Short communication

The adaptive benefit of leaf transfer in *Atta colombica*

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Summary. We studied leaf transfer on trails of the leafcutter ant *Atta colombica*. 78.6% (N = 210) of leaves were not transferred, 12.4% (33) were cached and the remaining 9% (24) were transferred directly to another individual. Directly-transferred leaves travelled significantly faster post-transfer. There was no difference between the speeds of leaves that were not transferred and those post-transfer, although there was a significant difference among the pre-direct-transfer, pre-cache, and non-transfer speeds. We suggest that there may be a critical transportation speed, and that if this speed is not met, an individual will relinquish its leaf.

Key words: Task partitioning, leaf-transfer, foraging trails, *Atta colombica*.

Introduction

Little quantitative data exist on the costs and benefits of task partitioning – the process in which material is passed from worker to worker in a relay fashion (Jeanne, 1986; reviewed in Ratnieks and Anderson, 1999; see also Anderson and Ratnieks, 2000). However, such data is necessary to help elucidate the conditions in which task partitioning is favoured over other forms of work organisation (Ratnieks and Anderson, 1999).

Task partitioning is known to occur in the retrieval of leaf fragments in *Atta* leafcutter ants. *A. cephalotes* sometimes transfer leaves – either directly by passing it to another individual, or indirectly by caching it on the ground – when establishing a trail to a new food source (Hubbell et al., 1980; Ratnieks and Anderson, 1999). In *A. sexdens* however, retrieval may occur in three distinct stages; "arboreal cutters" clip through petioles allowing leaves to fall to the ground, where they are later collected, cut into fragments and deposited at the main trail by "cache exploiters." "Carriers" transport the fragments to the nest (Fowler and Robinson, 1979).

In all cases though, further task partitioning along the trail cannot be ruled out. Lugo et al. (1973) report leaf transfer on *A. colombica* trails, and we confirm and quantify such task partitioning.

There are numerous examples of partitioned resource retrieval on foraging trails (Ratnieks and Anderson, 1999). One possible hypothesis for such transfer is that transporter ants may be going too slow, or at least slower than the receiving ant could travel, and therefore transfer occurs in order to increase the leaf's transportation speed (perhaps resulting in an increase in the overall rate of resource transportation). Under this scenario, which we term the "speedy leaf hypothesis," we predict that slow-moving ants are more likely to transfer their leaves (either directly or indirectly), than faster-moving ants. We would also expect that post-transfer speed is greater than pre-transfer. The aim of this study is to test these two predictions as well as to quantify the amount of task partitioning on *A. colombica* trails.

Methods

We studied three colonies of *A. colombica* on the banks of the Corobici River at "Hacienda La Pacifica," 5 km Northwest of Cañas, Guanacaste, Costa Rica (10°25′N, 85°7′W). Cañas is within the Tropical Dry Forest life zone, which is marked by strong wet-dry seasonality. The research was conducted from mid-June until mid-August 1999, which corresponded with the middle of the wet season (May–October, mean annual rainfall 1369 mm).

Data for each colony were collected along a smooth and cleared one metre section of the active foraging trail at the base of the source tree, which was 45.3 m (colony 1) and 18.2 m (colony 2) from the main nest entrance (colony 3 ≈ 50–60 m). As individual leaf-toting ants crossed the zero metre mark, a stopwatch was started. In most cases, the ant did not transfer and the watch was stopped after they passed the one metre mark. However, for ants that cached their load, location at which caching occurred was measured, and the time was recorded. For ants that directly transferred their loads, distance and time at which transfer to a second ant occurred were recorded. The lap function was used to time the journey of the second (recipient) ant over the remaining dis-

Table 1. Speeds of various categories of leaf transportation. The transportation speeds of non-transferred leaves were not normally distributed and hence non-parametric statistical tests were used in analysis of this group (see text)

Leaf-category	N	Transportation speed cm/s	
		Mean (s.d.)	Median (I.Q. range)
Non-transferred *	210	1.62 (0.76)	1.46 (1.06–2.05)
Pre-cached	33	1.05 (0.55)	1.10 (0.64–1.42)
Pre-direct transfer	24	0.79 (0.54)	0.85 (0.21–1.21)
Post-direct transfer	18	1.40 (0.74)	1.28 (0.82–1.88)

* Non-normal data.

tance (mean 47.1 cm, 95% C.I. 35.6–58.6 cm) to the one metre mark. To avoid sampling bias, the first ant passing over the start point after the note-taker was ready was used.

Results

Of 267 leaves, 78.6% (210) were not transferred, 12.4% (33) were cached, and the remaining 9% (24) were directly transferred (Table 1). There was a highly significant difference among the median speeds of leaves pre-transfer, pre-caching and those that were not transferred (Kruskal-Wallis H = 36.66, df = 2, p < 0.0001). Non-transferred leaves travelled significantly faster than directly transferred leaves (1.46 vs. 0.85 cm/s; Mann-Whitney U = 963, N = 210, 24, p < 0.00001) and than cached leaves (1.46 vs. 1.1 cm/s; U = 1959.5, N = 210, 33, p < 0.0001). However, cached and directly transferred leaves did not differ in their mean speeds (1.06 vs. 0.79 cm/s; t = 1.81, df = 50, p > 0.076).

For those leaves that were directly transferred (N = 18 as 6 of the 24 ants were lost sight of), there was a significant increase in their speeds post-transfer (0.9 vs. 1.4 cm/s; paired-t = 2.94, df = 17, p < 0.009). (15/18 leaves were transported faster post-transfer.) Additionally, there was no significant difference between the post-transfer speeds and the speeds of non-transferred leaves (1.28 vs. 1.46 cm/s; U = 1592, N = 18, 210, p > 0.25) but the power of this test is very

low (approximately 0.23). Finally, the proportion of leaves not transferred is clearly a function of transportation speed (Fig. 1). As speed increases, the ants are less likely to directly transfer or cache their material but to continue its transportation along the trail. Above 0.8 cm/s, less than 25% of leaves are transferred, and at speeds greater than 2.4 cm/s no transfer (direct or indirect) was observed (Fig. 1).

Discussion

Task partitioning occurred at a surprisingly high rate – more than one in five leaves – on the trails of our study colonies and our data suggest an adaptive benefit of such transfer. The data confirm the predictions of the "speedy leaf hypothesis" in that fast-moving ants are less likely to transfer their material (Fig. 1) and that slow-moving ants do indeed transfer their leaves to faster and more capable individuals. Although these findings may suggest that donor-ants are not well-suited to their load and would be better to transport lighter leaf fragments, this is not necessarily so. Some of the ants were clearly slowed by gusts of wind or by interference from loads carried by other ants (especially when transporting large petal fragments) but more detailed research is required.

Unfortunately, it was not possible to obtain an accurate estimate of the average time cost of transferring material from one ant to another, although it ranged from near-zero to 21 s. However, in a similar study of a laboratory colony of *Atta cephalotes* housed at the University of Aarhus (C.A., unpublished data), the results of which prompted this field study, the mean delay (± s.d.) of transferring to another ant was 14 ± 10 seconds (N = 78). A further 16 ± 17 s (N = 76) was required for the recipient ant to adjust her leaf, get it into the right position for carrying, and set off. If similar delays exist in field colonies, our data suggest these transfer costs might easily be compensated by the increase in post-transfer speed along the remainder of the trail, which may reach 100 m or more.

Acknowledgements

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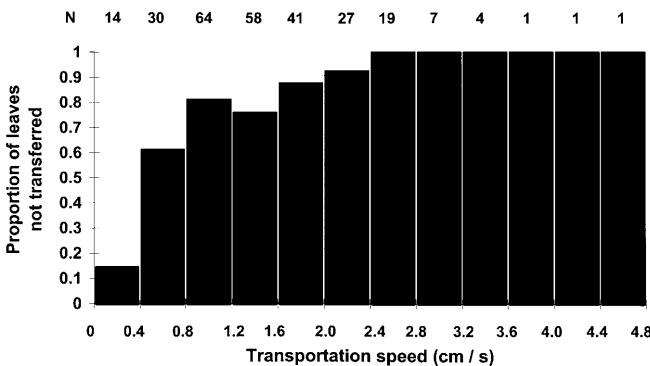
Figure 1. Proportion of leaves not transferred (versus direct transfer or caching) as a function of transportation speed (cm/s). The sample size, N, for each speed interval is given above the relevant bar