

Body size effects on locomotion and load carriage in the highly polymorphic leaf-cutting ants *Atta colombica* and *Atta cephalotes*

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Leaf-cutting ants reduce their walking speed under the weight of the leaf fragments they carry, an effect likely to have some consequence for the foraging performance of a colony. I manipulated loads carried by workers from two *Atta* species to determine how load mass and body size affect walking speed. A comparison of speeds before and after load manipulation indicates that change in load mass has a linear effect on velocity. Several different regression models of speed as a function of loads and body size have similar fit to the data, so a single best model cannot easily be identified. However, there is statistical evidence that the slope of the linear effect is more pronounced for smaller ants, an outcome most consistent with a regression model based on loading ratio, a metric that scales load mass relative to body mass. I then examined the effect of loading ratio on the leaf transport rate (the product of load mass and carriage velocity). It has been claimed that this rate is maximized over a range of loading ratios that is the same for all ants regardless of their size. However, I found that a latent body mass effect persists in the relation of transport rate to loading ratio, even though loading ratio is already scaled relative to body mass. The maxima seem to be reached only at artificially elevated loading ratios, so that transport rates with natural fragments tend to be sub-maximal. This conclusion is in agreement with analytical predictions of rate-maximizing load masses derived from the regression models. Thus, loading ratio does not adequately scale load mass relative to body size when used in this context (effect on leaf transport rate), and should be used cautiously. Ants are likely to accommodate loads through modulation of both stride length and step frequency, but precisely how this takes place requires future study. *Key words:* ants, *Atta*, central place foraging, Formicidae, walking speed, scaling. [*Behav Ecol* 11:125–131 (2000)]

Carrying leaf fragments is a central foraging activity of leaf-cutting ants of the genus *Atta* (Attini: Myrmicinae) (Hölldobler and Wilson, 1990). Workers that transport fragments may vary by an order of magnitude in body mass, and the fragments typically range from one to several times body mass. Such heavy loads reduce locomotion speed (Burd, 1996a; Lutz, 1929; Roces and Núñez, 1993; Rudolph and Loudon, 1986) and increase energetic outlay (Lighton et al., 1987) of laden ants as they return to the nest with substrate for the fungal gardens. Thus, foraging success of the colony would seem to be closely tied to load size and locomotion. But despite much research on the load size-to-worker size relation in attine ants (Roces and Hölldobler, 1994; Shutler and Mullie, 1991; Waller, 1989; Wetterer, 1990, 1991, 1994; Wilson, 1980), there is little certainty about the functional significance of the relation.

The polymorphism of attine workers presents a difficulty for analysis and interpretation of data. Many kinematic and metabolic features of locomotion and load carriage are expected to scale allometrically with body size (Schmidt-Neilson, 1984). It seems appealing, therefore, to account for within-species polymorphism in attine ants in some fashion that maintains functional similarity among workers of greatly different size. However, it is not always a straightforward task to compensate for body size variation in a functional or ecological analysis (LaBarbera, 1989).

In this article I address two issues: (1) how does load mass affect the speed of laden ants? and (2) what effect does laden

speed have on foraging performance? The influence of body size is a central concern for both questions.

Scaling of load with body size can be represented in several ways. Lutz (1929) and many others have represented load mass in relative terms by using the “burden” or “loading ratio,” L , defined by

$$L = (M_a + M_l) / M_a \quad (1)$$

in which M_a is the body mass of the transporting ant, and M_l is the load mass. Thus, a loading ratio of unity signifies an unladen animal, whereas a loading ratio of 1.25 indicates a load of 25% of body weight.

The main utility of the loading ratio in functional morphology derives from the finding that the proportional increase in an animal's metabolic rate during load carriage (measured as rate of oxygen consumption) equals the proportional increase in total mass caused by addition of the load (Lighton et al., 1987; Taylor et al., 1980). For instance, two animals of different size having equal loading ratios of 1.25 both experience a 25% increase in metabolic rate over their unladen travel. Thus, loading ratios are an index of functionally similar burdens with respect to relative metabolic rates. It does not immediately follow that the loading ratio is also an index of functionally similar loads with respect to locomotion velocity or foraging performance. Indeed, the analysis below suggests that loading ratio can be an incomplete or even misleading metric of relative load size.

Load mass is not the only variable that can be scaled to body size. Locomotion velocity, usually expressed as absolute distance per second, might be more appropriately measured in body lengths per second, or possibly defined as the non-dimensional Froude number (Alexander and Jayes, 1983). Yet another means of accounting for body size is to retain variables in their absolute units but to include body size as an

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Received 9 July 1998; revised 18 May 1999; accepted 9 June 1999.

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additional independent variable in a statistical model. Body size, along with other independent variables, may have linear or nonlinear effects on locomotion and foraging performance. It is not easy to choose among these options in the absence of a strong theoretical argument, but it is clear that the possibilities for data analysis are broader than have been used in past studies of attine ants.

In this article I reexamine load carriage in two Central American attine species, *Atta colombica* and *A. cephalotes*. I begin with an "agnostic" view of locomotion in these ants by calculating six different regression models of laden speed in relation to other variables. No clearly best model emerges on statistical grounds alone, but experimental data in which I compare speed before and after manipulation of a load mass suggests that absolute load mass has a linear effect on laden speed. Why this should be so in biomechanical terms is unknown.

I also consider the locomotion data in relation to a measure of foraging performance, the "leaf transport rate" (Rudolph and Loudon, 1986), in which locomotion velocity is a factor. Rudolph and Loudon (1986) have claimed that the leaf transport rate of *Atta cephalotes* ants is maximized under any loading ratio from approximately 3.5 to 6.5, irrespective of the size of the ant. My analysis reveals a more complex pattern in which the relation between loading ratio and transport rate differs for ants of different body size. Additionally, I show analytically that none of the regression models of walking speed I examined is consistent with the Rudolph-Loudon range of body-size independent, rate-maximizing loading ratios.

METHODS

Sites and species

I studied a colony of *Atta colombica* Guérin on Barro Colorado Island (BCI), Panama, in September–October 1989 during the BCI rainy season, and four colonies of *Atta cephalotes* L. in the La Selva Biological Station (LS), Costa Rica, January–March 1998, during the LS dry season. Both sites contain lowland Central American rainforest (Leigh et al., 1982; McDade et al., 1994) and numerous *Atta* colonies. The BCI colony of *A. colombica* foraged diurnally, and the LS colonies of *A. cephalotes* foraged nocturnally in January and early February, with a shift toward daylight foraging beginning in late February. Despite these differences, the two species are ecologically and morphologically similar (Weber, 1969).

Measurements

I measured walking speed of ants traversing 1-m sections of cleared, level foraging trails during peak hours of leaf harvesting. The sections chosen had smooth soil bases and were free of major obstacles. Air temperature during the measurements on BCI varied from 25° to 28°C; trail temperatures during measurements at LS varied from 24.5° to 27°C.

At BCI, the *Atta colombica* workers were transporting leaf fragments from a *Cordia alliodora* (Boraginaceae). I arbitrarily selected 100 laden workers, altered their loads by cutting the fragment with a small scissors or by adding a piece of aluminium foil, and timed to the nearest 0.1 s their transit over a 1-m segment of trail. Experimental manipulation of loads breaks up the natural covariance between ant size and load mass, an essential procedure to test load effects on performance.

At LS, I obtained data from 30 *Atta cephalotes* workers in a colony foraging nocturnally on an *Ampelocera holteii* (Ulmaceae), 15 workers in a colony foraging nocturnally on a *Virola sebifera* (Myristicaceae), 100 workers in a colony foraging di-

urnally on an *Inga* sp. (Mimosaceae), and 90 workers in a colony foraging diurnally on a vegetation source that was not identified. At LS I altered load masses to allow comparison of speed before and after the manipulation. Laden ants were timed with their natural loads over the first meter of a 3-m course. Upon completion the load was either reduced by clipping or increased by adding aluminium foil weighing approximately 5, 10, or 20 mg, and the ants were allowed to equilibrate to the new load in the second meter of the course. Transit time with the manipulated load was measured over the third meter.

The timed ants and their loads were collected and stored in individual vials. Leaf fragments were weighed to the nearest 0.1 mg within 2–3 h of collection for BCI fragments and after overnight storage at 4°C for LS fragments. I weighed ants to the nearest 0.1 mg and measured femur lengths (suture with trochanter to articulation with tibia) to 0.05 mm (BCI) or 0.02 mm (LS) under a dissecting microscope with an ocular micrometer.

To determine the pattern of natural load mass carriage by ants, I made random collections of 710 laden *A. colombica* workers at 3 vegetation sources on BCI and of 1582 laden *A. cephalotes* workers at 5 vegetation sources at LS. Load masses, ant weights, and femur lengths were determined in the manner described above.

Statistical analyses

For each ant species I analyzed the following regression models relating locomotion velocity to load mass and ant size (the error terms are omitted for clarity):

$$v = b_0 + b_1L \quad (2a)$$

$$v = b_0 + b_1M_l + b_2M_a \quad (2b)$$

$$v = b_0 + b_1M_l + b_2F \quad (2c)$$

$$v = b_0M_l^{b_1}M_a^{b_2} \quad (2d)$$

(logarithmically transformed for regression)

$$v = b_0M_l^{b_1}F^{b_2} \quad (2e)$$

(logarithmically transformed for regression)

$$v_{rel} = b_0 + b_1M_l \quad (2f)$$

In these equations v is velocity, v_{rel} is relative velocity in units of femur length per second, F is femur length, the b 's are regression coefficients, and the other terms are as in Equation 1. Because all measured variables contained intrinsic variance, ordinary least-squares (OLS) regression, which assumes that independent variables are experimentally fixed and free of variance, is not the most appropriate statistical technique to estimate parameter values (LaBarbera, 1989; McArdle, 1988). Instead, I used reduced major axis (RMA) regression, a technique that is robust to variation in the error structure of the variables (McArdle, 1988). When \log_e -transformed variables were used to estimate parameters for models 2d and 2e, a correction factor, $\exp(s^2/2)$, in which s is the standard error of estimate, was applied for back-transformation (LaBarbera, 1989).

Using the same data, I calculated for each laden ant of each species its leaf transport rate, defined by Rudolph and Loudon (1986) as the product of load mass and velocity, $M_l v$. I then examined $M_l v$ as a function of loading ratio, L , using nonlinear regression (least-squares criterion of fit with Gauss-Newton iteration) to fit the equation $y = a(1 - e^{-bx})$. This equation allows the regression curve to reach an asymptote at a , with a more rapid approach to the asymptote the greater

Table 1
Analysis of regression models in Equations 2a–f

Ant species	Model	Parameter estimates			<i>R</i>
		b_0	b_1	b_2	
<i>Atta colombica</i>	2a	57.90	-6.10		.77
	2b	39.46	-0.67	1.20	.65
	2c	-1.26	-0.70	13.89	.64
	2d	25.68	-0.40	0.66	.73
	2e	8.69	-0.44	1.99	.63
	2f	13.94	-0.19		.62
<i>Atta cephalotes</i>	2a	42.90	-5.40		.64
	2b	21.12	-0.59	1.78	.65
	2c	-18.73	-0.61	14.50	.69
	2d	13.35	-0.50	0.91	.64
	2e	2.89	-0.50	2.60	.67
	2f	9.59	-0.15		.62

Models refer to equation numbers in the text. Units for the regression equations: v , velocity (mm/s); v_{rel} , relative velocity (femur lengths/s); M_b , load mass (mg); M_a , ant mass (mg); F , metathoracic femur length (mm); L , loading ratio. Sample sizes: *A. colombica*, 100; *A. cephalotes*, 224. The simple or multiple correlation, R , is given as the absolute value. All correlations are significantly different from zero with probability $p < .0001$.

the value of b . The square of the correlation between predicted and observed values is used as the nonlinear regression R^2 . I initially analyzed all data pooled across ant body size and then analyzed separately three subsets of body size to determine if the transport rate-loading ratio relations differ among size classes and in comparison to the overall relation.

RESULTS

Carriage velocity

Reduced major axis regression coefficients for the models in Equations 2a–f are presented in Table 1, along with the simple or multiple correlation for the variables involved. In each of the 12 regressions, the correlations are significantly different from zero ($p < .0001$), as expected. There seems to be no clearly superior model judging on the correlations alone, and certainly no single model that seems best for both species, although they are similar morphologically and might be expected not to differ much in the biomechanics of load carriage. Unmeasured factors such as intensity of trail traffic and number of collisions with other workers probably produce a scatter of data that allows a similar statistical fit to several models. However, experimental manipulation of loads provides more insight into *Atta* locomotion.

Comparison of velocity before and after manipulation of load masses of *Atta cephalotes* workers shows that speed changes linearly with change in absolute load mass (Figure 1). Some of the scatter in the data of Figure 1 may be due to alarm or escape reactions after experimental manipulations, especially because adding weights required somewhat intrusive handling. The linear correlation for the data in Figure 1 is -0.76 (significantly different from 0 at $p \ll .0001$). There is no suggestion of nonlinearity judging by the significance of quadratic ($p = .26$) or cubic ($p = .37$) terms in polynomial regression.

A linear effect of absolute load mass on speed is incompatible with Equations 2d and 2e but consistent with the other models. Equation 2a predicts that smaller ants suffer a steeper decline in speed with added load mass than larger ants, and equation 2f predicts the decline would be steeper for larger

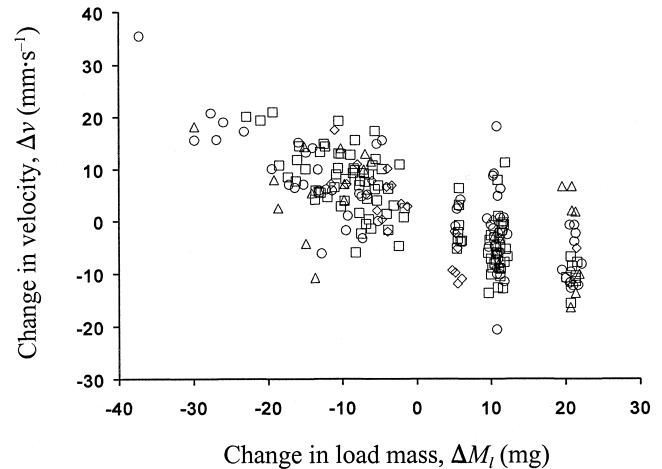


Figure 1

Results of experiment measuring laden speed before and after load manipulation in *A. cephalotes*. Ants are identified by size class: (diamonds) $M_a < 5$ mg; (squares) $5 \text{ mg} \leq M_a < 10$ mg; (circles) $10 \text{ mg} \leq M_a < 15$ mg; (triangles) $M_a \geq 15$ mg.

ants. Equations 2b and 2c imply that the effect of load mass on speed would be independent of ant size.

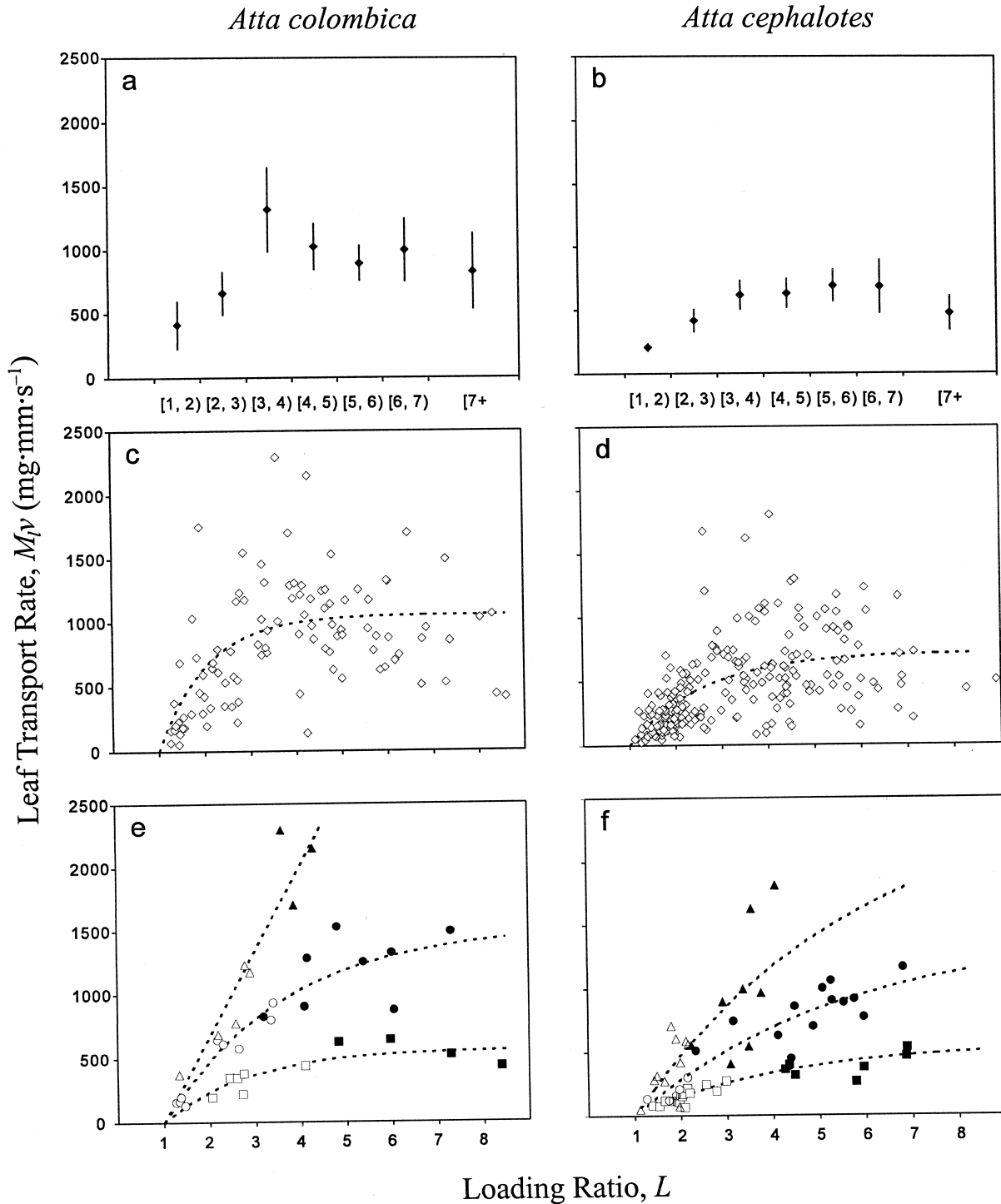
To test whether the pattern in Figure 1 is independent of ant size, I calculated a generalized linear model of Δv as a function of ΔM_b , M_a , and the $\Delta M_l \times M_a$ interaction. The interaction effect (evaluated after ΔM_l and M_a direct effects) was significant (semipartial $r^2 = .024$, $t = 3.69$, $df = 221$, $p < .001$), indicating that the linear effect of load mass on speed is not independent of ant size. Inspection of Figure 1 suggests that ants in the smallest size class ($M_a < 5$ mg) display a steeper slope, whereas ants in the largest size class ($M_a \geq 15$ mg) display a more shallow slope. Based on these results, Equation 2a is supported as a model of laden locomotion. However, there are few data for the largest and smallest size classes, and the apparent difference in slopes needs confirmation from additional study.

Moreover, Equation 2a contains an unlikely implication: if a load that slows an ant to zero velocity is taken to be the largest load it can carry, then Equation 2a implies that all ants reach $v = 0$ at the same loading ratio, $L = -b_0/b_1$, or 9.5 for *A. colombica* and 7.9 for *A. cephalotes*. However, my manipulations of load weight suggest that small workers more readily sustain high loading ratios than do larger ants (see Figure 2). Equations 2b and 2c are more realistic in this regard because they imply (upon solving for $v = 0$) that small ants can tolerate higher maximum loading ratios than large ants.

Leaf transport rate

Figure 2 shows the leaf transport rate, $M_l v$, of laden workers of each species as a function of loading ratio. Figure 2a,b presents the data in the same fashion used by Rudolph and Loudon (1986): mean ± 2 SE of $M_l v$ is shown for unit intervals of loading ratio (except for $L \geq 7$). For both species, there appears to be an approximate plateau in mean $M_l v$ across loading ratios of about 3–7 (with a possible decline for higher L). This broad maximum closely resembles the pattern found by Rudolph and Loudon. Visual assessment of this apparent plateau was the basis for their claim that leaf transport rate is maximized by any loading ratio from 3.5 to 6.5, for ants of any size.

Figure 2c,d displays the individual data underlying the means. Nonlinear regressions through these data produce

**Figure 2**

Leaf transport rate in relation to loading ratio in *Atta colombica* (left) and *A. cephalotes* (right). (a, b) Means \pm 2 SE within unit intervals of loading ratio (except for $L \geq 7$). (c, d) Raw data from which the means were calculated ($n = 100$ for *A. colombica*; $n = 224$ for *A. cephalotes*). The curves represent best-fit nonlinear regressions to an equation of the form $y = a(1 - e^{-bx})$. *Atta colombica*, $R^2 = .28$; *A. cephalotes*, $R^2 = .34$. (e, f) Subset of the raw data for three worker size classes: 5–6 mg body mass (squares), 10–11 mg (circles), and 15–20 mg (triangles). Open symbols are experimentally reduced load masses, filled symbols are experimentally increased load masses. Curves are best-fit nonlinear regressions to an equation of the form $y = a(1 - e^{-bx})$, except for the *A. colombica* 15–20 mg class, which shows the best-fit linear relation. *Atta colombica* 5–6 mg, $R^2 = .68$; 10–11 mg, $R^2 = .87$; 15–20 mg, $R^2 = .97$. *Atta cephalotes* 5–6 mg, $R^2 = .86$; 10–11 mg, $R^2 = .83$; 15–20 mg, $R^2 = .60$.

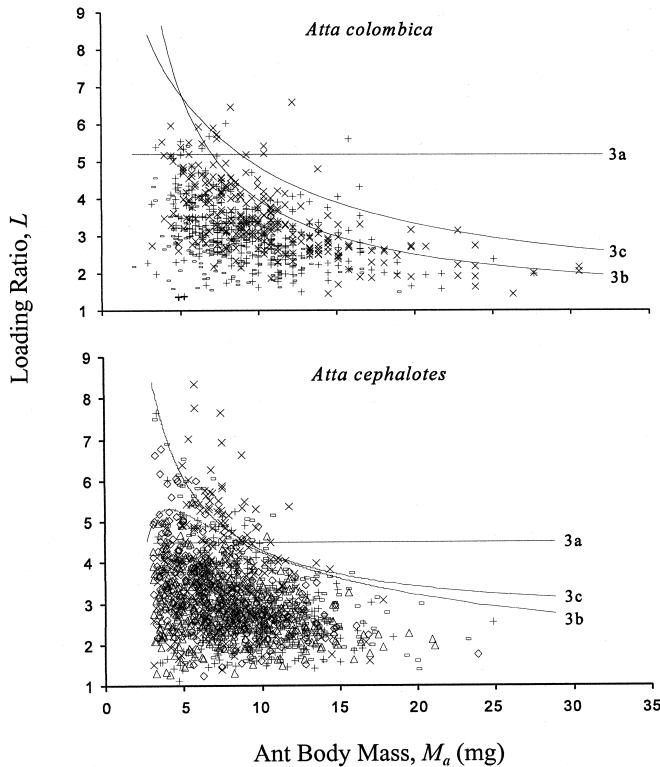


Figure 3 Loading ratios in relation to body mass of randomly collected laden ants. Data for *A. colombica* ($n = 710$ ants) from three trees (indicated by different symbols) harvested by one colony. Data for *A. cephalotes* ($n = 1582$ ants) from five trees (indicated by different symbols) each harvested by a different colony. Lines and curves represent loading ratios that would maximize the rate of biomass transport, as given by Equations 3a–c.

curves similar to the putative plateaus of Figure 2a,b, but the scatter of data about the curves is obviously large (R^2 is .28 for *A. colombica* and .34 for *A. cephalotes*). The data in Figure 2a–d are pooled across ants of all body sizes, thereby tacitly accepting the assumption that a 5-mg load on a 5-mg ant has the same effect on leaf transport rate as a 20-mg load on a 20-mg ant because the loading ratios are the same in both cases. Separate consideration of three distinct size classes in Figure 2e,f indicates that this assumption is not correct.

Figure 2e,f presents data for ants of 5–6 mg, 10–11 mg, and 15–20 mg (the last category is wider to include a sufficient number of points). Nonlinear regressions within each of the size classes of *A. cephalotes* and within the two smaller size classes of *A. colombica* show good fit to the data, with R^2 values ranging from 0.60 to 0.87. [For the largest size class of *A. colombica*, nonlinear regression did not converge on a solution, and the linear relation is shown instead ($R^2 = .97$).]

Two important patterns are evident in Figure 2e,f. First, regressions within individual size classes provide a much better fit to the data than does a single regression that pools all body sizes. This suggests that the relation of $M_l v$ to L is not the same for ants of all sizes. Indeed, the scatter of data in Figure 2c,d is due largely to differences among body size classes. Second, the regression curves do not closely approach their asymptotes until loading ratios are large (particularly for the larger ants). There is little support for the contention of Rudolph and Loudon (1986) that all ants, whatever their size, reach a performance plateau with loading ratios of 3.5–6.5.

Figure 3 shows loading ratio in relation to body mass for randomly collected laden ants of both species. The majority

of loading ratios for 5- to 6-mg ants are below 5; for 10- to 11-mg ants below 4; and for 15- to 20-mg ants below 3. Thus, most natural loads are below the loading ratios at which their bearers come near the asymptotic maxima of leaf transport rates shown in Figure 2e,f.

Analytical prediction of $M_l v$ -maximizing loading ratios

Another way of considering the question of rate maximization is to use the regression equations for walking speed as functions for further analysis. Any conclusion about leaf transport rate should be compatible with conclusions about laden velocity, in that laden velocity is a factor in the term $M_l v$. The data do not point clearly to a single best regression model of velocity, but a single best model is not needed to establish an important point: none of the alternatives examined is compatible with the Rudolph and Loudon (1986) claim of a universal range of rate-maximizing loading ratios for all ants.

If velocity is related linearly to loading ratio (Equation 2a), then $M_l v$ would be greatest at

$$L = (b_1 - b_0) / (2b_1) \quad (3a)$$

(derivation in the appendix, case 1). If load mass and ant mass have independent linear effects on speed (Equation 2b), then $M_l v$ is maximized when

$$L = -(b_0 - 2b_1 M_a + b_2 M_a) / (2b_1 M_a) \quad (3b)$$

(appendix, case 2). If a linear dimension such as femur length, rather than body mass, is used as the measure of ant size (Equation 2c), then the $M_l v$ -maximizing solution is

$$L = -(b_0 - 2b_1 M_a + b_2 F) / (2b_1 M_a) \quad (3c)$$

(appendix, case 3). The linear measure F that appears in Equation 3c could be converted to M_a using their allometric relationship (e.g., Feener et al., 1988). The locomotion Equations 2d and 2e predict that $M_l v$ reaches a maximum only at infinite load mass (appendix, case 4). Equation 2f is largely uninformative with respect to an optimal loading ratio because relative velocity, v_{rel} , is not a term in $M_l v$.

Consider what these alternative $M_l v$ -maximizing optima indicate. Equation 3a gives an optimum loading ratio that applies to all ants regardless of body size, but the optimum is a single value of L (for a given set of regression parameters) and not a broad range. For the parameter estimates obtained in this study (Table 1), Equation 3a implies rate-maximizing loading ratios of 5.2 for *Atta colombica* and 4.5 for *A. cephalotes*. In contrast, Equations 3b and 3c imply that transport rate is maximized over a range of loading ratios, but, because the body size variables M_a or F appear in the right-hand side expressions, the predicted optima necessarily depend on the size of the ants involved. The infinite optimal loading ratios implied by Equations 2d and 2e are biologically meaningless, and Equation 2f is inapplicable to the problem at hand.

Thus, none of the locomotion models is compatible with a single broad range of rate-maximizing loading ratios for all ants regardless of their size. Either laden speed follows peculiar rules which these equations do not even approximate (unlikely, given the reasonably high correlations in Table 1), or the Rudolph and Loudon plateau hypothesis is incorrect. Curiously, Rudolph and Loudon (1986) report laden locomotion using a regression model like Equation 2c (except they use head width rather than femur length as the size measurement). Thus, their locomotion model and their plateau hypothesis cannot both be correct.

Figure 3 shows the rate-maximizing optima from Equations 3a–c (using parameter values from Table 1) superimposed on the random samples of laden ants. No matter which locomotion equation is used to predict peak performance, the ma-

majority of loads for both species are below the theoretically optimal sizes. Equations 3b and 3c seem to form an approximate upper boundary for the scatter of natural loads, but this may be fortuitous.

DISCUSSION

The results of this study confirm that intraspecific variation in body size affects both laden velocity and leaf transport rate in *Atta* ants. Six locomotion models that account for body size variation in different ways were analyzed for each species (Table 1). Judging by the simple or multiple correlation among the variables involved, all six models are reasonably successful at explaining laden walking speed. However, speed changes after experimental load manipulation suggest that load mass has a linear effect on speed (Figure 1). A statistically significant interaction effect, in which the linear relation is steeper for smaller ants, is most compatible with the model in Equation 2a, which scales loads to body size by use of the loading ratio. However, Equations 2b and 2c give a more realistic prediction about maximum possible loads, if we assume that maximum loads slow an ant to zero velocity.

Although loading ratio rescales load size relative to body size, it does not completely incorporate all body-size dependence in the relation between fragment size and leaf transport rate (Figure 2e,f). Indeed, by pooling ants of different body size, as in Figure 2a,b and in Rudolph and Loudon (1986), the latent body-size dependence is obscured, leaving the incorrect impression of a single plateau in leaf transport rate for all ants. Plateaus in transport rate may occur, but Figure 2e,f shows that it is not the same plateau for large and small workers.

I have used leaf transport rate in the present analysis to allow comparison with other literature on attine foraging, but it may not be an appropriate or useful measurement of foraging performance. The quantity $M_l v$ has some appeal because the units can be interpreted as the leaf biomass carried a given distance per unit time. But these units are different from the more conventional foraging measure of (gross or net) gains per time, and the two measures do not predict the same optimal load masses (Burd, 1996a). One problem with $M_l v$ is that it pertains only to an ant's return laden journey, although the outbound journey and leaf cutting are time- and energy-demanding components of a foraging excursion. Furthermore, the leaf transport rate takes no account of the way in which large numbers of workers interact to collectively yield the colony level rate of resource acquisition. Thus, despite the common use of leaf transport rate to measure attine performance, it may at best serve an heuristic function in foraging studies.

If, as Figure 3 implies, natural loads are too small to maximize $M_l v$ or to maximize the gross rate or energetic efficiency of tissue delivery to the nest (Burd, 1996a), does this mean the ants are not foraging optimally? Two hypotheses have been offered to explain how suboptimal individual performance of *Atta* ants may be a component of optimal group foraging. Roces and Núñez (1993) proposed that small loads allow laden ants to return more quickly to recruit nest mates, thereby increasing the rate at which the whole colony exploits a resource. However, rapid return to the nest would seem irrelevant for the majority of foraging time when nearly continuous flows of outgoing and returning traffic prevail.

I have proposed (Burd, 1996b) that ants engaged in cutting hinder their nest mates' access to leaf margin. By taking smaller fragments they relinquish the resource more quickly and allow more workers to obtain fragments per unit of colony foraging time. A model of this process based on queuing theory predicted load sizes for optimal colony performance that

correspond well to natural load sizes (Burd, 1996b), but the detailed behaviors assumed in the queuing model have not been tested.

Schmid-Hempel et al. (1985) have suggested that small nectar loads taken by honey bees (*Apis mellifera*) maximize the ratio of energetic gains to energetic expenditure of foraging. This strategy would maximize the total energy delivery of a worker over its lifetime if it could spend only a fixed amount of energy, but whether such considerations are important for walking, rather than flying, insects is not certain (Fewell, 1988; Weier et al., 1995).

There remains the biomechanical issue of why load mass affects velocity in the linear manner indicated in Figure 1. A simple explanation would be that load mass has a linear effect on either step frequency or stride length alone, without affecting the other. However, loading is unlikely to alter an ant's gait in so simple a fashion. Step frequency in crayfish is reduced by loading (walking on land rather than in water), due to increased duration of the power stroke during which legs are in contact with the ground (Grote, 1981). But loads also cause postural changes (legs tucked more closely under the body to provide greater mechanical advantage against the load), and these changes reduce the stride length. Similarly, in hermit crabs (Herreid and Full, 1986) and in painted turtles (Zani and Claussen, 1995), velocity during load carriage is related to modulation of both stride length and step frequency. In ants, maintaining laden speed seems to depend largely on the ability to maintain balance, with relatively long legs being advantageous (Nielsen et al., 1982). Leaf-cutting ants holding fragments in their mandibles must experience considerable rotational force, and they generally position fragments above their backs in an apparent attempt to improve balance. The gait changes imposed by gravitational and rotational forces may be the fundamental cause of the load effect on velocity in attines, but this awaits detailed kinematic study of these ants.

APPENDIX

Case 1

Assume that locomotion follows an equation of the form $v = b_0 + b_1 L$. Substitution for v in $M_l v$ yields $M_l v = M_l (b_0 + b_1 L)$. Because $M_l = M_a (L - 1)$ by the definition in Equation 1 of the main text, further substitution into $M_l v$ yields

$$M_l v = M_a (L - 1) (b_0 + b_1 L).$$

Differentiating the above equation with respect to L produces

$$\partial M_l v / \partial L = M_a (b_0 + 2b_1 L - b_1),$$

and setting the right-hand side equal to zero and solving for L yields the critical point

$$L = (b_1 - b_0) / (2b_1),$$

which is Equation 3a of the main text. The second derivative, $\partial^2 M_l v / \partial L^2 = 2b_1 M_a$, is negative if b_1 is negative (higher loading ratio decreases velocity), indicating that Equation 3a specifies a maximum.

Case 2

Assume a locomotion equation of the form $v = b_0 + b_1 M_l + b_2 M_a$. Substitution of this and of $M_l = M_a (L - 1)$ into $M_l v$ yields

$$M_l v = M_a (L - 1) [b_0 + b_1 M_a (L - 1) + b_2 M_a].$$

Differentiating this equation with respect to L results in

$$\partial M_l v / \partial L = M_a [b_0 + b_1 M_a (L - 1) + b_2 M_a] + b_1 M_a^2 (L - 1),$$

and by setting the right-hand side equal to zero and solving for L , we obtain

$$L = -(b_0 - 2b_1M_a + b_2M_a)/(2b_1M_a),$$

which is Equation 3b of the main text. The second derivative, $\partial^2 M_l v / \partial L^2 = 2b_1 M_a^{-2}$, is negative provided the regression coefficient b_1 is negative, so the critical point in Equation 3b is a maximum.

Case 3

Assume a locomotion equation of the form $v = b_0 + b_1 M_l + b_2 F$. By a derivation similar to that in case 2, the critical point is found to be

$$L = -(b_0 - 2b_1 M_a + b_2 F)/(2b_1 M_a),$$

which is Equation 3c of the main text. The second derivative is the same as for case 2, so the critical point is a maximum provided b_1 is negative.

Case 4

Assume a locomotion equation of the form $v = b_0 M_l^{b_1} M_a^{b_2}$. Substitution into $M_l v$ as in the previous cases yields

$$M_l v = M_a(L - 1) b_0 M_l^{b_1} M_a^{b_2},$$

and differentiation produces,

$$\partial M_l v / \partial L = b_0 M_a^{(1+b_1+b_2)} (L - 1)^{b_1} (1 + b_1).$$

When the above equation is set equal to zero, a solution occurs only at $L \rightarrow \infty$, provided b_1 is negative. If the locomotion equation is originally based on F rather than on M_a (Equation 2e), then

$$\partial M_l v / \partial L = b_0 M_a^{(1+b_1)} F^{b_2} (L - 1)^{b_1} (1 + b_1).$$

As before, when the above equation is set equal to zero, a solution occurs only at $L \rightarrow \infty$.

I thank the Smithsonian Tropical Research Institute and the Organization for Tropical Studies for making their field stations at Barro Colorado Island and La Selva available, and the responsible ministries of the governments of Panama and Costa Rica for permission to conduct the research. Susan Giles provided unflinching assistance with the field work at La Selva. I thank N. Aranwela, I. Cuthill, G. D. Sanson, and three anonymous reviewers for helpful comments on the manuscript. This study was funded by the Australian Research Council.

REFERENCES

- Alexander RM, Jayes AS, 1983. A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J Zool* 201:135–152.
- Burd M, 1996a. Foraging performance by *Atta colombica*, a leaf-cutting ant. *Am Nat* 148:597–612.
- Burd M, 1996b. Server system and queuing models of leaf harvesting by leaf-cutting ants. *Am Nat* 148:613–629.
- Feener DH, Lighton JRB, Bartholomew GA, 1988. Curvilinear allometry, energetics, and foraging ecology: a comparison of leaf-cutting ants and army ants. *Funct Ecol* 2:509–520.
- Fewell JH, 1988. Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. *Behav Ecol Sociobiol* 22:401–408.
- Grote JR, 1981. The effect of load on locomotion in crayfish. *J Exp Biol* 92:277–288.
- Herreid CF, Full RJ, 1986. Locomotion of hermit crabs (*Coenobita compressus*) on beach and treadmill. *J Exp Biol* 120:283–296.
- Hölldobler B, Wilson EO, 1990. The ants. Cambridge, Massachusetts: Belknap Press.
- LaBarbera M, 1989. Analyzing body size as a factor in ecology and evolution. *Annu Rev Ecol Syst* 20:97–117.
- Leigh EG, Rand AS, Windsor DM (eds), 1982. The ecology of a tropical forest. Washington, DC: Smithsonian Institution Press.
- 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*. *Physiol Zool* 60:524–537.
- Lutz FE, 1929. Observations on leaf-cutting ants. *Am Mus Nov* 388:1–21.
- McArdle BH, 1988. The structural relationship: regression in biology. *Can J Zool* 66:2329–2339.
- McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS, 1994. La Selva: ecology and natural history of a neotropical rain forest. Chicago: University of Chicago Press.
- Nielsen MG, Jensen TF, Holm-Jensen I, 1982. Effect of load carriage on the respiratory metabolism of running worker ants of *Camponotus herculeanus* (Formicidae). *Oikos* 39:137–139.
- Roces F, Hölldobler B, 1994. Leaf density and a trade-off between load-size selection and recruitment behavior in the ant *Atta cephalotes*. *Oecologia* 97:1–8.
- Roces F, Núñez JA, 1993. Information about food quality influences load-size selection in recruited leaf-cutting ants. *Anim Behav* 45:135–143.
- Rudolph SG, Loudon C, 1986. Load size selection by foraging leaf-cutter ants *Atta cephalotes*. *Ecol Entomol* 11:401–410.
- Schmid-Hempel P, Kacelnik A, Houston AI, 1985. Honeybees maximize efficiency by not filling their crop. *Behav Ecol Sociobiol* 17:61–66.
- Schmidt-Nielsen K, 1984. Scaling: why is animal size so important? Cambridge: Cambridge University Press.
- Shutler D, Mullie A, 1991. Size-related foraging behavior of the leaf cutting ant *Atta colombica*. *Can J Zool* 69:1530–1533.
- Taylor CR, Heglund NC, McMahon TA, Looney TR, 1980. Energetic cost of generating muscular force during running. *J Exp Biol* 86:9–18.
- Waller D, 1989. Size-related foraging in the leaf-cutting ant *Atta texana* (Buckley) (Formicidae: Attini). *Funct Ecol* 3:461–468.
- Weber NA, 1969. Ecological relations of three *Atta* species in Panama. *Ecology* 50:141–147.
- Weier JA, Feener DH, Lighton JRB, 1995. Inter-individual variation in energy cost of running and loading in the seed-harvester ant, *Pogonomyrmex maricopa*. *J Insect Physiol* 41:321–327.
- Wetterer JK, 1990. Load-size determination in the leaf-cutting ant, *Atta cephalotes*. *Behav Ecol* 1:95–101.
- Wetterer JK, 1991. Allometry and the geometry of leaf cutting in *Atta cephalotes*. *Behav Ecol Sociobiol* 29:347–351.
- Wetterer JK, 1994. Forager polymorphism, size-matching, and load delivery in the leaf-cutting ant, *Atta cephalotes*. *Ecol Entomol* 19:57–64.
- 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.
- Zani PA, Claussen DL, 1995. Effects of extrinsic load on locomotion in painted turtles (*Chrysemys picta*). *Copeia* 1995:735–738.