Allometric scaling of foraging rate with trail dimensions in leaf-cutting ants

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Leaf-cutting ants (Atta spp.) create physical pathways to support the transport of resources on which colony growth and reproduction depend. We determined the scaling relationship between the rate of resource acquisition and the size of the trail system and foraging workforce for 18 colonies of Atta colombica and Atta cephalotes. We examined conventional power-law scaling patterns, but did so in a multivariate analysis that reveals the simultaneous effects of forager number, trail length and trail width. Foraging rate (number of resource-laden ants returning to the nest per unit time) scaled at the 0.93 power of worker numbers, the –1.02 power of total trail length and the 0.65 power of trail width. These scaling exponents indicate that individual performance declines only slightly as more foragers are recruited to the workforce, but that trail length imposes a severe penalty on the foraging rate. A model of mass traffic flow predicts the allometric patterns for workforce and trail length, although the effect of trail width is unexpected and points to the importance of the little-known mechanisms that regulate a colony’s investment in trail clearance. These results provide a point of comparison for the role that resource flows may play in allometric scaling patterns in other transport-dependent entities, such as human cities.

Keywords: allometry; Atta; foraging; leaf-cutting ants; scaling; traffic flow

1. INTRODUCTION

The scaling of vital rates with body size has interested biologists for decades [1–3]. Recently, the scaling of metabolism with colony size in social insects has also been studied and an important parallel between organisms and colonies has been found: larger colonies tend to have lower rates of energy consumption per capita or per unit mass [4–7], similar to the metabolic scaling pattern found in unitary organisms [1]. Metabolic scaling in organisms has been attributed to constraints imposed by vascular networks on the delivery of energy and materials to cells [8,9]. Here, we ask whether transport networks impose constraints on resource flows in colonies of leaf-cutting ants (Atta spp., Attini: Formicidae). In particular, we ask how resource acquisition rates scale with respect to the size of the transport network and the number of workers engaged in harvesting resources [5,10,11]. Although the analogy between organismal vascular systems and ant trail networks is intriguing, flows through these pathways can have different dynamical properties. For example, traffic is bidirectional on Atta trails [12], while vascular flow is unidirectional or rhythmically alternating. Fluid flows necessarily maintain conservation of momentum, while the self-driven components of traffic flows need not [13]. These and other mechanistic differences suggest that scaling properties involving resource transport could differ between organisms and colonies.

Leaf-cutting ants are notable for trails that are not merely pheromone-defined paths over existing substrates. Instead, they make physical transportation corridors as long as 200 m by cutting and clearing debris and vegetation along paths to foraging sites, and they maintain these pathways in the face of a rain of leaf litter [14]. These trails direct and restrict forager searching and foraging effort [15,16], so that essentially all resource movement occurs along these transportation corridors. Trails carry the traffic of workers to and from leaf sources where ants harvest leaf tissue that is used as a substrate for their mutualist fungal gardens in the nest [14,17]. A colony’s cumulative trail network used over the course of a year tends to form a highly branched pattern radiating in all directions from the central nest [18], although only one or a few minimally branching trails may be in active use on a given day. Thus, the more central, permanent portions of a colony’s trail system represent a legacy of its foraging history.

The ‘macroscopic’ dynamical behaviour of trail traffic has already been empirically characterized for Atta colombica using a model based on fluid dynamics [12]. The collective traffic flow of these ants is a function of their density because interactions between moving ants impede their progress. We use the traffic flow model to derive an expression for the expected scaling relationship between colony foraging rate and size of the foraging workforce and foraging trails on which they move. We then compare these expectations with the actual scaling patterns among field colonies of two Atta species in Central America. A close correspondence suggests that the traffic dynamics embodied in the model are a mechanistic basis for the scaling pattern. Understanding the effect of size on resource acquisition in ant colonies can help explain the ecology and life history of a species, and may provide insights into size-dependent resource flows and economic activity in human cities.
2. MATERIAL AND METHODS

(a) Prediction of scaling patterns

The total flow of bidirectional traffic of A. colombica ants is described by

\[ q = kv_0 \left( 1 - \frac{k}{k_f} \right)^n \]  

in which \( q \) is the flux of ants per unit width of trail, \( k \) is the density of ants per unit area of trail, \( k_f \) is the density at which traffic velocity slows to zero (a traffic jam), \( v_0 \) is the free-flow velocity of ants as density approaches zero and \( n \) is an empirically fitted parameter. Parameter values were estimated from experimental manipulation of A. colombica trails to be \( k_f = 1.11 \text{ ants cm}^{-2} \), \( v_0 = 4.04 \text{ cm s}^{-1} \) and \( n = 0.64 \) [12].

In order to derive scaling properties from this model, we assume that a colony deploys a foraging workforce of \( F \) ants distributed along a foraging trail of length \( L \) and width \( W \), so that traffic density is \( k = F/(LW) \). If the only effect of trail width on traffic flow is through its effect on ant density, then the total flux on a trail of width \( W \) becomes \( Q = qW \), and with appropriate substitution from equation (2.1), this becomes

\[ Q = \frac{F}{L} v_0 \left( 1 - \frac{F}{LWk} \right)^n. \]  

Peak foraging traffic tends to be at equilibrium, with half of the workers outbound to a foraging site and half returning to the nest [15,19]. Only a fraction of returning ants carry a leaf fragment: 87 per cent in a colony in Trinidad [15], 42 per cent in an Atta cephalotes colony in Guyana [19], 51 per cent among five colonies at La Selva (M.B. 1998, unpublished data) and 33 per cent among six colonies at La Selva (A.I.B. 2009, unpublished data). Variability in this component of foraging is potentially important in understanding the allometry of foraging rate and we return to this issue below. However, the scaling exponents predicted by the model will not be affected by the assumed proportion of carriers, provided that the proportion is the same for all colonies. To predict foraging rates from equation (2.2), therefore, we assume that, on average, half the returning flow, and thus one-quarter of the total bidirectional flow, is composed of laden ants. Then the predicted foraging rate, \( R_q \), for a given combination of \( F \), \( L \) and \( W \) will be given by \( Q/4 \).

Leaf fragments transported by A. colombica and A. cephalotes workers typically have a mean fresh mass of about 14–21 mg and dry mass of 5.6–8.4 mg, depending on the species being harvested [20]. Dry leaf tissue has an energetic content of approximately 19 J mg\(^{-1}\), of which the fungal gardens extract about 45 per cent [21]. Thus, a foraging rate of \( R = 1 \text{ laden ant s}^{-1}\) represents approximately 48–72 J s\(^{-1}\) (Watts) ultimately obtained by the colony’s fungal gardens during equilibrium trail traffic.

From equation (2.2), we can predict the traffic flux for each colony in a sample, given its values of \( F \), \( L \) and \( W \). A colony’s foraging rate should increase as more foragers are recruited until an optimal density of workers is reached, and then decline with further growth of the workforce (figure 1). Increasing trail length while holding forager number and trail width constant is expected to reduce the foraging rate (filled circles in figure 1) because travel time increases, the workforce is distributed more thinly, and the traffic flux declines. Increasing trail width while holding length and forager number constant has a large effect only when the workforce is very large (filled squares in figure 1).

(b) Sites and colonies

We gathered data from 12 A. colombica colonies in lowland, closed-canopy forest on Barro Colorado Island (BCI), Panama, and nearby mainland areas during April and May 2006, and from six A. cephalotes colonies at La Selva Biological Station in the Atlantic lowlands of Costa Rica during November and December 2009. Atta colonies can grow to several million workers [17]. These colonies were mature but varied in size, judging from the cleared area of the nest surface, which is allometrically related to the length of the longest foraging trail in A. cephalotes [15]. All 12 Atta colombica colonies were foraging diurnally, while five of the six A. cephalotes colonies foraged nocturnally and the remaining one diurnally.

(c) Measurements

For each colony, we mapped the shape, branching points and segment lengths of all active trails from the nest to the base of the leaf harvesting sites, and noted whether these sites were mature trees or smaller saplings. We could not directly measure the vertical lengths of trails up tree trunks where leaf harvesting occurred. For the Atta colombica colonies on BCI, we assumed such vertical trails were 25 m high for trees (corresponding to the mid-canopy height of trees in the BCI forest) and 4 m for saplings. For the A. cephalotes colonies at La Selva, we had measured the diameter at breast height (DBH) of each tree where foraging occurred, so we used the height–DBH relationship for mixed dipt trees at La Selva of Rich et al. [22] to estimate vertical trail length. The total trail network length, \( L_t \), for a colony was the sum of all ground trail segments and vertical trail lengths.

To measure traffic properties and foraging rate, we recorded the trail activity at 25 frames per second with a digital video camera positioned on a tripod directly above the

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Figure 1. Foraging rate in relation to forager number as predicted by equation (2.2). The curves represent trails of different dimensions (dotted line, 25 m length × 10 cm width; thin solid line, 50 m × 10 cm; dashed line, 50 m × 15 cm; thick solid line, 100 m × 10 cm). Filled circles and arrows indicate the effect of increasing trail length while holding width constant at 10 cm and forager number constant at 10 000. Filled squares and arrow indicate the effect of increasing the width of a 50 m trail from 10 to 15 cm, for a foraging workforce of 30 000 ants. Foraging rate is assumed to be one-quarter of the total bidirectional traffic flux (see text).
trail surface, giving a field of view of a 50 cm segment of the trail. A ruler was placed next to the trail to provide a scale in each recording frame and allow measurement of the trail width. Recordings were made for 5 min at the nest entrance of a colony and for 1 min at each of several positions along each active trail: immediately to the basal (nest) side of any branching point in a trail, immediately distal to any branching point on the daughter trails, and at the base of any tree or sapling where leaf harvesting was occurring. From these recordings, we determined the mean density of ants at each recording point along the trail, determined from counts of all ants in a known area on five still frames chosen randomly from the 1 min of video recorded traffic. We assumed that this mean density at one point characterized the trail segment outward to the next point where recording occurred. The product of the worker density and the area of the trail segment gave an estimate of the number of foragers on a given segment. The sum of these estimates over the entire trail network yielded the workforce size, $F$. The recordings of traffic at the nest entrance provided data on the foraging rate from the entire trail network, $R$, measured as the number of ants returning to the nest with a leaf fragment (laden ants) per second. We also used the trail width at the nest entrance to characterize the width, $W$, of the trail network in the regression analyses, since the nest entrance must accommodate all the traffic flow from a given trail. All recordings were made at least 2 h after the start of foraging, during traffic with well-established outbound and returning flows of ants. Recordings for a single colony were made on a single day, with minimal delay between the recordings at different trail positions.

**Table 1.** Trail dimensions and activity characteristics for 18 colonies of *A. colombica* and *A. cephalotes.*

<table>
<thead>
<tr>
<th>variable</th>
<th>mean</th>
<th>s.d.</th>
<th>range</th>
</tr>
</thead>
<tbody>
<tr>
<td>forager number, $F$</td>
<td>12,646</td>
<td>1974</td>
<td>877–27,569</td>
</tr>
<tr>
<td>forager density (ants m$^{-2}$)</td>
<td>2,225</td>
<td>268</td>
<td>505–4932</td>
</tr>
<tr>
<td>total trail length, $L$ (m)</td>
<td>74.3</td>
<td>9.0</td>
<td>18.5–157.9</td>
</tr>
<tr>
<td>basal trail width, $W$ (cm)</td>
<td>15.5</td>
<td>1.6</td>
<td>4.1–24.1</td>
</tr>
<tr>
<td>foraging rate, $R$ (laden ants s$^{-1}$)</td>
<td>1.80</td>
<td>0.25</td>
<td>0.20–3.73</td>
</tr>
</tbody>
</table>

(d) **Analysis**

We determined scaling relationships in the usual way from linear regression analysis of log-transformed variables. We used reduced major axis (RMA) regression because it is often more robust than ordinary least squares (OLS) regression to departures from assumptions about error structure [23]. To describe the trail networks, we calculated the bivariate scaling relationships between $W$ and $L$, $F$ and $L$, and $F$ and $W$.

Foraging rate for the two species appeared to follow indistinguishable scaling patterns (figure 2), but to confirm this impression, we conducted an ANCOVA to determine whether the species differed significantly in their regression slopes or intercepts. Slopes were not significantly heterogeneous ($\text{species } \times \text{ forager number interaction}: F_{1,14} = 0.044, p = 0.84$). We therefore assumed homogeneity of slopes and calculated the ANCOVA without an interaction term. The species effect was not significant, indicating that the regression intercepts did not differ significantly between the two species, ($F_{1,15} = 2.54, p = 0.13$). Based on this lack of significant difference between *A. colombica* and *A. cephalotes*, we combined data from the two species for further analysis.

To derive predictions for the scaling relationships, we used the measured values of $F$, $L$ and $W$ for each colony to calculate the expected traffic flux from equation (2.2), and then took the predicted foraging rate to be $R_p = Q/4$. We then calculated an RMA regression analysis for the model

$$\log_{10}(R_p) = b_1 \log_{10}(F) + b_2 \log_{10}(L) + b_3 \log_{10}(W).$$

The slope coefficients $b_i$ of this model correspond to scaling exponents in the multivariate allometric relationship $R_p \propto F^{b_1} L^{b_2} W^{b_3}$. Standard errors of parameter estimates are identical for RMA and OLS regression [23], and we used the OLS standard errors calculated in $R$ to determine 95% confidence intervals (CIs) for the slope coefficients.

To find the actual scaling exponents, we followed the same regression procedures with the measurements of $F$, $L$ and $W$ for each colony, but used the observed foraging rate, $R$, as the dependent variable, rather than the rate predicted from equation (2.2). Slope coefficients and their 95% CIs were determined and compared with the predicted values. Matrix manipulations for the multivariate RMA regressions were performed in a MATHCAD (Mathsoft, Cambridge, MA, USA) program available from M.B.

For comparison with this multivariate scaling relationship, we also calculated the predicted and observed scaling exponents for the bivariate relationships between foraging rate and each of the independent variables $F$, $L$ and $W$ independently. The difference between the multivariate and bivariate scaling exponents for a given variable indicates the effect the other variables have on the foraging rate.

**3. RESULTS**

The variables of the analysis for the 18 colonies ranged over more than an order of magnitude, except for trail width, which varied by a factor of six (table 1). Longer trails tended to be wider but somewhat less than isometric ($W \propto L^{0.93}$), although the 95% CI (0.64–1.22) includes
Table 2. Predicted and observed multivariate scaling relationships between foraging rate (laden ants s⁻¹) and the variables indicated, determined from the regression model $\log R = k + b_1 \log F + b_2 \log L + b_3 \log W$. Confidence intervals were calculated from the standard errors with a $t$-distribution with d.f. = 16.

<table>
<thead>
<tr>
<th>slope coefficient ± s.e. (95% CI)</th>
<th>$b_1$</th>
<th>$b_2$</th>
<th>$b_3$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>predicted ($R_p$)</td>
<td>0.93 ± 0.008 (0.91, 0.95)</td>
<td>−0.94 ± 0.013 (−0.97, −0.91)</td>
<td>0.07 ± 0.015 (0.04, 0.10)</td>
<td>0.96</td>
</tr>
<tr>
<td>observed ($R$)</td>
<td>0.93 ± 0.130 (0.66, 1.20)</td>
<td>−1.02 ± 0.210 (−1.47, −0.57)</td>
<td>0.65 ± 0.240 (0.14, 1.16)</td>
<td>0.95</td>
</tr>
</tbody>
</table>

Table 3. Bivariate scaling relationships between foraging rate (laden ants s⁻¹) and the variables indicated. Confidence intervals were calculated from the standard errors with a $t$-distribution with d.f. = 16.

<table>
<thead>
<tr>
<th>variable</th>
<th>slope ± s.e.</th>
<th>95% CI</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>forager number, $F$</td>
<td>0.79 ± 0.089</td>
<td>(0.60, 0.98)</td>
<td>0.80</td>
</tr>
<tr>
<td>trail length, $L$</td>
<td>1.34 ± 0.27</td>
<td>(0.75, 1.92)</td>
<td>0.33</td>
</tr>
<tr>
<td>trail basal width, $W$</td>
<td>1.44 ± 0.22</td>
<td>(0.96, 1.91)</td>
<td>0.69</td>
</tr>
</tbody>
</table>

isometric scaling. The estimated size of the workforce and the measurements of foraging rate were similar to those for other *Atta* colonies in the field [14,24,25]. Forager number scaled at the 1.68 power of trail length (95% CI: 1.15–2.22), at the 1.82 power of basal trail width (95% CI: 1.23–2.36) and at the 1.55 power of total trail area (95% CI: 1.11–2.00). This last result suggests that trail systems with greater cleared area have proportionately more workers on them, although the wide confidence interval reflects the variability in forager density among the colonies we measured.

Regression of the predicted foraging rate from equation (2.2), $R_p$, against $F$, $L$ and $W$ shows the expected multivariate scaling relationship to be $R_p \propto F^{0.93} L^{-0.94} W^{0.07}$ (confidence intervals and regression statistics are given in table 2). The empirical scaling exponents determined from the regression for the observed foraging rate was $R \propto F^{0.93} L^{-1.02} W^{0.65}$ (table 2). These exponents agree well with predictions for two of the three independent variables. Only the role of trail width was anomalous: wider trails enhanced the foraging flux more than expected, with a scaling exponent of 0.65 rather than the predicted 0.07. However, the most dramatic effect of the trail system on colony performance was the approximately inverse relationship of the foraging rate with trail length in both predicted (−0.94) and empirical (−1.02) relationships. The 95% CI for this exponent is strictly negative: longer trails reduce the equilibrium flux of resources to the colony. In contrast, additional foragers enhanced the resource flux, as intuition suggests they would. But if foragers interfered with each other as workforces grew larger [26], the foraging rate should scale less than isometrically with forager number. The predicted and observed scalings at the 0.93 power of forager number suggest that any such interference plays only a small role. Because the scaling exponents are determined from the slope coefficients of a multiple regression analysis, they have the statistical interpretation of such coefficients; that is, they represent the effect of each independent variable when the others are held constant. The agreement of predicted and observed scaling for $F$ and $L$ suggests that the scaling pattern emerges at least in part from the traffic dynamics modelled by equation (2.2).

Additional insight into the scaling of foraging rate can be gained from comparing the multivariate pattern with the separate bivariate relationships. These are shown in table 3. The observed relationship between foraging rate and forager number is $R \propto F^{0.79}$ (figure 2). The 95% CI for the scaling exponent excluded unity. Interpreted without reference to the trail systems on which foraging took place, this allometry would suggest that *per capita* performance declines substantially in larger workforces. Foraging rate scaled at the 1.34 power of trail length and 1.44 power of trail width (table 3). In contrast to the negative exponent on trail length in the multivariate relationship, the positive exponent in the bivariate relationship misleadingly implies that long trails enhance foraging performance. The beneficial effect of trail width is exaggerated in the bivariate relationship compared with the multivariate one.

4. DISCUSSION

Inspired by an analogy with metabolic scaling, we have asked how the foraging rate of leaf-cutting ant colonies scales with the size of the foraging workforce and the trail network, and, in particular, whether the trail network constrains the foraging rate. Although the scaling exponents we observed have wide confidence intervals, some very clear conclusions can be drawn. The most striking pattern is a negative relationship between foraging rate and trail length when the statistical effects of forager number and trail width are held constant (table 2). The scaling exponent of −1.02 suggests a nearly perfectly inverse relationship. This scaling effect supports the general idea of vascular hypotheses for metabolic scaling [8–10] that transport paths can restrict the rate of resource supply in a consuming entity, organismal or superorganismal.

Trail length defines the travel time for an individual foraging worker, and a longer trail can reduce individual efficiency because of the additional time needed for a round trip between the nest and foraging site. But from the colony’s perspective, the equilibrium rate of returning laden ants per unit time would be unaffected by individual travel time if recruitment continually brought new workers onto the trail to maintain the traffic stream (although investment of the colony’s workforce would increase). Indeed, equation (2.2) implies that colonies will maximize their resource harvesting rate at an optimal density of ants on a trail (figure 1). For the parameter values noted above, the optimum occurs at 0.512 ant cm⁻² or 5120 ants m⁻² [12]. This is above the highest density observed in our sample, 4932 ants m⁻² (table 1). Thus, the scaling pattern...
we found is not a consequence of traffic volumes exceeding the capacity of the trail system. It is possible that the cleared area of a trail system at the time we measured traffic flow was a legacy of previous higher flows that left excess trail area for current traffic. However, the accumulation of litter on the forest floor would limit the duration of any such ‘legacy effect’ and the BCI data were collected on newly cleared trails just after the dry season accumulation of leaf litter. Some other factor is a more likely source of the observed scaling. We believe the apparent under-utilization of trail capacity is related to the recruitment dynamics of Atta colonies.

Mass recruitment of nest-mates to foraging sites plays a central role in the ecological success of ants [27]. We do not know, however, how trail length affects the recruitment behaviour of leaf-cutting ants. Moreover, only a fraction of recruited workers end up carrying leaf tissue back to the nest, and almost nothing is known about what regulates that fraction. Among the six A. cephalotes colonies at La Selva, the fraction of laden ants among the returning workers had no relation to trail length (\( r = 0.08, p = 0.71 \)) or number of foragers (\( r = 0.12, p = 0.58 \)) (A.I.B. 2009, unpublished data). The behavioural basis of matching workforce size to trail dimensions is complicated further by the role that trail width plays in our results. Trail width was predicted to have little effect, but foraging rate scaled positively, albeit sublinearly, with trail width. This may indicate that trail edges impose an unexpected effect on traffic that is not accounted for in equation (2.2). If contact with vegetation or leaf litter at the trail margin impedes foragers more than interactions with other ants in the traffic flow, then wider trails would enhance the flow because proportionally fewer ants are at the margins. The distance from the nest to a desired foraging site is a feature of the environment, but the width of a trail is under the control of the leaf-cutting ants, although how trail clearing activity is regulated is not well known. These gaps in current knowledge are unfortunate, but our analysis shows that social insect colonies can be usefully dissected into components, whose contribution to scaling patterns can then be studied separately.

Trail-building among ant species is associated with larger colony size [28], suggesting that the potential traffic flow must be large enough for the payback from physical trail construction to outweigh the investment. The negative scaling of foraging rate with trail length implies that there is likely to be a maximum foraging distance beyond which the colony obtains no net benefit. Furthermore, if larger trail networks limit the return per worker, there may be a maximum colony size beyond which there would be no net benefit from further growth. Trail networks may, therefore, play a central role in life-history patterns by determining how the gap between metabolic demands of a colony and foraging supply scales with colony size. This gap provides the net productivity, which can be devoted to the production of additional workers or reproductives.

The trails in Atta colonies seem analogous to the transport and supply networks of cities [11,29,30]. Resources conveyed along these transport paths determine the economic activity and ultimate productivity (population growth or economic output) of the societies they serve. Although the geometry of transportation networks is more decentralized in cities than in Atta colonies or organismal vascular systems [30], traffic volume is highly concentrated on a small portion of the total road length in cities [31], much as the traffic of Atta foragers is concentrated on permanent, central trunk trails, while smaller, peripheral trails to particular foraging sites change over time [16,18]. Road length scales below isometry (i.e. scaling exponent less than unity) with the population size of cities [32] and with the geographical area of countries [33]. Similarly, the maximum distance from the nest at which leaf harvesting occurs scales at only the 0.37 power of nest size in A. cephalotes [15]. This kind of similarity in scaling properties suggests some functional correspondence between supply networks in Atta and human societies, and these analogies deserve further exploration.

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