

# Effects of trail gradient on leaf tissue transport and load size selection in leaf-cutter ants

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Leaf-cutter ants in the genus *Atta* are frequent model organisms in studies of central-place foraging. Workers carry leaf fragments from the foraging site to the nest. Larger workers carry heavier loads, but it has been noted repeatedly that workers typically carry fragments lower in mass than appropriate to maximize leaf tissue transport. Here, we suggest and test a previously unconsidered explanation for this discrepancy. Previous calculations of rate-maximizing load sizes have been based on data from smooth, horizontal trails. However, foraging ants will in reality experience a variety of trail gradients, with implications for locomotion speeds of laden ants and consequently for rate-maximizing loads. In the field, we manipulated trail gradient for 389 laden *Atta cephalotes* workers and found that gradient had marked effects on leaf tissue transport rates, which were highest on downhill and horizontal gradients and considerably lower when ants carried loads uphill. In a captive colony where the whole length of the foraging trail was manipulated, ants apparently adjusted their loading ratios in response to gradient, carrying smaller loads relative to their mass on uphill gradients. Significantly higher loading ratios were recorded for ants carrying loads vertically downhill, perhaps because ants use gravity to reduce the energetic costs of carrying heavy loads. Our results suggest that optimal loads will differ markedly under differing trail conditions and that leaf-cutter ants show previously unsuspected plasticity in load size selection, allowing them to maintain foraging efficiency under a range of trail conditions. *Key words:* *Atta*, central-place foraging, gradient, leaf-cutting ants, loading, slope. [*Behav Ecol* 19:805–809 (2008)]

Central-place foraging theory suggests that individual organisms should act to maximize rates of resource delivery from a foraging site to a central location (Orians and Pearson 1979; Schoener 1979). Examples of central-place foragers include birds bringing resources to a nest (e.g., Kacelnik and Cuthill 1990), beavers collecting timber to build lodges (Basey et al. 1988), marine molluscs foraging from an intertidal resting site (e.g., Focardi and Chelazzi 1990), and humans exploiting natural fishery resources (e.g., Bird DW and Bird RLB 1997). Social insects such as bees (e.g., Schmid-Hempel et al. 1985; Kacelnik et al. 1986) and ants (e.g., Bailey and Polis 1987) also typically act as central-place foragers.

Leaf-cutter ants in the genus *Atta* (Formicidae: Attini) are ideal model organisms for studies of central-place foraging (Kacelnik 1993; Burd and Howard 2005a). Worker ants cut leaf fragments from plants growing up to 100 m from their nests and carry these in their jaws along clearly defined foraging trails to chambers deep within the nests, where they provide the medium for the growth of mutualistic fungi, the sole food source for the ants (Weber 1972). The selection of fragment size by individual *Atta* workers has been of particular interest to behavioral ecologists. Foraging workers vary markedly in size and consequently in their ability to carry different size loads (Lutz 1929; Rudolph and Loudon 1986; Burd 2000a, 2000b). If a worker carries a relatively heavy load, its walking speed is reduced. If a worker carries a smaller load, then it may cover the distance from the foraging site to the nest more rapidly, but the mass of leaf tissue transported will be smaller. In general, individual ants might be expected to select the mass of the fragments that they carry in a way that maximizes leaf tissue transport per unit time. Given information on ant walking speeds under different loading ratios, it is

possible to predict the loads that would maximize the net rate of resource delivery to the nest (e.g., Lopez 1987; Burd 2000a, 2000b, 2001).

Existing data suggest that, up to a point, heavier loads increase the total mass of leaf tissue transported to the nest per unit time (Rudolph and Loudon 1986). However, studies of load size selection in *Atta* have found that loads are typically smaller than would be predicted to maximize leaf tissue transport (Burd 2000a, 2001). For example, in *Atta cephalotes*, leaf tissue transport rate would be maximized if individual workers carried, on average, considerably larger loads than were observed; only 2–6% of workers were carrying loads that could be classified as rate maximizing (Burd 2001). The discrepancy between actual and optimal loads was particularly marked for workers in larger size categories (Burd 2001). Two main explanations have been put forward to explain this apparent anomaly in load size selection. First, by taking smaller fragments, workers may reduce congestion at the cutting site, allowing more ants to obtain fragments per unit of colony foraging time (Burd 1996, 2000a). Second, in eusocial insects, it might be expected that the foraging performance of colonies rather than individuals would be optimized, and behaviors that are apparently suboptimal at the individual level may in fact maximize colony-level efficiency (e.g., Rocés and Núñez 1993; Burd 1996; but see Burd 2000a). Recently, Burd and Howard (2005a) have shown for *Atta columbica* that leaf fragment size affects the speed at which leaf tissue is processed within the nest. Burd and Howard (2005b) modeled the complete sequence of tasks outside and within the nest and calculated that observed loads are broadly consistent with global optimization when foraging is interpreted in this broad sense.

Here, we suggest and test an additional explanation for the selection of smaller than expected loads by foraging leaf-cutting ants. Calculations of rate-maximizing loads in previous studies have universally used measurements collected for workers carrying fragments along smooth, horizontal sections of trail (Lutz 1929; Rudolph and Loudon 1986; Lighton et al. 1987; Rocés and Núñez 1993; Burd 1996, 2001). In reality,

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foraging trails of *Atta* (including trails used in previous studies to investigate load size selection) will have numerous uphill and downhill sections. Uphill and downhill load carriage is likely to have markedly different energetic consequences for load-carrying ants (Full and Tullis 1990; but see Lipp et al. 2005), and rate-maximizing load sizes under these conditions may be reduced if loads of differing sizes are favored at different trail gradients. Furthermore, if rate-maximizing load sizes vary with trail characteristics, selection may favor plasticity in load carrying behavior sensitive to these changes. We explored the effects of trail gradient on load size selection and leaf tissue transport rates in the leaf-cutter ant, *A. cephalotes* (L.), by manipulating trail gradient experimentally, both in the field and using a laboratory colony. We ask 1) whether mean leaf tissue transport differs at different trail gradients, 2) how the relationship between loading ratio and speed is affected by trail gradient, and 3) whether individual workers in the captive colony adjust load size in response to trail gradient. We discuss our results in the context of central-place foraging theory.

## MATERIALS AND METHODS

### Data collection

#### *Field manipulation of trail gradient*

To establish how trail gradient affects the speed and leaf transport rates achieved by laden ants, we exposed laden *A. cephalotes* worker ants to trails at a range of gradients at the La Selva Biological Station in northeastern Costa Rica (10°25'52"N, 84°00'12"W) during July and August 2006. We selected 8 large (>82 m<sup>2</sup>), well-established *A. cephalotes* colonies in the vicinity of the field station and drew approximately equal numbers of laden ants at random from each colony by selecting the first laden ant to walk past an arbitrarily selected point on the foraging trail. Workers with hitchhiking minima ants on their leaf fragments were not selected. Selected ants were lifted by their load using flat-nosed entomological tweezers and transferred to a 2 × 50-cm wooden runway marked with a 1-cm scale. After allowing the ant to settle for 30 s with the runway in a horizontal position, the runway was rotated to a preselected gradient. The time it took an ant to walk a particular distance along the upper surface of the runway was recorded to 0.1 s with a handheld stopwatch, along with the distance walked (to the nearest centimeter). Data for distances <5 cm were usually discarded unless the ant was moving sufficiently slowly to allow accurate timing. Eleven runway gradients were tested at intervals of 18°, ranging from 90° (ant walking vertically upward) through 0° (ants walking horizontally) to -90° (ants walking vertically downward). One measurement is analyzed per ant individual for a randomly selected gradient. We analyze data for 390 individual ants, with sample sizes ranging from 28 to 45 for each gradient. Data collection occurred between 0800 and 1800 h, and no data were collected during or 2 h subsequent to heavy rain. When measurements on an ant were completed, the ant and leaf fragment were placed in a 1-ml Eppendorf tube and returned to the laboratory. The wet masses of ants and leaf fragments were measured on a Scientech SA 80 analytical balance (readability and repeatability = 0.0001 g).

#### *Manipulation of trail gradient for a captive colony*

To investigate the response of ants to manipulation of the gradient of the entire foraging trail, a captive colony of *A. cephalotes* was established in a controlled temperature room, using stock originating in Trinidad. The colony consisted of approximately 1000 individual ants when obtained in April 2003. The colony was maintained at 25 °C and >75% relative humidity.

The nest chamber was linked to a foraging platform by a 1 m length of garden cane, roughened with coarse sandpaper. Depending on the treatment, the foraging platform was either lowered or raised relative to the nest platform, to generate a range of trail gradients. We tested ants at 5 trail gradients over a 3-week period in May 2003: -90° (vertical trail, foraging platform above nest), -45°, 0° (horizontal trail), +45°, and +90° (vertical trail, foraging platform below nest). Treatments were applied sequentially and in randomized order, with at least 2 discrete recording periods at each gradient. At least 12 h separated measurements at each gradient. Data collection began once a foraging trail was established to the food source (typically 1–3 h after any change in trail gradient). Foraging ants were supplied with an ad libitum supply of fresh privet (*Ligustrum vulgare*) shoots. The same plant was used throughout the experiment because varying quality food resources can result in altered foraging patterns (Cherrett 1972; Roces and Núñez 1993; Roces and Hölldobler 1994). Ants for observation were selected haphazardly as the first laden ant to move onto the bamboo trail once the observer was ready to begin data collection. Only a single ant was observed at any one time. Ants were timed (to the nearest 0.1 s) with a handheld stopwatch over the 1-m course, and then the ant and its leaf fragment were collected and the mass of each measured (to 0.1 mg) on a microbalance. Ants were not returned immediately to the colony as distressed ants were found to disrupt foraging, and so that individual ants could not be measured twice within a trial. We made no attempt to mark individual ants. When ants "collided" with workers moving in the opposite direction on the cane, the time delay (typically <0.5 s for each collision) was recorded and subtracted from the total time taken on the trail. Burd (2001) found that calculated rate-maximizing load sizes were similar, whether or not collisions were taken into account, and all results were qualitatively identical using unadjusted walking speeds or when ants that experienced 5 or more collisions were excluded from the analyses.

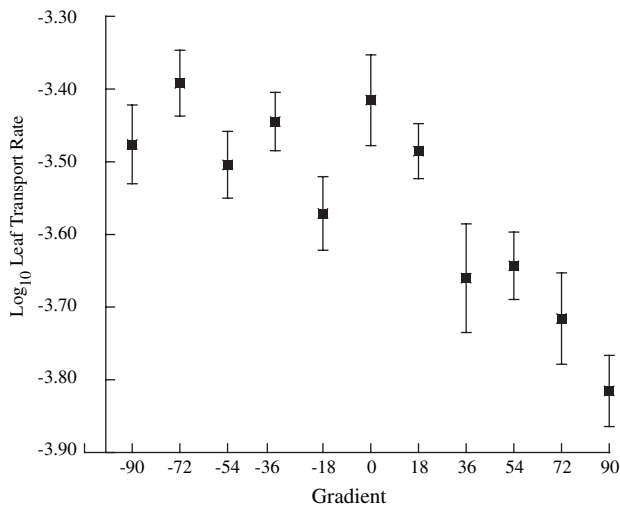
#### *Data analysis*

Following Rudolph and Loudon (1986), we use leaf transport rates (load mass × velocity) to measure resource gain and loading ratios ([ant mass + load mass]/ant mass) to quantify relative load size for individual ants. Loading ratios and tissue transport rates were compared among treatments using analysis of variance (ANOVA), with trail gradient as a categorical variable. We carried out model criticism (plots of residuals against fitted values and histograms of residuals) to ensure that our data met the normality and homogeneity of variance assumptions for parametric tests. All 3 response variables (leaf transport rate, ant mass, and loading ratio) were log<sub>10</sub> transformed to improve normality of residuals and homogeneity of variance. The interacting effects of log<sub>10</sub> loading ratio and gradient on log<sub>10</sub> ant speed (meter per second) were investigated further using analysis of covariance, with gradient again treated as a categorical variable. To check for potential confounding effects on foraging in the captive colony, we investigated whether the mean body size of workers (using ANOVA) and levels of traffic measured as the number of collisions per ant transit (using a Kruskal–Wallis test) differed under different gradient treatments.

## RESULTS

### Does trail gradient affect leaf transport rate?

For ants in the field, there were marked effects of gradient on leaf transport rate ( $F_{10,379} = 6.74$ ,  $P < 0.001$ ; Figure 1). Leaf tissue transport was highest on downhill and horizontal trails



**Figure 1**  
Effects of trail gradient on leaf tissue transport (grams per second) for workers from 8 natural colonies of *Atta cephalotes*. Error bars show standard errors of the mean. Sample sizes are as follows: 31 at  $-90^\circ$ , 37 at  $-72^\circ$ , 42 at  $-54^\circ$ , 37 at  $-36^\circ$ , 33 at  $-18^\circ$ , 33 at  $0^\circ$ , 40 at  $18^\circ$ , 28 at  $36^\circ$ , 45 at  $4^\circ$ , 32 at  $74^\circ$ , and 32 at  $90^\circ$ .

but declined sharply and progressively when ants carried loads uphill. For the captive colony, leaf tissue transport (grams per second) for individual ants also differed significantly among treatments ( $F_{4,150} = 16.76$ ,  $P < 0.001$ ) and was lowest on the 2 uphill gradients. However, for the captive colony, there was some evidence that leaf transport rate was lower on downhill gradients compared with a horizontal trail (Figure 2a).

#### How is the relationship between loading ratio and speed affected by trail gradient?

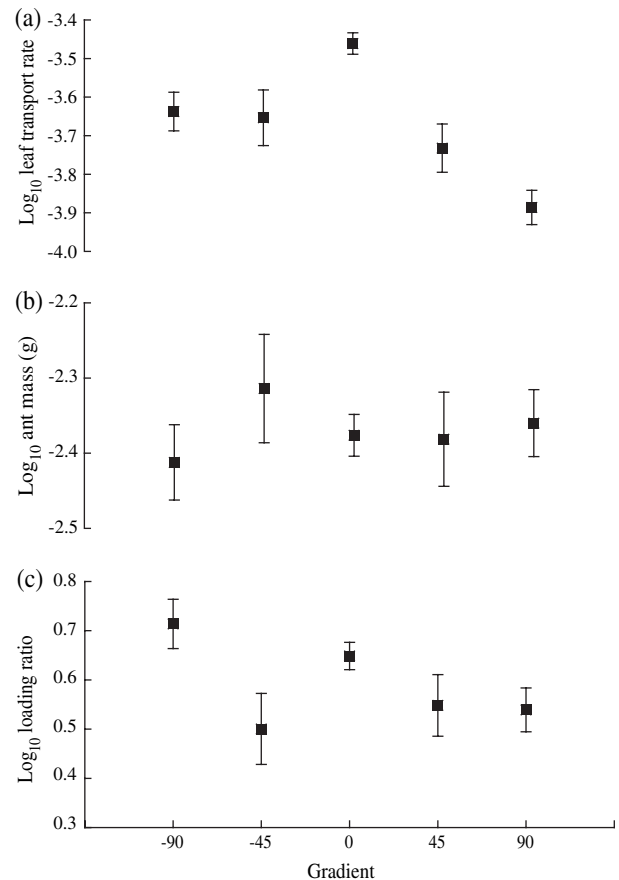
For ants measured in the field, walking speed declined with loading ratio ( $F_{1,368} = 86.97$ ,  $P < 0.001$ ), trail gradient had a significant effect on walking speed ( $F_{10,368} = 3.21$ ,  $P = 0.001$ ), and there was no significant gradient  $\times$  loading ratio interaction ( $F_{10,368} = 1.44$ ,  $P = 0.162$ ). Similarly, for the captive colony, walking speed decreased with loading ratio ( $F_{1,145} = 28.49$ ,  $P < 0.001$ ), trail gradient had a significant effect on speed ( $F_{4,145} = 4.69$ ,  $P < 0.001$ ), and there was no evidence that the slopes of the relationship between loading ratio and walking speed varied among gradient treatments ( $F_{4,145} = 1.77$ ,  $P = 0.138$ ).

#### Do individual workers adjust load size in response to trail gradient?

In the captive colony, gradient had a highly significant effect on loading ratio ( $F_{4,150} = 5.99$ ,  $P < 0.001$ ; Figure 2c). *Atta cephalotes* workers operate under the highest loading ratio when the foraging site is vertically above the nest. The next highest loading ratio is for horizontal foraging trails. The loading ratios for uphill gradients of  $+90^\circ$  and  $+45^\circ$  and for the downhill gradient  $-45^\circ$  are similar and lower.

#### Potential confounding variables

In the captive colony, the mean body mass of foraging ants was unaffected by gradient treatment ( $F_{4,150} = 1.06$ ,  $P = 0.378$ ; Figure 2b). The median number of collisions experienced by laden ants was 1. There was no significant effect of trail gradient on the number of collisions, which acts as a measure of



**Figure 2**  
Effects of trail gradient on (a) leaf tissue transport (grams per second), (b) forager mass (grams), and (c) loading ratio for a captive colony of *Atta cephalotes*. Error bars show standard errors of the mean. Sample sizes are as follows: 30 at  $-90^\circ$ , 15 at  $-45^\circ$ , 63 at  $0^\circ$ , 15 at  $45^\circ$ , and 32 at  $90^\circ$ .

trail congestion (Kruskal–Wallis test, adjusted for ties:  $H = 6.94$ ,  $df = 4$ ,  $P = 0.139$ ).

## DISCUSSION

Maximization of central-place foraging might be achieved by alterations in the mass of loads carried by individual workers. Previous studies have investigated load size selection in leaf-cutting ants in relation to travel distance, both in the field and in the laboratory, but have failed to find consistent relationships (e.g., Roces 1990; Wetterrer 1990; Burd 1995). To the best of our knowledge, this is the first study to investigate foraging efficiency and load size selection in relation to trail gradient.

We found that trail gradient had marked effects on *A. cephalotes* foraging (Figure 1). Leaf transport rates were reduced on uphill gradients because of lower walking speeds (Lipp et al. 2005). We made no attempt to calculate rate-maximizing loads (cf., Burd 2001) because we did not manipulate load sizes of individual workers. However, the marked differences in leaf tissue transport rates observed among gradients suggest that calculations of rate-maximizing loading ratios based on data collected solely from flat trail sections will be misleading. Because *Atta* species often forage in the canopy of trees (Wirth et al. 2003), downhill sections will represent a major element of many foraging trails. Furthermore, even if the foraging trail is largely along the ground, at the scale of an ant, even a nominally horizontal trail will comprise numerous uphill and downhill sections.

A novel result from our captive colony study is that *A. cephalotes* workers appear to alter their loading ratios according to gradient, with observed differences in loading ratios consistent with the apparent ease with which loads are transported over the different gradients. In general, smaller loads were carried on the gradients where ant walking speeds are lowest. Thus, on uphill gradients, there was a decrease in loading ratio of around 20% relative to a horizontal trail. Reduced walking speed at a given loading ratio is to be expected for ants carrying loads on uphill gradients, where they need to do extra work to overcome gravity (Taylor et al. 1972). Such responses may have an adaptive explanation if they result in enhanced leaf tissue transport rates under the prevailing trail conditions. We excluded the possibility that differences in trail congestion were responsible for the differences observed and also found no evidence for a colony-level response to trail gradient in terms of forager mass. This makes it unlikely that the observed differences in leaf tissue transport among treatments are a consequence of differences in ant mass. In the relatively young captive colony, there was little heterogeneity in worker mass, so the possibility that such effects occur in more established colonies cannot be excluded.

*Atta* ants are known to respond to gravitational cues (Vilela et al. 1987), and our results suggest that on vertical, downhill trails, they may be able to exploit gravity to reduce the energetic costs of carrying heavy loads, making higher loading ratios feasible. Experimental augmentation of load mass can cause laden workers descending vertical tree trunks to fall (Burd M, personal communication, July 2006), but there is no evidence for such an effect (which could potentially limit load size to a lower value than would be possible if loads were only carried horizontally) in our data set, perhaps because loads have been selected by individual ants rather than manipulated artificially. An apparent exception to the general pattern of higher loading ratios on level and downhill gradients occurred when ants carried loads at  $-45^\circ$ , when loading ratios were lower than on either a horizontal trail or a vertically downhill trail ( $-90^\circ$ ). Perhaps at  $-45^\circ$ , any beneficial effects of gravity are insufficient to counteract the negative effect of the turning moment generated around the ant's head by the weight of the leaf and the associated difficulty of maintaining traction on the trail surface. However, there is no indication from the analysis that the relationship between loading ratio and speed has a steeper slope on intermediate, downhill gradients.

Burd and Howard (2005a, 2005b) show that apparently sub-optimal loads in *A. columbica* can be explained if fragment processing within the nest is taken into account. We made no attempt to measure this component of the foraging process because we focused solely on aboveground foraging. However, our results and those of Burd and Howard (2005a, 2005b) are not necessarily mutually exclusive: both trail gradients and handling constraints could act together to limit optimal load sizes. *Atta* trail gradients in nature will be downhill on average (because foraging sites are above ground and the nest is underground), so based on our results we would predict *Atta* workers to carry larger (not smaller) loads than those calculated in previous optimum foraging studies. If this is the case, the processing costs identified by Burd and Howard (2005a, 2005b) might after all be the best explanation of the discrepancy between rate maximizing and actual loading ratios. However, the variance in gradients on a typical *Atta* foraging trail may be more critical than the mean gradient, and even nominally level trails will have numerous short uphill and downhill sections (e.g., where trails cross fallen trunks and branches). Thus, load size selection may be determined by these extreme gradients, rather than by the overall mean gradient. A final but perhaps unlikely possibility

is that different mechanisms limit load size selection in *A. cephalotes* and *A. columbica*.

Careful field experiments involving large colonies with a full range of worker sizes will be required to understand fully the importance of trail gradient in determining load size. In particular, it remains to be seen whether ants adjust their load size on "real" foraging trails where both uphill and downhill sections occur. Such experiments will be challenging because of the necessity to manipulate the gradient of all or at least a substantial proportion of the foraging trail. Precisely how ants "anticipate" trail gradients will also be of considerable interest and should be amenable to experimental investigation. For example, it is possible that selection of load sizes may be based on their experience of the outward journey or on a chemical cue provided by other workers.

Our results have implications for central-place foraging models in general. Environmental conditions that exert differing energetic costs on foragers between the foraging point and the central point, and which vary in both time and space, are likely to be the rule rather than the exception. Gradient effects, as considered here, are a particular example that will apply widely to terrestrial vertebrates and invertebrates (Taylor et al. 1972), and parallel situations may occur for aerial locomotion. For example, optimal foraging strategies of birds are likely to differ markedly under different wind vectors relative to potential foraging sites (Shamoun-Baranes and van Loon 2006). Such effects will inevitably complicate models of central-place foraging. Although few such models are used to generate specific quantitative predictions, researchers will need to consider whether models that neglect environmental factors such as the gradient, which foragers must traverse, will lead to altered conclusions. However, testing these effects using manipulative experiments of the kind we describe here will only be feasible for a restricted range of species.

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