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Load size selection by foraging leaf-cutter ants (*Atta cephalotes*)

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ABSTRACT. 1. Velocity of load-carrying *Atta cephalotes* (L.) foragers increases with increasing ant size and decreasing load size.

2. Foragers are selective in the sizes of loads they carry, but heavier loads would apparently increase their rate of leaf transport to the nest (mg of leaf m s^{-1}).

3. Even for very thin leaves, leaf diameter is not correlated with ant body size despite the method of cutting (rotating around a fixed point on the leaf edge).

4. When cutting leaves of different densities, load mass is more closely matched to ant size than is load surface area. This implies that ants choose loads based on mass rather than surface area, and thus the several possible disadvantages associated with carrying loads of large surface area (e.g. increased disturbance by wind or rain) are unlikely explanations of why ants do not select larger loads.

5. The relationship beween forager size and load size is made more complex by further selectivity at the level of colony recruitment: larger ants recruit to higher-density (thicker) leaf types.

6. Gross leaf transport rate is not maximized by foraging *A.cephalotes*, but net rate of energy intake cannot be assumed to follow the same pattern. If costs/time (not measured) are constant with changing load size, then the net rate of energy intake is not maximized. An alternative hypothesis is that costs/time increase with larger loads, thereby decreasing net rate of gain for larger loads.

Key words. Ants. *Atta cephalotes,* Attini, Costa Rica, foraging behaviour, Formicidae, leaf-cutter ants, load carrying, optimal foraging, prey selection.

Introduction

Leaf-cutter ants (Formicidae: Attini) are abundant and conspicuous consumers of foliage in lowland tropical wet forests of the New World. They use the leaf material they cut to culture fungi which are harvested and fed to the developing brood and, to a lesser extent, the adult ants (Quinlan & Cherrett, 1979). Defoliation by leaf-cutters can be swift and extensive. Colonies may consist of up to several million

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workers (Wilson, 1971; Weber, 1972), with several thousand foragers cutting and carrying vegetation along any single trail. Foragers may spend from 20 min to 7 h per round-trip journey from the nest, and foraging trails 60 m long or more are frequently reported (Hodgson, 1955; Cherrett, 1968; Lewis *et al.*, 1974a; Hubbell *et al.*, 1980).

Foraging theory predicts that ants should select loads that maximize the net rate of resource delivery to the nest. Because the size of a leaf fragment chosen by an ant influences the ant's speed while carrying this fragment to the nest (Rissing, 1982; Traniello *et al.*, 1984), leaf size selection may represent a compromise between maximizing load size and speed. Brown *et al.* (1975) and Taylor (1978) have suggested that desert seed-harvesting ants (*Pogonomyrmex* spp.) select intermediate-sized seeds because larger seeds, though containing more energy, take disproportionately longer to transport to the nest.

Previous work on the foraging behaviour of leaf-cutters has addressed the problem of tree species selection (Cherrett, 1972a, b; Rockwood, 1976; Stradling, 1978; Rockwood & Glander, 1979) and the spatial distribution of foraging effort around the colony (Rockwood, 1976; Shepherd, 1982). In this study we focus on the sizes of loads carried by *Atta* workers and test the hypothesis that foragers select leaf fragments that maximize the rate at which leaf biomass is delivered to the nest. After determining the velocities of ants carrying loads they cut naturally, we experimentally altered load sizes to examine the effects of increased or decreased loading on individual foragers' velocities and leaf transport rates.

Wilson (1980a, b) analysed the ergonomics of *Atta* polyethism, asking what size distribution of workers should be produced to best carry out the various tasks of the colony. In contrast, we ask how a particular group (foragers) should behave, given their observed size distribution.

Atta cephalotes (L.) is particularly suited for studying load size selection because in this species individuals exploiting established leaf sources normally cut the leaf fragment they subsequently carry (Hubbell *et al.*, 1980). In contrast, *A.sexdens*, and *A.cephalotes* exploiting new sources, may employ a multi-stage harvesting method where cut leaves or fragments are deposited on trails for other workers to transport (Fowler & Robinson, 1979; Hubbell *et al.*, 1980).

Upon delivery to the nest, leaf fragments are passed on to a series of ever smaller workers who cut them into smaller fragments in 'assembly-line' fashion and process them for eventual insertion into the fungus garden (Wilson, 1980a). A fragment's size should have little effect on the processing effort required per unit mass. Thus in *A.cephalotes*: (1) the resource is available for packaging into loads of any size; (2) most individual foragers directly select the loads they carry; and (3) load size probably has little effect on any aspect of leaf-processing beyond the carrying stage.

The indirect use made of leaf resources by *Atta* precludes a direct measurement of the value of these resources to the colony in energetic or other common units. Our assumption has been that more leaf biomass provides greater value, and we have used leaf transport rates (mass·velocity) to measure resource gain.

Methods

This study is based on observations of four colonies of *Atta cephalotes* in Costa Rica during July and August 1982. Three of the colonies were located at the La Selva Field Station, Provincia Heredia, and one was at Sirena, Parque Nacional Corcovado, Provincia Puntarenas. A few additional observations were made on a colony of *Acromyrmex octospinosus* (Reich) at La Selva.

The ants foraged diurnally at La Selva in July and at Corcovado in August, but changed to nocturnal foraging in August at La Selva. Temporal switches from daytime to nocturnal foraging are apparently common among attines (Lewis *et al.*, 1974a, b; Rockwood, 1975).

Load manipulation experiments

To determine the effects of load size on ant velocity and leaf transport rate (mg of leaf m s^{-1}), we measured velocities of 276 ants (171 at one La Selva colony and 105 at Corcovado) over two 1 m portions of the same trail. At each site we selected a straight section of established trail (as evidenced by steady ant traffic) 2.4 m long. Two 1 m runs were separated by a 0.4 m zone where manipulations of load size were performed. At La Selva the experimental trail section was along the top of a concrete wall that sloped gently upward towards the nest 5 m away. At Corcovado the experimental trail section was on horizontal ground, more than 20 m from the nest.

Three types of load manipulations were performed. We decreased or increased ants' loads by grasping the leaf with forceps and cutting off a portion of the leaf or adding a small (16–64 mm^2) piece of tape (Shamrock Speciality Labeling Tape) to the leaf, respectively. Ants in the control-manipulated group we lifted off the ground for 3 s by grasping their leaf with forceps, to imitate the treatment received by the other two groups. We timed each ant as it traversed the two 1 m trail sections, and recorded the number of riders on each carrier's leaf at 0.1 m intervals. Riders are smaller workers that perch on the leaves carried by foragers, and are thought to defend the foragers from attack by parasitic phorid flies (Eibl-Eibesfeldt & Eibl-Eibesfeldt, 1967). At the end of the second 1 m run, we collected each forager with its load including tape, riders, and fragments cut off for decreased-load manipulations. These items were stored fresh in closed vials until they could be weighed and measured (within 24 h) to determine pre- and post-manipulation load sizes. To control for changes in temperature and other environmental variables, treatments were alternated so that the category of treatment changed after every ten ants. Air temperature varied no more than 5°C over the course of each experiment.

We used data from the first metre (before manipulations were performed) to determine the relationships between ant size, load size, and ant velocity for ants carrying unaltered loads. Data from the second metre were used to determine the effect of a given change in load size on velocity and leaf transport rate (mg of leaf m s^{-1}). Implicit in this comparison is the assumption that any adjustment of ant velocity occurred within the 0.4 m manipulation zone, so that velocities measured for the second metre were representative of the rest of the nestward trip. We will return to this assumption in later discussion.

Measurement

Ant head widths were measured with an ocular micrometer as the maximal width of the head when viewed dorsally (Wilson, 1980a, b). The precision of these measurements is ±0.025 mm (range of repeated measurements of a single ant head). Wet weights of ants and leaf fragments were determined using a Mettler balance, which was recalibrated after every five measurements. Average calibration error was 0.2 mg.

Leaf areas were estimated by tracing the fresh leaf fragment on to paper, and using a planimeter to trace the image. The precision of this method, as estimated by repeated tracing and measuring, is ±7.1% (coefficient of variation) within the range of leaf sizes measured.

We weighed forty-seven ants individually to obtain an expression relating ant mass (M_a) in mg to head width (H) in mm. The resulting equation,

$$M_a=1.27\ H^{2.57}\ (r^2=0.96)$$

was used throughout the study to estimate ant masses from head width measurements.

Results

Load sizes

For three collections of 143–168 ants each, head widths (H) ranged from 1.2 to 3.4 mm (median 1.9 mm) and load masses (M_l) ranged from 2 to 77 mg (median 14 mg). Larger ants carried larger loads ($r^2=0.12$–0.39, $P<0.0001$ for regression of M_l on H, for the three collections separately). Pooling these collections ($n=461$) yielded the relationship

$$M_l=21.0\mathrm{H}-21.3\ (r^2=0.33,\ P<0.0001).$$

Since the majority of *A.cephalotes* workers cut the loads they carry, this result implies that ants cut loads adjusted to their body size. Correlations between load size and carrier size have also been reported by Wilson (1980a) for *A. sexdens* workers transporting pupae ($r^2=0.16$, calculated from Wilson's Fig. 15a), and by Davidson (1978) for desert seed-harvesting ants (*Veromessor pergandei*) ($r^2=0.08$–0.27). In each of these cases, correlations of load size with ant size are highly significant, but explain only a portion of the variance in load size.

To confirm that loads are generally retained by the ants that cut them, we watched twenty-five ants from the point of cutting until they had travelled 2 m or given up their leaf fragment to another worker. Transfer activity is greater near

TABLE 1. Velocity (V) is positively correlated with ant size (head width, H) for loaded and unloaded ants on paths. Table gives coefficients for the equation $V=a+bH$, where V is in m 10^{-2} s^{-1} and H is in m 10^{-3}.

Group	a	b	r^2	P	N
Unloaded ants, La Selva	1.12	1.40	0.35	0.0019	25
Loaded ants, La Selva	−0.38	1.67	0.37	0.0001	167
Loaded ants, Corcovado	0.02	1.12	0.42	0.0001	105

the cutting site than elsewhere on the trail because obstacles and stalled ants are commoner and many unladen workers mill about the cutting site, contacting and grasping the leaves of stalled carriers. Despite this, eighteen (72%) of the carriers we watched retained their leaves at the end of the 2 m observation zone.

In the few instances where we did observe loads being transferred to other ants, these transfers tended to support the idea that load size is somehow matched to ant size. During our load-manipulation experiments, fourteen ants carrying leaves toward the nest were observed passing their loads to ants approaching from the nest, within 1 m after load manipulation. After transfer, both ants reversed direction. The relative sizes of the two ants almost always corresponded to the change in load size; that is, three of four increased loads were transferred to larger ants, and eight of eight decreased loads were transferred to smaller ants (multinomial exact $P=0.00027$). Only two transfers of control-manipulated loads were observed: both were to larger ants.

Velocity

Larger ants walk faster than smaller ants, whether they are carrying leaves or not, as seen by the significant positive relationship between ant size and velocity (Table 1). Carrying a leaf fragment slows an ant down. Together, ant mass and leaf mass explain approximately half of the variance in ant velocity under constant conditions on a particular trail (multiple regression, $r^2=0.45$ for La Selva, $r^2=0.51$ for Corcovado). Riders can add significantly to the load. At La Selva 42% of loads carried riders, and rider mass averaged 15% of the mass of the carried leaf. 47% of loads at Corcovado had riders, and rider mass averaged 8% of leaf mass. Using total load (M_{l+r}=mass of leaf+riders) rather than leaf mass alone, multiple regression of velocity (V) as a function of load and head width yields slightly higher correlation coefficients and the following equations:

$$V=2.16H-0.05M_{l+r}-0.58 \quad \text{(La Selva, } r^2=0.47\text{)}$$

$$V=1.68H-0.05M_{l+r}+0.25 \quad \text{(Corcovado, } r^2=0.58\text{)}$$

where V is in m 10^{-2} s^{-1}, H is in m 10^{-3}, and M_{l+r} is in mg.

Load manipulation experiments

In our load manipulation experiments, 96% of ants with decreased loads responded by running faster, and 82% of those with increased loads slowed down. The percentage change in velocity for these ants is negatively correlated with percentage change in total load (Fig. 1, Spearman correlation, $r_s^2=0.58$, $P<0.0001$ for La Selva, $r_s^2=0.52$, $P<0.0001$ for Corcovado), but the slope of this relationship is shallower than −1,

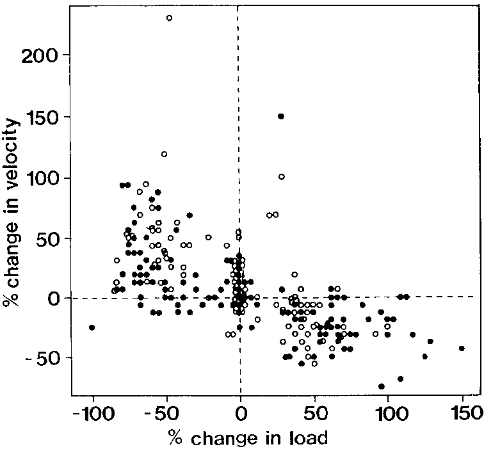

FIG. 1. Changes in velocity reflect changes in load. Each point represents the change in velocity of one ant after experimental increase, decrease, or dummy-manipulation of the load it carried (closed circles=La Selva site, open circles=Corcovado site).

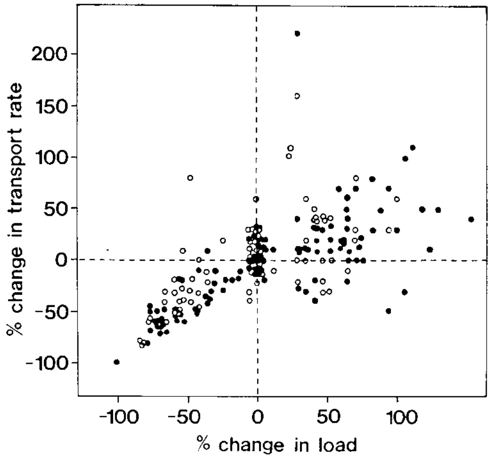

FIG. 2. Total biomass transport rate (mg of load m s^{-1}) increases when loads are experimentally increased, despite the partially compensatory adjustment of velocity to load size (Fig. 1). Each point represents one ant (closed circles=La Selva site, open circles=Corcovado site).

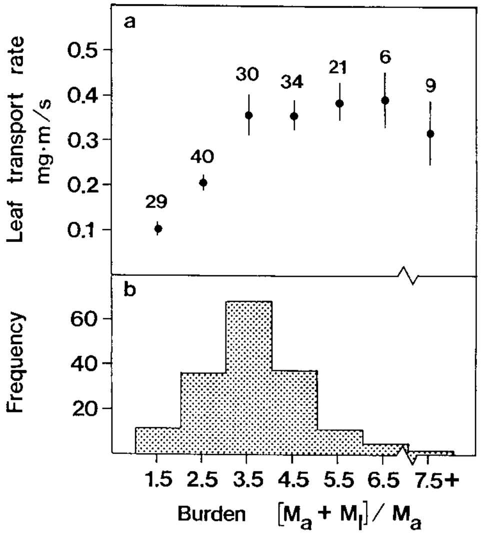

FIG. 3. Gross leaf transport rates achieved for different burden sizes (a), and frequency with which those burden sizes were selected by the ants (b). Burden is calculated as (ant mass+leaf mass)/ant mass. Sample sizes for leaf transport rate measurements are shown above standard error bars. Frequencies (b) are for loads selected naturally by the ants.

indicating that an increase in load size does not lead to a proportionate decrease in velocity. Thus ants could have increased gross leaf transport rate by carrying larger loads (Fig. 2).

Although leaf transport rates increase with load size over the range of our manipulations, ants clearly cannot carry loads of infinite size. Eventually workers will be slowed enough that leaf transport rate will level off and then begin to decline. What is the load size that produces this maximal leaf transport rate? Since we already know that load size is correlated with ant size, it is most appropriate to express load size here in relative terms, as a multiple of the ant's body mass. We therefore computed an ant's burden (B) as

$$B=(M_a+M_l)/M_a.$$

This measure has been used previously in studies of the effects of loading on velocity in seed-harvesting ants (Rissing, 1982) and mammals (Taylor *et al.*, 1980). For the La Selva observations, burden did give a measure of load size that was independent of ant size ($r=0.046$), although in some of our other collections a weak but significant correlation persisted. In this analysis we consider only the La Selva observations. We manipulated ants' burdens to increase sample sizes (and thus the precision of our estimates of leaf transport rates) for the largest and smallest burden size classes. We report the results for the manipulated loads; however, a similar pattern is seen for antiselected loads.

Leaf transport rate is maximized between burdens of 3.5 and 6.5, and may begin to decline for burdens above this size (Fig. 3a). Despite the breadth of this plateau, the mode of the frequency distribution of burdens selected occurs at the lower bound of this range (Fig. 3b), and a significant fraction (28%) of ants selected smaller loads giving lower transport rates. Thus, although decreasing leaf transport rate would eventually make larger loads unprofitable, other factors apparently cause ants to select loads that are correlated with ant size, but are in a size range well below the point where loads become too heavy to be transported profitably.

Loads smaller than those which maximize gross leaf transport rate might be selected for several reasons: (1) loads are selected on the basis of leaf area rather than leaf mass, because loads of large surface area pose manoeuverability problems independent of their mass; (2) the method of cutting imposes a ceiling on the fragment size that can be cut; (3) load size selection is related to the maximum mass that can be successfully held and manoeuvred into carrying position at the time of cutting, rather than the maximum mass that can be carried once lifted into position; (4) the energetic cost of transport rises faster than gross leaf transport rate with increasing load size, making net gain maximal at intermediate load sizes.

In the following sections we describe experiments designed to test the first three of these alternatives.

Leaf area v. leaf mass

Leaf fragments with larger areas might be 'discriminated against' by a number of physical factors: overhanging vegetation might selectively obstruct the passage of large loads; rains might force the abandonment of large fragments sooner, as their weight is increased by wetting or their large wet surfaces adhere together or to other objects. Finally, winds might slow or overturn workers in proportion to the surface areas of their loads.

A general test of the ants' tendency to select leaves by area *v.* mass was performed at La Selva. On a forking trail, ants travelling the two forks were cutting leaves of widely differing densities at equal distances from the nest. On one fork ants carried thin leaves cut from the herbaceous layer (density=159 g/m^2, standard error 3, $n=71$), while on the other fork ants were cutting an epiphyte (*Souroubea gilgii*) with density 575 g/m^2 (standard error 11, $n=72$). We collected seventy-two ants from each fork and measured ant size (H), leaf mass, and leaf area.

Ants were larger ($t=8.37$, $P<0.001$) on the fork with denser leaves, confirming observations by Cherrett (1972a) that ants carrying leaf fragments were larger than those carrying less dense flower fragments. Wilson (1980b) similarly found that 'harder' vegetation was cut by larger ants. When this difference in forager size is controlled for, our forking trail provides a 'natural experiment' for testing whether ants of a given size tend to select loads of similar mass or area.

Analyses of covariance using ant size as a covariate and leaf mass or area as the dependent variable showed that both measures were affected by differences in leaf density: for ants of a given size fragments cut from thick leaves were both smaller ($P<0.001$) and heavier ($P<0.001$) than those cut from thin leaves. When ants from both forks are considered together, ant size is more strongly correlated with leaf mass ($r^2=0.388$, $n=143$, $P=0.001$) than leaf area ($r^2=0.022$, $n=143$, $P=0.039$). Taken together, these analyses suggest that the foraging group responds to leaf density by adjusting the sizes of workers recruiting to different food sources, with the overall result that ant size is more strongly correlated with load mass than with area. An analysis of the combined data from all ants and loads measured at both sites throughout the study shows this result clearly: overall, ant size explains 30% of the variance in load mass ($n=671$), but only 11% of the variance in leaf area ($n=601$).

Does cutting method determine load size?

Leaf-cutters position themselves with the rear legs at the leaf edge and cut in an arc to detach a leaf fragment, thus the width of the fragment might be determined directly by the ant's body length. This causal relationship was suggested by Weber (1972), but has not been investigated quantitatively despite subsequent mention in the literature (e.g. Gamboa, 1975). It predicts that ant size should be correlated with the radius of the leaf fragment cut, measured at the point around which the ant pivoted while cutting (Fig. 4a). For many of the leaf fragments we collected, we were able to reconstruct the ant's position by finding the longest continuously cut arc and taking the position of the ant's rear feet as the midpoint of the opposite side (Fig. 4b). For 194 leaf radii measured in this way from all ants over the entire study, we found a very weak correlation between carrier size and leaf radius ($r^2=0.124$). However, we know (see previous section) that denser leaves are usually carried in smaller pieces, and ants might not be reaching to their full extent in cutting these leaves. Body length is most likely to limit load size for the least dense leaf types. We repeated our analysis with the leaf collection of lowest density (137 g/m^2, standard error=3, $n=13$) and found that even in this case carrier size was a very poor predictor of leaf radius ($r^2=0.001$).

Finally, it might be argued that later transfer of cut fragments from one ant to another destroys any initial correlation between ant size and fragment radius. Analysis of three data sets

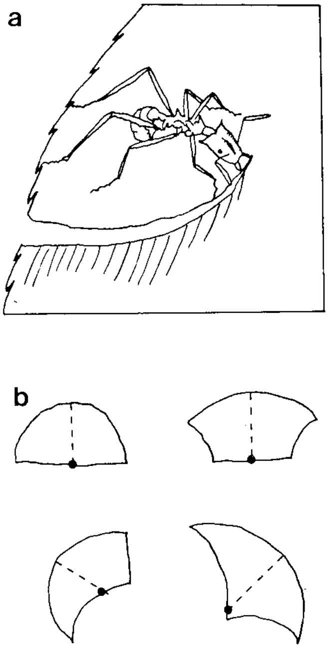

FIG. 4. Method of cutting employed by leaf-cutters (a), and method by which we inferred the position of the cutter for measurement of fragment radii (b).

in which ants were collected immediately after severing the leaf fragment from the leaf also led to low correlations (r^2=0.002, n=7 *Atta cephalotes* cutting *Souroubea gilgii*; r^2=0.380, n=15 *A.cephalotes* cutting *Theobroma cacao*; r^2=0.021, n=14 *Acromyrmex octospinosus* cutting an unidentified plant intermediate in density between *S.gilgii* and the thinner *T.cacao*). Only in the case of *T.cacao* did ant size explain a substantial proportion of the variance in leaf radius. Clearly, leaf load size is not determined by any mechanism so simple as the ant's body length when extended in cutting.

Manoeuvring the load into carrying position

Leaf-cutters carry their loads held vertically overhead, in a balanced position. While heavier loads can be carried, it is possible that they could not be manoeuvered into the carrying position initially, or that they are more likely to be dropped at the critical point when the load has just been severed from the leaf. To examine the effect of load mass on manoeuverability, we added pieces of tape within the margins of leaf fragments being cut by ants, just before the last connection to the plant was severed. This resulted in ants lifting loads of greater mass but the same area and shape as they had chosen to cut. We compared the time required to lift these loads, and the frequency of leaf-dropping, with unmanipulated loads cut from the same leaf.

These observations were made on a heterogeneous group of ants: twenty were *Atta cephalotes* cutting *Theobroma cacao,* six were *A.cephalotes* cutting *Souroubea gilgii,* and sixteen were *Acromyrmex octospinosus* cutting an unidentified plant of intermediate density. We combined these groups for analysis because all leaf fragments were of the dimensions chosen by the ants, and control and taped fragments were in equal proportions in each group.

The time required to manoeuvre a leaf into position for carrying was increased by only 9 s by the addition of tape (M_d unmanipulated=19.5 s, M_d increased load=28.5 s, P=0.007, one-tailed Mann-Whitney test). This small increase in time is probably trivial when compared with variations in the time required to traverse $\geq$60 m of trail. For instance, the average difference in time to run the first and second metres for ants with unaltered loads in the load manipulation experiments was 5 s (La Selva, n=75).

Very few leaves were dropped once they had been cut, and no difference in dropping frequency between unmanipulated and increased loads could be detected: two of twenty-four unmanipulated loads and two of twenty-two increased loads were dropped.

Discussion

This study investigated the interplay of three factors (ant size, load size and velocity) in determining leaf transport rates in *A.cephalotes*. Both ant size and load size affect velocity. Our findings agree with Lutz's (1929) report that velocity is positively correlated with body size in *Atta* and contrast with Wilson's (1980b) data and Hill's (1950) static scaling model which predicts that velocity should be independent of size. Within-species size–velocity correlations have been reported for one other ant (*Veromessor pergandei*: Rissing, 1982), and for an amphibian (*Bufo boreas*; Huey, 1980) and a reptile (*Stellio stellio*; Huey & Hertz, 1982).

The apparently compensatory changes in

velocity observed when we increased or decreased ants' loads suggest that ants 'trade off' load size and velocity. A simple optimal foraging model would predict that ants should choose loads that maximize the product of these two factors, leaf transport rate. Lutz (1929), in observations on load-carrying in unmanipulated *A.cephalotes,* found that leaf transport rate peaked at intermediate burden sizes. Although his presentation of means without variances or sample sizes does not allow evaluation of the significance of this trend, his findings do suggest that some sort of optimal load size selection might be expected in *A.cephalotes*. Our load-manipulation experiments allowed us to confirm that gross leaf transport rate shows a broad plateau between burdens of 3.5 and 6.5 (i.e. loads 2.5–5.5 times the carrier's body mass), a range that encompasses the maximum found by Lutz (1929).

However, we have shown that 28% of ants select loads below the range that would yield maximal gross leaf transport rates (Fig. 3), and that after manipulation, 75% of increased loads yielded greater transport rates (Fig. 1). No obvious physical constraint associated with leaf area or cutting method prevents them from selecting larger loads. Neither the difficulty of manoeuvring heavy loads into carrying position nor the risk of dropping a heavier newly-cut leaf poses a limit to load size.

We did not examine the effects of wind on leaf fragments of different sizes. Wind speeds are normally quite low on the forest floor where our experiments were conducted. However, winds could be important in the canopy where ants cut leaves. Weber (1972, p. 81) reports one instance in which an 'intermittent breeze . . . caused the ants with the larger loads to be momentarily stopped, and in one case an ant was blown over'. If common, this effect could potentially cause ants to limit the areas of their loads.

Rain is an unlikely determinant of leaf size selection because most fragments are dropped during rain. We frequently observed a total cessation of all trail traffic during rainy periods, and other authors have also reported mass leaf-dropping during rains (Hodgson, 1955; Lewis *et al.,* 1974a, b). Large piles of discarded and browning leaves are common sights along *Atta* trails.

Our experiments have established size selectivity, both by individual cutters and carriers and by recruitment of different-sized foragers to resources of differing densities. We are left with the question: why don't ants select larger loads?

Our initial prediction that leaf choice would correspond to loads that maximize gross leaf transport rate was based on the observation that ants apparently traded off load mass for velocity. If power output remained constant, this would cause net and gross energy intake rates to follow parallel curves (Fig. 5a), so that optimal behaviour could be predicted without direct measurement of absolute costs. This rests on the assumption of direct trade-offs between load and velocity. However, if ants varied velocity depending on behavioural modes or 'goals', the assumption of constant costs would be invalid. For instance, Rissing (1982) found that unloaded granivorous ants (*Veromessor pergandei*) travelling away from the nest moved more slowly than inbound, loaded ants. If ants with larger loads achieve high speeds and high gross leaf transport rates at the expense of markedly higher energetic costs of transport, then the larger loads produced by our manipulations might actually yield lower net rate of gain to the colony when carried at the speeds we measured (Fig. 5b).

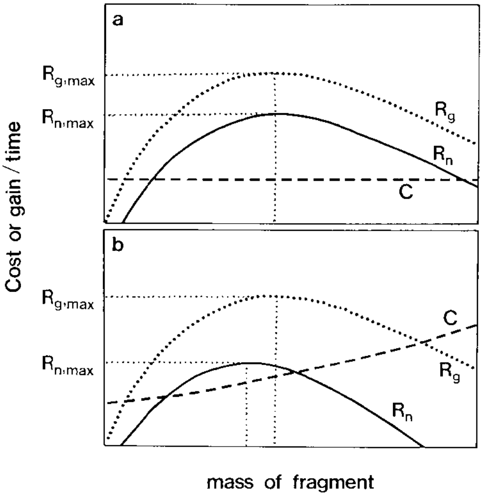

FIG. 5. Relationship between gross leaf transport rate (R_g), cost/time of transport (C), and net rate of energy uptake (R_n). (a) When cost/time is constant (constant power output), maxima for gross and net rates of gain coincide. (b) If cost/time increases with fragment mass, net rate of gain will be maximized by smaller loads than those which maximize gross leaf transport rate.

We measured velocities of ants for only 1 m after load manipulation. If ants with increased loads walked slower later on, then the gross leaf transport rates we calculated would be overestimates for these larger loads. Although we cannot entirely dismiss this possibility, the close correspondence of leaf transport rates for ant-selected and manipulated loads of similar sizes suggests that adjustment occurs quickly enough to be reflected in our measurements.

Finally, our measurements of leaf transport rate deal with single foraging trips and assume that the time spend in rest or other activities following each trip is independent of load size. If a longer 'recovery period' was required following a trip with a heavy load it would have the same effect as higher energetic costs of transport, lowering net gain to the colony for large loads. In this vein, Schmid-Hempel *et al.* (1985) found that honeybees (*Apis mellifera*) frequently returned to the hive with only partly filled crops, and showed that loading in honeybees conformed to a rule which maximized efficiency rather than net gain. They argued that workers are constrained by a fixed amount of flight 'performance' rather than a fixed lifespan, and that this limit on the calories available for foraging activity results in the bees choosing smaller, more efficient loads. In contrast to *Atta,* honeybees apparently did not increase travel time as their burdens increased.

It is clear that information on the metabolic costs associated with load-carrying in ants would greatly facilitate our efforts to understand leaf size selection in this species. In fact, the literature on energetics of load-carrying in general has been extremely limited until recently. However, Taylor *et al.* (1980) report that energetic costs rise linearly with total mass (animal+load) in running mammals carrying loads of up to 27% of their own mass. Nielsen *et al.* (1982) also found that metabolic rate increased linearly with total mass in loaded ants (*Camponotus herculeanus*), up to loads of 1.4 times the ant's mass. Their ants were apparently run at constant speeds (regardless of load size). As yet, the interactive effects of load size and speed have not been studied in any ectotherm, and the linear relationship between load size and metabolic rate has not been confirmed for burdens as large as those carried by *Atta.*

Our results clearly demonstrate load size selection by *Atta cephalotes,* both at the individual forager level and in recruitment by the colony to different leaf sources. Load size in turn affects forager velocity and leaf transport rate, which is used as a measure of gross rate of gain while foraging. Gross leaf transport rates were not maximized during our experiments, leading to the prediction that cost/time must increase with load size if net leaf transport rates are maximized.

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