Size-related foraging behaviour of the leaf-cutting ant *Atta colombica*

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In a Costa Rican forest adjacent to cattle pasture, larger individuals of the leaf-cutting ant *Atta colombica* carried heavier loads and foraged farther from the colony, as predicted by foraging theory. Counter to foraging theory, individual ants did not increase their load mass if they foraged farther from the colony. However, the colony avoided this apparent inefficiency by sending larger ants to more distant trees. The colony harvested simultaneously from several individuals of the same tree species, even though distant trees were twice as far from the colony as nearby trees. The reasons for this behaviour require further investigation. In a wide foraging trail, larger ants travelled faster than their smaller counterparts. In addition, ant velocity was reduced when loads were experimentally supplemented, and increased when loads were experimentally reduced. Ants using narrow trails in the leaf litter may all be constrained to travel at the same speed, irrespective of load or body size, simply because they get in each other's way.

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Dans une forêt du Costa Rica adjacente à un pâturage, ce sont les individus les plus gros de la fourmi découpeuse *Atta colombica* qui transportent les fardeaux les plus lourds et qui s'éloignent le plus de la colonie pour chercher leur nourriture; c'est d'ailleurs ce que laissait prévoir la théorie de la quête optimale. Contrairement à la théorie cependant, les fourmis ne transportent pas des fardeaux de masse plus grande lorsqu'elles s'éloignent davantage de la colonie. Cependant, la colonie compense l'inefficacité apparente de ce système en envoyant des individus de plus grande taille aux arbres les plus reculés. La colonie glane sa nourriture simultanément sur plusieurs arbres de la même espèce, même si les arbres reculés sont deux fois plus éloignés de la colonie que des arbres avoisinants. Les raisons de ce comportement nécessitent des recherches plus poussées. Le long d'un sentier large, les fourmis les plus grosses se déplacent plus rapidement que les individus plus petits. De plus, la vitesse de déplacement diminue lorsque les fardeaux sont rendus plus lourds expérimentalement et augmente lorsque les fardeaux sont rendus plus légers. Les fourmis qui utilisent des sentiers étroits dans la litière de feuilles peuvent être forcées de se déplacer toutes à la même vitesse, quelle que soit la masse de leur fardeau ou leur masse corporelle, simplement parce qu'elles s'entre-nuisent.

[Traduit par la rédaction]

Introduction

Feeding strategies, in their simplest form, involve maximizing intake per unit of energy expended (Pyke 1984). The rate of energy intake for an individual is often a function of its body size. In this paper, we report on relationships between foraging behaviour and body size in the leaf-cutting caste of the leaf-cutting ant *Atta colombica*.

Using data on the velocity and transport costs of seed-harvester ants, Lopez (1987) developed models to predict optimal foraging strategies for these insects. One of these models predicts that an ant's optimal load mass increases exponentially with its body size. Thus, the observation that larger seed-harvester (Davidson 1977a, 1977b, 1978a; Hansen 1978) and leaf-cutting ants (Oster and Wilson 1978: p. 257; Waller 1989; Wetterer 1990) carry heavier loads fits theoretical expectations.

Lopez's (1987) model also predicts that larger ants travel greater distances more efficiently than their smaller counterparts. Evidence that this relationship may affect foraging strategies comes from a study of three sympatric *Pogonomyrmex* seed-harvester ants, where the largest species foraged the farthest from its colony (Hansen 1978). At an intraspecific level, however, larger individuals of *Veromessor pergandei* seed-harvesters did not forage at greater distances than their smaller counterparts (Rissing and Pollock 1984). This prediction has not been tested within leaf cutters.

Greater travelling distances entail greater energetic costs; thus ants making longer foraging trips should carry back food of greater value (Orians and Pearson 1979; Kacelnik *et al.* 1986). Davidson (1978b) found that *Pogonomyrmex rugosus* seed-harvesters preferentially selected larger seeds the farther they foraged from the colony. However, if larger ants travel greater distances more efficiently than smaller ants (Lopez 1987), Davidson's (1978b) results may indicate that a greater percentage of large ants forage at more distant food sources, and not that ants increase their load masses at greater distances irrespective of body size. In contrast to Davidson (1978b), Rissing and Pollock (1984) found that ants spent more time sampling seeds at greater distances from the colony, but they did not choose larger seeds at greater distances. In leaf cutters, larger individuals of *Atta texana* carried larger seeds (Waller 1989), and larger *Atta cephalotes* individuals selected thicker leaves (Rudolph and Loudon 1986). However, the prediction that leaf cutters should cut larger leaves the farther they forage from the colony has not been tested.

The models of Rudolph and Loudon (1986) and Lopez (1987) predict that each size of ant has a single optimum load that maximizes its rate of return per unit effort. The first implication from these models is that larger ants have greater return per unit effort, either because of the larger loads they are able to carry (see above), or because of their greater speed. Larger *V. pergandei* (Rissing 1982) and *A. cephalotes* (Rudolph and Loudon 1986) are indeed able to travel faster. The second implication of these models is that small loads are not worth the invested time

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and energy, and large loads incur a penalty in speed. As partial evidence for this, Rudolph and Loudon (1986) found that *A. cephalotes* velocity was inversely related to load mass.

In this paper, we first report on relationships between ant size, load mass, and foraging distance for the leaf-cutting species *A. colombica*. We predicted that (*i*) larger ants would forage at greater distances from the colony, and (*ii*) independent of their size, ants would carry heavier leaf fragments the farther they foraged from the colony. Second, we tested for effects of ant size and load mass on travelling velocity. We predicted that (*iii*) larger ants would travel faster, (*iv*) ants with lightened loads would travel faster, and (*v*) ants with supplemented loads would travel slower.

Study area and methods

We conducted these experiments at an elevation just below the Monteverde cloud forest in Costa Rica on 22 February 1989 between 1100 and 1700. The ant colony was partly under the canopy of a forest and partly in a cattle pasture. The ants used in this study probably made up less than 1% of the leaf-cutting caste of this colony. Air temperatures ranged between 20 and 25°C during data collection. Statistical methods followed Steel and Torrie (1980).

Ant size, load mass, and foraging distance

By following ants from the colony, we found four trees from which ants were cutting and carrying leaf fragments. We concluded that all four trees were the same species after comparing their leaf, trunk, and seed morphology. To test if larger ants were carrying heavier loads, we captured burdened ants as they descended the trunks of the trees. While we were at a given tree, we used every burdened ant encountered. We measured the size of each ant with a micrometer (using head width as an index; Wilson 1980a), traced the outline of each ant's leaf fragment, and then released the ant. Because we were sampling leaves from the same species of tree on the same day in the same location, we assumed that leaf fragment size was a consistent index of leaf fragment mass and of leaf fragment nutritional value.

To test whether larger ants foraged farther from the colony, and whether ants selected heavier loads if they foraged farther from the colony, two groups were sampled: 100 ants (and their leaf fragments) were from two "nearby" trees that were 20 m from the colony, and 44 ants were from two "distant" trees that were 40 m from the colony. We could not tell how high in the trees individual ants had foraged. However, no tree was more than 15 m high. This eliminated the possibility that foraging height in the trees made foraging distances the same for both groups.

The areas of the traced leaf fragment outlines were obtained with a Laboratory Systems, Inc., Microplan II Computer (distributed by Nikon, Inc.). The computer also calculated a form function that varied between 0, for a straight line, and 1, for a perfect circle. The form function enabled us to control for the possibility that small ants carried linear leaves to reduce carrying effort in windy conditions, whereas larger ants carried circular leaves. That ants would do so was plausible because we observed that strong winds often made burdened ants stop walking (see also Weber 1972).

Ant velocity, ant size, and load mass

To test for the effects of ant size and load mass on travelling velocity, we measured the velocity of burdened ants as they walked along a 7-m log. All ants had their leaves marked with paint to facilitate following them. The paint did not add significantly to the leaf fragment mass. In the group with a lightened load (the "lightened" group, $N = 11$), the travel time with the initial load was recorded for the first half of the log, then the top of the leaf fragment was cut off and collected, and the ant was timed again for the remaining 3.5 m of the log. In the group with a supplemented load (the "supplemented" group, $N = 10$) a dab of glue was added to the initial leaf fragment at the half-way point along the log, and travel time was recorded similarly. The control group ($N = 10$) was simply timed over both halves of the log. Ants that reversed direction after painting or treatment were excluded from the analysis.
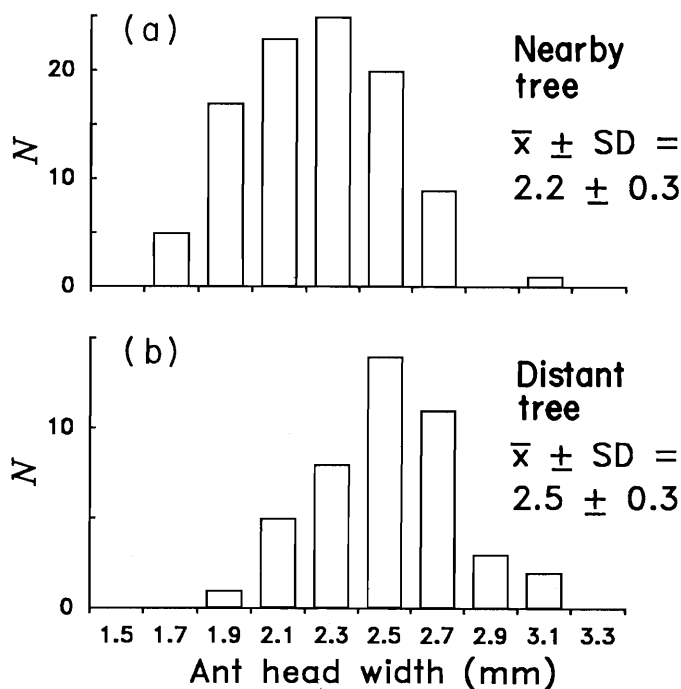

FIG. 1. The frequency distribution of ant sizes on (*a*) nearby and (*b*) distant trees ($t = -5.42$, $P < 0.001$).

At the end of the log, the size of each ant and the size (area) of its corresponding leaf fragment were recorded. The final load was expressed as a percentage of the initial load. For the lightened group, it was evaluated from the following equation: (area of remaining leaf fragment) / (area of cut piece + area of remaining leaf fragment). For the supplemented group, it was expressed as (mass of leaf fragment with dab of glue) / (mass of leaf fragment) − (average mass of glue dab). The average mass of a glue dab was estimated with a weigh scale and was about 30% of the mass of a 1-cm^2 leaf fragment.

Results

Ant size, load mass, and foraging distance

Larger ants carried heavier leaves ($r = 0.47$, $P < 0.001$). In addition, the average size of ants was greater on the trees most distant from the colony (Fig. 1). The leaf fragments that ants on distant trees carried (mean ± SD = 1.53 ± 0.5 cm^2) were larger than those from nearby trees (1.23 ± 0.4 cm^2; $t = -3.72$, $P < 0.001$). However, an analysis of covariance with ant size as the covariable indicated that ants did not select heavier loads when they foraged farther from the colony (Table 1), which is counter to what we predicted. In other words, the difference in load mass between distant and nearby trees was attributable to a greater percentage of large ants foraging on more distant trees.

We tested whether the difference in ant size between near and distant trees was the product of temperature and (or) diel effects (see Feener 1988; Wetterer 1990) by regressing ant size against order of capture. For the period in which we sampled, ant size did not change over time at any tree (Fig. 2, all |r| values < 0.20, all P values > 0.10). Furthermore, burdened ants' travel time from the base of the distant trees to the colony (35 min) was less than the total sampling time for the four trees (240 min). Thus, ants captured at nearby and distant trees could have left the colony at the same time. Thus, the patterns we obtained were consistent for the hours and temperatures in which we sampled.

Small ants did not carry leaf fragments that differed in form from those of large ants ($r = -0.11$, $P = 0.09$). Thus small ants were not cutting or carrying leaf fragments that minimized the
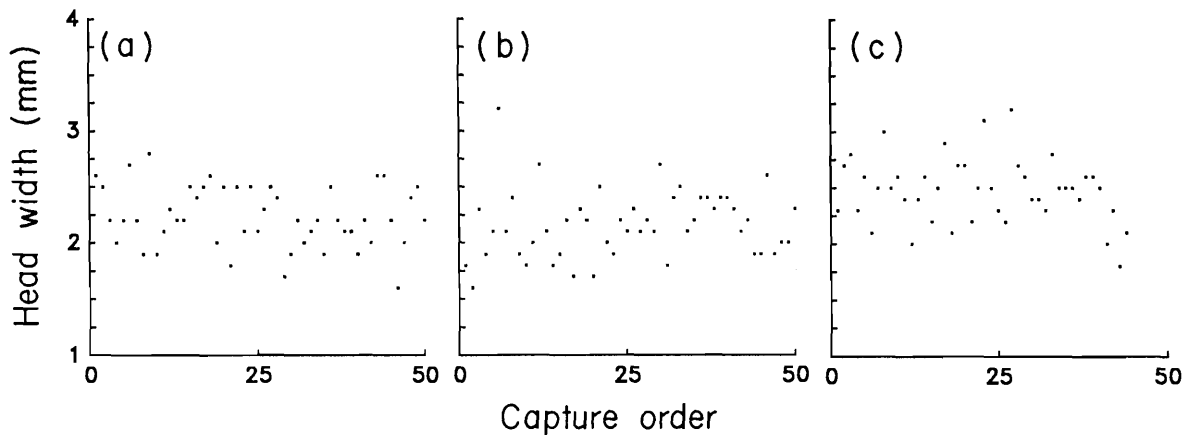
FIG. 2. The relationship between ant size relative to capture order on two nearby trees (*a*) and (*b*) and two distant trees (*c*). The distant trees are pooled.

TABLE 1. Analysis of covariance comparing leaf fragment sizes of ants foraging at nearby and distant trees, with ant size as the covariable

Source	Sum of squares	df	Mean square	F
Total	22.9	141	0.2	
Regression (head size on leaf fragment size)	4.4	1	4.4	26.9***
Nearby vs. distant	0.4	1	0.4	2.4 ns

NOTE: ***, significant at $P < 0.001$; ns, not significant.

effects of wind any more than large ants were. Nor were ants on distant trees carrying leaf fragments that differed in form from those carried from nearby trees ($t = -0.64$, $P = 0.53$).

Ant velocity, ant size, and load mass

Velocity for the first half of the log, head size, and leaf fragment mass did not differ between controls and experimental groups (two-tailed t-tests, all P values > 0.10). Neither the weight of the paint on ants' leaf fragments nor manipulation of the ants for the purpose of painting significantly affected velocity, because control ants travelled at the same speed on both halves of the log (Fig. 3, two-tailed paired t-test, $t = -1.09$, $P = 0.30$). Therefore, we assume that the effects of load manipulations were solely due to changes in load mass, and not to our interference.

Larger ants travelled faster ($N = 31$, $r = 0.50$, $P = 0.003$) as predicted. This relationship remained significant when we controlled for load mass by partial correlation ($r = 0.55$, $t = 4.42$, $P < 0.001$).

Eight of 11 ants increased their velocity when their loads were lightened (Fig. 3; one-tailed paired t-test, $t = -2.61$, $P = 0.01$). Velocity also increased as a function of the amount of leaf fragment removed ($r = -0.67$, $P = 0.01$). All of 10 ants travelled slower when their loads were supplemented (Fig. 3; one-tailed paired t-test, $t = 6.13$, $P < 0.001$). Together, these results indicate that velocity is inversely related to load mass.

Discussion

In leaf cutters, it has been suggested that an ant's body size determines the arc of its cut (Weber 1972). However, ant size explains only a small part of the variance in load mass (Rissing and Pollock 1984; Rudolph and Loudon 1986). Weather conditions, temporal factors, competition, etc. also contribute a large
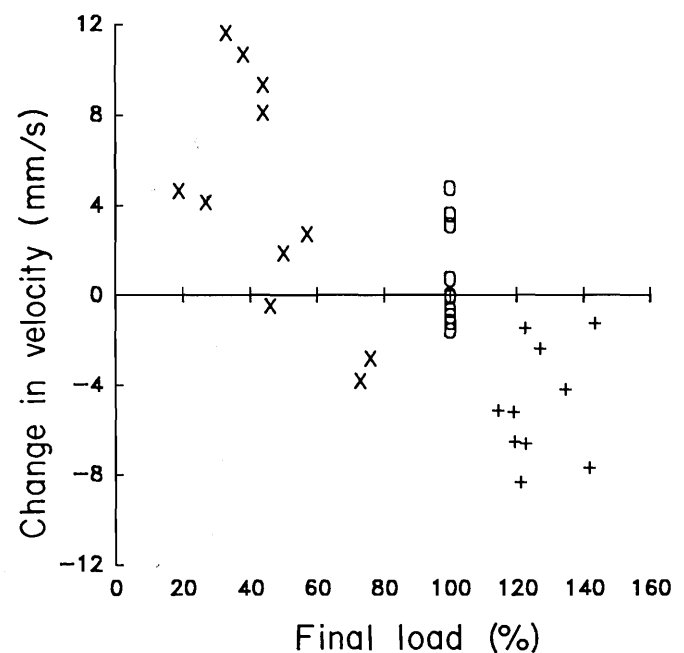

FIG. 3. The effect of changes in load size on ant velocity. The final load was expressed as a percentage of the load size before manipulation (initial load). ×, ants with lightened load; +, ants with supplemented load; 0, ants with unmanipulated load.

percentage of the variation in the relationship between ant size and load mass (Mehlhop and Scott 1983; Rissing 1982, 1988; Wetterer 1990).

Our results were obtained over a brief time interval. Nonetheless, our findings match theoretical expectations in many cases and suggest possibilities for further exploration. The finding that larger ants forage farther from the colony is consistent with one of the predictions from Lopez's (1987) model. The considerable overlap in ant sizes at nearby and distant trees (Fig. 1) indicates that the proximate mechanism regulating size-related recruitment in *A. colombica* colonies is not absolute. Waller (1989) found no evidence that size-specific trail pheromones or previous success (within 6 days) acted as proximate mechanisms regulating size-related recruitment in *A. texana*. Because the ants in our experiments were using food sources that lasted more than 6 days, it is still possible that previous feeding experience or simply distance may have influenced size-related recruitment for

A. colombica. As previously discussed, the evidence for larger seed harvesters foraging farther from their colonies is equivocal (Hansen 1978; Rissing and Pollock 1984).

Ants did not carry heavier loads when they foraged farther from the colony. This inefficiency in foraging is partially avoided in that larger ants are the individuals most likely to forage far from the colony. However, if a tree species is an appropriate food source, why spread the colony's effort over many individual trees? The fact that larger ants are found at more distant trees suggests that the colony tries to balance the return per unit effort from each tree it is using, because the larger ants collect heavier loads. An alternative hypothesis, according to which leaf cutters would use a conservational harvesting strategy, has not received empirical support (see Rockwood and Hubbell 1987). Clearly, more rigorous testing is required to determine how and why leaf cutters regulate their foraging columns.

Previous studies have also found that larger ants travel faster (Rissing 1982; Rudolph and Loudon 1986). However, Wilson (1980b) only found a weak relationship between ant size and velocity in *Atta sexdens*, which he suggested was an adaptation to maintain linear traffic flow along the congested columns of foraging ants. Wilson's results may differ because he measured velocity on a narrow foraging trail where large and small ants would interfere more with each other, preventing larger ants from travelling at maximum speed. We measured velocity along a log, and Rudolph and Loudon (1986) measured velocity on a concrete wall. In these latter situations, the ant column is much wider than we observed on the trails in the leaf litter in the surrounding forest, hence ants are less likely to interfere with each other.

Wilson's (1980b) hypothesis, according to which leaf cutters behave to maintain smooth traffic flow, predicts that load mass, within limits, will not affect ant velocity. However, *A. colombica*, and *A. cephalotes* (Rudolph and Loudon 1986) travelled at velocities inversely related to their load mass, as has also been reported for the seed harvester *V. pergandei* (Rissing 1982). This contrasts with *A. sexdens*, where velocities were only weakly related to load masses (Wilson 1980b). Because leaf cutters consistently cut similar load masses, Wilson's unmanipulated ants would not have exhibited the conspicuous decrease in velocity associated with above-normal load masses. For below-normal load masses this explanation cannot explain Wilson's results, as he also found little difference between the velocities of burdened and unburdened ants. Once again, Wilson's narrower ant columns may explain his contrasting results. In any case, the data do not support Wilson's hypothesis that foraging velocity of leaf cutters will be similar for all individuals.

Acknowledgements

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