1). Parameter values are those in Table 1, with leaf fragment area of $a = 109 \text{ mm}^2$

oratory colonies with two gardens studied by Burd and Howard (2005) attained an average peak performance rate of $6,136 \text{ mm}^2 \text{ h}^{-1}$, or $3,068 \text{ mm}^2 \text{ h}^{-1}$ per garden, approximately commensurate with the model. At equilibrium, upstream chambers in the model contain more tissue than downstream chambers (Fig. 1). Indeed, for some parameter values and fragment sizes, the downstream chambers may contain less leaf material than their garden capacity, C . We observed a similar pattern in the laboratory colonies: downstream fungal gardens sometimes appeared to be processing below their capacity, even while a surplus of fragments had accumulated in an upstream chamber. Thus, it appears that transport between chambers can sometimes limit the function of the entire system.

The overall foraging rate in the model colony is strongly affected by leaf fragment size. At a ‘typical’ garden size ($C = 10,000 \text{ mm}^2$) foraging rate reaches a maximum with fragments of 109 mm^2 (Fig. 2A). Performance is low at the extremes of fragment size because the delivery rate is low (either trivially small fragments delivered rapidly or large fragments delivered very slowly); thus, some or all gardens operate below their capacity. The maximum delivery rate would occur with fragments of $\hat{a} = 187 \text{ mm}^2$ (Eq. (4), using the values of v_0 and k_v in Table 1), well above the overall optimal size of 109 mm^2 (Fig. 2A). Moreover, this overall optimum would not optimize the two other components of broad-sense foraging. The internal transport rate, $ak_T e^{-0.017a}$, reaches a maximum at $a = 1/0.017 = 59 \text{ mm}^2$ (Burd and Howard 2005). The rate of handling of individual fragments on a fungal garden, $p = a^{0.68}/1088$ (Eq. (7)), reaches a maximum at infinite fragment size (in a mathematical sense) or at the largest size that garden workers can physically handle (in a biological sense), which is at

least 246 mm² (Burd and Howard 2005). Thus, the model shows that rate-maximization of foraging *sensu lato* can be achieved by serially linked processes that are, individually, operating below their potential maximum rate.

Sensitivity to parameter values

Fungal garden capacity has a strong effect on both total foraging rate and the rate-maximizing fragment size. Total foraging rate increases with garden size, from 7,614 mm² h⁻¹ at $C=5,000$ mm² to 16,010 mm² h⁻¹ at $C=25,000$ mm². Because of this variation, we scale the rates so that they peak at unity, in order to facilitate comparison among rate-maximizing fragment sizes (Fig. 2A). Small fragments are optimal when gardens are small, and the optimum fragment size increases as the garden processing capacity rises (Fig. 2A). For the largest gardens represented in Fig. 2A ($C=25,000$ mm²), the optimal fragment size for overall performance is 175 mm², very near the optimum for delivery rate alone (187 mm²). The potential foraging rate saturates as garden size increases, so that there is no further change in output at higher garden capacities. We believe the garden capacity of colonies in the field is well below this large value, as explained under *Parameter values* above, but the sensitivity of model output to the value of the garden capacity, C , does focus attention on garden size, hence on chamber size and nest architecture.

If the distance, d , from the nest to the vegetation source is altered, the model follows the prediction of the classic patch model: larger loads are optimal at patches further from the central place (Stephens and Krebs 1986). But this occurs in the model only if the number of foragers, N , is held constant. If N changes in proportion to the change in distance, the optimal fragment size does not change at all. Indeed, the entire behavior of the model remains identical when both d and N make the same proportional change.

When the parameter regulating foraging activity, k_d , is increased, the negative feedback from tissue accumulation in the nest becomes stronger and less new plant material is delivered. If the value of k_d in Table 1 is doubled to 0.001, the gardens often receive less plant material than their processing capacity, and overall performance declines as the optimal fragment size increases to about 150 mm² (Fig. 2B), closer to the delivery-maximizing size, \hat{a} . However, it seems unlikely that colonies would regulate their leaf harvesting so strongly that the fungal gardens fail to receive adequate substrate. In contrast, if the value of k_d in Table 1 is halved to 0.00025, more workers harvest leaves and the colony's overall rate increases, while the optimal fragment size is reduced to about 70 mm² (Fig. 2B). At even smaller values of k_d , more leaf tissue accumulates during the 12-h foraging period than the model colony can process in 24 h. This does not accord with our observations of the lab colonies, suggesting that such low values of k_d are unrealistic.

Variation in the internal transport parameter, k_T , which might reflect motivation of the work force or nutritional urgency in the colony, has little effect on the colony's over-

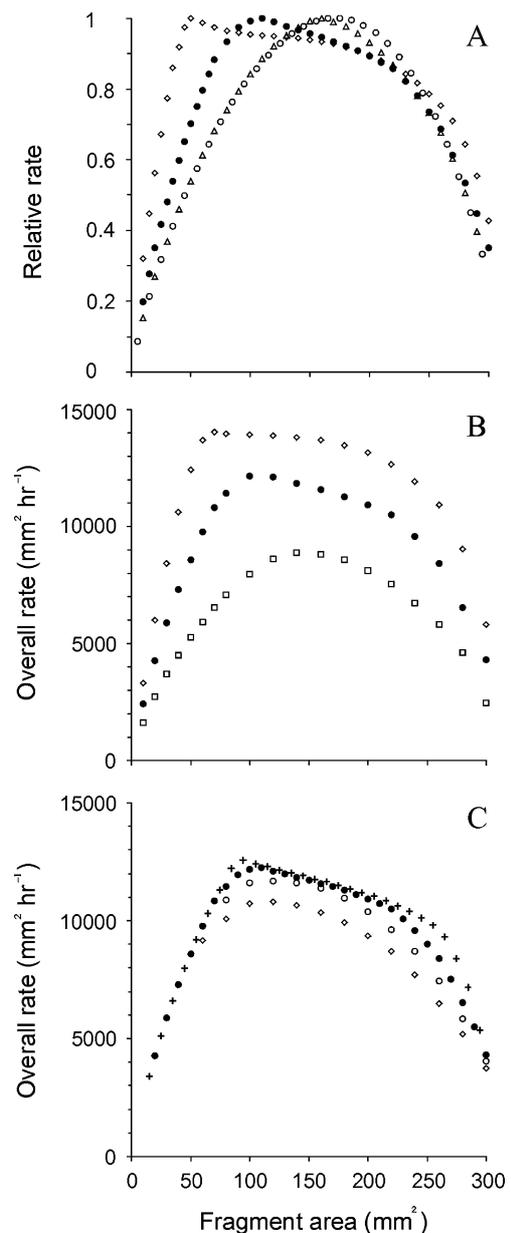


Fig. 2 Relationship between leaf fragment size and overall rate of foraging *sensu lato* by the model colony over 24 h. Output for the parameter values given in Table 1 is shown by filled circles (●) in each panel. (A) Effect of garden capacity. Symbols represent different values of C (in units of mm²): ◇ – 5000; ● – 10,000; △ – 20000; ○ – 25000. The foraging rates on the vertical axis are scaled so that each curve peaks at unity, to allow easier visual comparison. Absolute values of the peak rates (in units of mm² h⁻¹) are: ◇ – 7614; ● – 12247; △ – 15898; ○ – 16010. (B) Effect of negative feedback regulation of harvesting activity. Symbols represent different values of k_d : ◇ – 0.00025 s⁻¹; ● – 0.0005 s⁻¹; □ – 0.001 s⁻¹. (C) Effect of internal distribution of leaf fragments. Symbols represent values of k_T : ◇ – 0.05 sec; ○ – 0.1 sec; ● – 0.2 sec; + – 1.0 s

all foraging rate (Fig. 2C). Better distribution of fragments (higher value of k_T) provides slightly better colony performance, but there is a diminishing effect on the overall rate as higher k_T brings a more uniform distribution of material among the three chambers. In any case, there is little effect of k_T on the rate-maximizing fragment size (Fig. 2C).

Discussion

Model predictions and observed behavior

The model results indicate that apparent failure of above-ground *Atta* foragers to maximize their individual delivery performance can be better understood when this behaviour is examined as one component in a series of tasks that feed the fungal gardens. Harvesting small leaf fragments may compromise the gross rate of tissue delivery to the nest, but because smaller leaf fragments arrive in a more 'digested' state, the distribution and processing of tissue within the nest proceeds more rapidly. Our empirical measurements of these underground activities had previously suggested that small fragments would enhance a colony's overall rate of leaf tissue input to the fungal gardens (Burd and Howard 2005). This model confirms that it is possible for global rate-maximization to occur even when above-ground foraging appears to be suboptimal.

How well do model predictions compare to real behaviour? Mean leaf fragment sizes from several published field studies of *Atta* foraging are summarized in Table 2. Habitat, leaf density, mean body size of the foragers, and other factors differed among the colonies listed in this table, but mean fragment sizes are almost always in the range of about 90–125 mm², or 19–24 mg. This compares well with the model's predicted rate-maximizing fragment size of 109 mm² (which corresponds to 22 mg for leaves with area-specific density of $\rho=0.20$ mg mm⁻², a density near the middle of the range reported by Wetterer (1994a) for leaves of woody species harvested by *Atta cephalotes* in Costa Rica).

The predicted optima depend on the parameter values used. Our sensitivity analysis suggests that the optimal fragment size would remain in the range of about 50–120 mm² (10–24 mg for $\rho=0.20$ mg mm⁻²) under fairly wide variation in parameter values (Fig. 2B and C). This range remains consistent with the field data in Table 2, and still well below the delivery-maximizing size of about 35–40 mg determined empirically for *A. colombica* and *A. cephalotes* by Burd (1996a). Only large increases in the fungal garden capacity, *C*, would raise the model's predicted optimal fragment size close to the delivery-maximizing size (Fig. 2A).

The model may explain another feature of load selection in leaf-cutting ants. Researchers have had difficulty finding consistent relations between load size and travel distance for *Atta* colonies in both field and laboratory settings (Roces 1990; Wetterer 1991; Shutler and Mullie 1991; Burd 1995). In this model, the optimal fragment size is invariant under changes in travel distance, provided the number of foragers varies in proportion to distance. In real colonies, such correspondence could be achieved if recruitment occurs until the entire length of a trail attains a target density of workers in the traffic stream. If this occurs, investigators should observe that the work force, rather than prey loading, increases with travel distance.

Optimality is sometimes thought to be a suspect concept in behavioural ecology, so it is worth recapitulating the

nature of the model. We start by noting that the model does not assume that load selection by leaf-cutting ants is optimal. Rather, the model predicts the consequences of load selection across the entire range of biologically possible load sizes (those loads that ants are able to lift). The model could predict a rate-maximizing size very different to the loads actually taken by *Atta* colonies in the field (indeed, high values of the parameter *C*, and low values of *k_d*, produce exactly this result). We attempt to use realistic parameter values for our model evaluation, and, where we must admit uncertainty over some values, we vary them to see how sensitive the output is to such variation. This offers the potential for falsification: if better estimates of parameter values yield predicted optimal loads that depart consistently from observed behaviour, the model would fail to explain load selection in leaf-cutting ants.

We do assume that selection favors colonies with higher foraging rates, and therefore favors the fragment selection that produces the maximum rate. But this is not an assumption of the model: it is an assumption we make about evolution when interpreting the model's output. This assumption could be falsified, in principle, by showing that colonies with higher foraging rates do not achieve higher reproductive success.

Garden size

The parameter the with greatest effect on the model output was the processing capacity of fungal gardens. As garden capacity rises, the global rate-maximizing fragment size moves closer to the delivery-maximizing size (Fig. 2A). Why, then, do *Atta* colonies not cultivate larger gardens? They are certainly capable of excavating larger chambers. For example, Weber (1972) notes that refuse chambers in *Atta* nests are much larger than the garden chambers. In one excavated *A. cephalotes* nest, a refuse chamber measured 192 cm in diameter, about 200 times larger in volume than garden chambers that are typically less than 30 cm across (Weber 1972).

It is possible that very large fungal gardens would not produce the nutritive gongyliidia with the same efficiency as smaller gardens, or that metabolic carbon dioxide would dissipate too slowly from a large garden. *Atta* workers are sensitive to carbon dioxide concentration (Kleineidam and Tautz 1996), and the nest structure is designed to facilitate ventilation (Kleineidam and Rocés 2000). Brood are placed in the interior of fungal gardens, so any difficulties with gas exchange may have particularly strong effects on brood development.

While these effects of garden size deserve further study, there may a simpler architectural reason to keep garden chambers small: it is more efficient to excavate several small chambers than a single large chamber of equal volume. This is because smaller gardens have greater surface area relative to their volume, and cleaning and shredding of leaf fragments take place over the garden surface. A single large spherical chamber provides only $n^{-1/3}$ as much

surface area as n smaller chambers that add up to the same volume. For example, a single large sphere of unit volume has only half the surface area of eight small spheres with the same combined volume. If construction costs are proportional to the volume of excavated soil, surface-to-volume scaling relationships would make large chambers – hence, large gardens – increasingly unprofitable. We know of no previous theoretical or experimental work that addresses a relationship between nest architecture and foraging behavior in social insects.

Polymorphism and task partitioning

Our model uses parameter values that reflect the behavior of foragers of average size, and we compare the model output with the mean load selection of foragers in field colonies. In reality, *Atta* leaf harvesters are highly polymorphic (about 2–40 mg). When we adjust the parameters of the model to reflect behaviour of foragers larger or smaller than the mean, the optimal fragment sizes change accordingly, i.e., smaller optima for smaller foragers and larger optima for larger foragers. Although we do not expect polymorphism to alter substantially the conclusions we draw from the model, it is an area requiring further investigation.

It is interesting to consider if variation *per se* in leaf fragment sizes could provide any advantages. Fragments of different size may be distributed at different rates through the network of chambers and tunnels in a nest. Smaller fragments should reach interior chambers more readily, leaving large fragments to be processed in chambers closer to nest entrances. Figure 2C shows that optimal fragment size decreases slightly when leaf tissue is distributed more rapidly within the nest, and increases with more restricted distribution. Forager polymorphism may allow distal and interior chambers to specialize on the fragment sizes they process, and thus maximize the foraging rate of a very large nest. We know of no data available at present that would allow us to address this speculation.

Efficient task partitioning requires an appropriate ratio of workers to be engaged in the component tasks (Anderson and Ratnieks 1999). Foraging task partitioning is associated with physical caste polymorphism in *Atta* colonies. Foragers in Wilson's (1983) study of *A. cephalotes* colonies had head widths of at least 1.6 mm while leaf processors had head widths no greater than 1.6 mm. Our model implicitly assumed that work force allocation within the nest is at the appropriate ratio, so that leaf processing is affected only by fragment size and never by worker shortages. Whether and how colonies maintain the most efficient worker ratios among tasks in the foraging sequence requires further investigation. In general, small colonies should have more difficulty achieving the benefits of task partitioning than large colonies (Jeanne 1986; Anderson and Ratnieks 1999; Ratnieks and Anderson 1999a, b), and changes in foraging behaviour as *Atta* colonies grow (Wilson 1983; Wetterer 1994b) may reflect changing caste ratios.

Conclusion

It will come as no surprise to observers of social insects that collective activity may emerge in unexpected ways from individual behaviors. Our model shows how dynamically linked tasks in *Atta* colonies yield this kind of effect. Under task partitioning, whole *Atta* colonies can forage at a maximum rate even when (indeed, precisely because) individual workers outside the nest perform below the maximal rate for their component task. By a loose analogy, task partitioning allows an *Atta* colony to function like a 'distributed' cow. Both *Atta* colonies and cows gather plant material and use it to culture an organism that converts plant tissue to useable nutrition. *Atta* foragers function like a cow's teeth: fragment cutting by the former and cud chewing by the latter determine the size of particles passed downstream to the fungal or bacterial cultures. Since particle size affects the rate of the downstream tasks, we can see the seemingly inefficient load selection by *Atta* foragers as analogous to cud chewing. Viewed in isolation, cud chewing by bovids appears to waste time, but in context it enhances the overall rate of nutrient acquisition. A similar conclusion holds for load size selection in *Atta*.

The model shows a surprisingly strong effect of fungal garden (hence chamber) size on optimal fragment size. If this interpretation is correct, it would appear that the behavior of foragers outside the nest has evolved within the context of an architectural constraint. Our results suggest that a full explanation of *Atta* behavioral ecology will require much greater attention to the structure and internal dynamics of *Atta* nests.

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References

- Anderson C, Jadin JLV (2002) The adaptive benefit of leaf transfer in *Atta colombica*. *Insectes Soc* 48:404–405
- Anderson C, Ratnieks FLW (1999) Task partitioning in insect societies. I. Effect of colony size on queueing delay and colony ergonomic efficiency. *Am Nat* 154:521–535
- Bass M, Cherrett JM (1996) Leaf-cutting ants (Formicidae, Attini) prune their fungus to increase and direct its productivity. *Funct Ecol* 10:55–61
- Burd M (1995) Variable load size–ant size matching in leaf-cutting ants, *Atta colombica* (Hymenoptera: Formicidae). *J Insect Behav* 8:715–722
- Burd M (1996a) Foraging performance by *Atta colombica*, a leaf-cutting ant. *Am Nat* 148:597–612
- Burd M (1996b) Server system and queueing models of leaf harvesting by leaf-cutting ants. *Am Nat* 148:613–629

- Burd M (2000a) Foraging behaviour of *Atta cephalotes* (leaf-cutting ants): an examination of two predictions for load selection. *Anim Behav* 60:781–788
- Burd M (2000b) Body size effects on locomotion and load carriage in the highly polymorphic leaf-cutting ants *Atta colombica* and *Atta cephalotes*. *Behav Ecol* 11:125–131
- Burd M (2001) Leaf tissue transport as a function of loading ratio in the leaf-cutting ant *Atta cephalotes*. *Ecol Entomol* 26:551–556
- Burd M, Aranwela N (2003) Head-on encounter rates and walking speed of foragers in leaf-cutting ant traffic. *Insectes Soc* 50:3–8
- Burd M, Howard JJ (2005) Central-place foraging continues beyond the nest entrance: the underground performance of leaf-cutting ants. *Anim Behav* (in press)
- Howard JJ (1991) Resource quality and cost in the foraging of leaf-cutter ants. In: Huxley C, Cutler D (eds) *Ant-plant interactions*. Oxford University Press, Oxford, pp 42–50
- Jeanne RL (1986) The organization of work in *Polybia occidentalis*: costs and benefits of specialization in social wasp. *Behav Ecol Sociobiol* 19:333–341
- Jeanne RL (1999) Group size, productivity, and information flow in social wasps. In: Detrain C, Deneubourg JL, Pasteels JM (eds) *Information processing in social insects*. Birkhäuser, Basel, Switzerland, pp 3–30
- Kacelnik A (1993) Leaf-cutting ants tease optimal foraging theorists. *Trends Ecol Evol* 8:346–348
- Kleineidam C, Tautz J (1996) Perception of carbon dioxide and other "air-condition" parameters in the leaf cutting ant *Atta cephalotes*. *Naturwissenschaften* 83:566–568
- Kleineidam C, Roces F (2000) Carbon dioxide concentrations and nest ventilation in nest of the leaf-cutting ant *Atta vollenweideri*. *Insectes Soc* 47:241–248
- Lighton JRB, Bartholomew GA, Feener DH (1987) Energetics of locomotion and load carriage and a model of the energy cost of foraging in the leaf-cutting ant *Atta colombica* Guer. *Physiol Zool* 60:524–537
- Lutz F (1929) Observations on leaf-cutting ants. *Am Mus Novit* 388:1–21
- Mueller UG, Rehner SA, Schultz TR (1998) The evolution of agriculture in ants. *Science* 281:2034–2038
- Ratnieks FLW, Anderson C (1999a) Task partitioning in insect societies. *Insectes Soc* 46:95–108
- Ratnieks FLW, Anderson C (1999b) Task partitioning in insect societies. II. Use of queueing delay information in recruitment. *Am Nat* 154:536–548
- Roces F (1990) Leaf-cutting ants cut fragment sizes in relation to distance from the nest. *Anim Behav* 40:1181–1183
- Roces F, Nuñez JA (1993) Information about food quality influences load-size selection in recruited leaf-cutting ants. *Anim Behav* 45:135–143
- Röschard J, Roces F (2002) The effect of load length, width and mass on transport rate in the grass-cutting ant *Atta vollenweideri*. *Oecologia* 131:319–324
- Rudolph SG, Loudon C (1986) Load size selection by foraging leaf-cutter ants (*Atta cephalotes*). *Ecol Entomol* 11:401–410
- Seeley TD, Tovey CA (1994) Why search time to find a food-storer bee accurately indicates the relative rates of nectar collecting and nectar processing in honey bee colonies. *Anim Behav* 47:311–316
- Shutler D, Mullie A (1991) Size-related foraging behaviour of the leaf cutting ant *Atta colombica*. *Can J Zool* 69:1530–1533
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton
- van Breda JM, Stradling DJ (1994) Mechanisms affecting load size determination in *Atta cephalotes* L. (Hymenoptera, Formicidae). *Insectes Soc* 41:423–434
- Weber NA (1966) Fungus-growing ants. *Science* 153:587–604
- Weber NA (1972) *Gardening ants: the attines*. American Philosophical Society, Philadelphia
- Wetterer JK (1989) Central place foraging theory – when load size affects travel time. *Theor Pop Biol* 36:267–280
- Wetterer JK (1991) Source distance has no effect on load size in the leaf-cutting ant, *Atta cephalotes*. *Psyche* 98:355–359
- Wetterer JK (1994a) Forager polymorphism, size-matching, and load delivery in the leaf-cutting ant, *Atta cephalotes*. *Ecol Entomol* 19:57–64
- Wetterer JK (1994b) Ontogenetic changes in forager polymorphism and foraging ecology in the leaf-cutting ant *Atta cephalotes*. *Oecologia* 98:235–238
- Wilson EO (1980) Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*) II. The ergonomic optimization of leaf cutting. *Behav Ecol Sociobiol* 7:157–165
- Wilson EO (1983) Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*) IV. Colony ontogeny of *Atta cephalotes*. *Behav Ecol Sociobiol* 14:55–60
- Wirth R, Herz H, Ryel RJ, Beyschlag W, Hölldobler B (2003) Herbivory of leaf-cutting ants: a case study on *Atta colombica* in the tropical rainforest of Panama. Springer, Berlin