Fallen Branches as Part of Leaf-Cutting Ant Trails: Their Role in Resource Discovery and Leaf Transport Rates in *Atta cephalotes*

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ABSTRACT

Fallen branches, logs, and exposed roots (fallen branches hereafter) commonly form part of the trunk trail system of leaf-cutting ants that inhabit the tropical rain forest. We studied the role of fallen branches on resource discovering and on leaf transport rates in *Atta cephalotes*. Fallen branches were common components of the *A. cephalotes* trail system; they were present in all the nests, and in the majority of the trunk trails examined (13/16). A field experiment revealed that, at the beginning of their foraging activity, ants discovered food sources located at the end of fallen branches earlier than those located on the leaf litter. Additionally, laden ants walked faster along a fallen branch than along soil tracks of the trunk trails. This increment in speed was higher in slow-walking ants (*e.g.*, with larger loads) than in fast-walking ants (*e.g.*, with smaller loads). These results suggest that the presence of fallen branches may direct the searching effort of leaf-cutters and increase the foraging speed of laden ants when these structures are part of the trunk trail system. The advantages of using fallen branches as part of a trail system, and their potential consequences in the spatial foraging pattern of leaf-cutting ants, are discussed.

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Key words: Costa Rica; foraging costs; scout; tropical rain forest; trunk-trails.

THE STRUCTURE OF FOREST UNDERSTORY LIKELY has a profound effect on the foraging patterns in central-place foragers. For instance, ants exploring and carrying resources to the nest through dense vegetation and abundant litter reduce their velocity as the three-dimensional distance increases. Consequently, several ant species preferentially use pathways that are relatively free of debris where their speed can increase when searching for resources and foraging (Fewell 1988, Farji-Brener & Sierra 1998, Denny *et al.* 2001). This preference decreases energy cost and time consumption (Fewell 1988). One way to reduce travel time through a dense forest understory is to use cleared trails to facilitate locomotion. The use of foraging trails by ants enhances foraging speed, and also is important in facilitating foraging on clumped resources and in providing marked routes (Hölldobler & Wilson 1990). However, the con-struction and maintenance of a large and permanent trail system free of debris may represent a large investment of time and energy in tropical forests, where litter is constantly falling to the forest floor.

One of the more formidable trunk-trail systems is constructed by the leaf-cutting ants of the genus *Atta*. Leaf-cutting ants travel up to 200 m or more along cleared trunk trails to the resource patches, where plant material is cut and transported back to the nest to cultivate the fungal food supply (Hölldobler & Wilson 1990). This trunk-trail system is particularly conspicuous because a single nest may maintain up to 3 km of trails free of debris per year (Howard 2001, Wirth *et al.* 2003). For example, a single trunk trail may exceed 200 m in length and 30 cm in width (Lewis *et al.* 1974) and represents a significant investment in time and energy for the colony (Lugo *et al.* 1973, Shepherd 1982, but see Howard 2001).

The role of trunk trails in the foraging activity of leaf-cutting ants has been extensively studied. These studies address the per-formance of workers using trails (Rudolph & Loudon 1986, Burd

1996), the use and design of trails in exploiting resources (Shepherd 1982, Rockwood & Hubbell 1987, Wetterrer 1990, Wirth *et al.* 2003), the cost of trail construction and maintenance (Lugo *et al.* 1973, Howard 2001), and the role of trails in discovering new resources (Shepherd 1982, Therrien & McNeil, 1990, Farji-Brener & Sierra 1998). However, little effort has been made to understand the role of fallen logs and branches as components of the trunk-trail system of leaf-cutting ants.

One striking characteristic of the trunk-trail system of *Atta* nests is the use of fallen logs and branches (fallen branches, hereafter) as part of the ants foraging trails. For example, in a tropical semideciduous forest in Panama, 9.3 percent of the *Atta columbica* trails consisted of fallen branches, where little or no litter accumulated (Howard 2001). The use of these fallen branches as part of the trail system is likely advantageous for the colony because these segments reduce the cost of trail construction and maintenance, and offer a smooth substrate where the walking speed of ants might be faster than on soil tracks of the trunk trails. Because reducing transport time of leaf fragments is beneficial for leaf-cutting ants (Roces & Nuñez 1993, Roces & Hölldobler 1994, Burd 1996, Roschard & Roces 2002), the use of fallen branches is expected to be relevant in the transport of leaves. Furthermore, fallen branches may play a role in discovering new resources.

Searching for new resources is a critical and little studied component of the foraging process in leaf-cutting ants (Howard 1991, Roces & Nuñez 1993, Howard *et al.* 1996, Farji-Brener & Sierra 1998). If scouting ants tend to explore along fallen branches, this behavior may represent an advantage for the scout itself and for the colony as a whole. First, the scout explores and returns faster, minimizing the time of information transfer to other members of the colony (Roces & Nuñez 1993). Second, if a resource is discovered, leaf-cutters use these fallen branches to transport the resources at higher walking speed without the costs of trail construction and maintenance. In this study, we present two lines of field evidence on the importance of fallen branches in both processes, analyzing whether: (1) laden ants walk faster along fallen branches than along cleared soil section of trunk trails; and (2) resources located at the end of fallen branches are discovered before those located on the forest floor. Additionally, if the presence of fallen branches plays a role in the trail design, we expect that a fallen branch will not be a simple continuation of an existing trunk trail (*i.e.,* that the angle between the trunk-trail direction and the fallen branch should differ from zero).

METHODS

We conducted this study at La Selva Biological Station of the Organization for Tropical Studies (10°26′ N, 83°59′ W) in the Atlantic lowlands of Costa Rica, in February 2005. The area is a lowland wet forest that receives a mean annual rainfall of 4000 mm (see McDade *et al.* 1994 for a full site description). Colonies of leaf-cutting ants, mainly *Atta cephalotes*, are common in La Selva (Farji-Brener 2001). We randomly selected six large nests of *A. cephalotes* located in forests with different successional stages. In

each ant nest we selected the main 2–3 trunk trails and measured their total length, and the length of all the fallen branches forming part of these trails. Whenever a fallen branch was a part of the trail system, we measured the angle between the trail direction and the fallen branch, considering 0° if the fallen branch followed the same direction of the trunk trail. These measurements were analyzed using circular statistics (Zar 1999).

We measured the traveling time of laden ants on both fallen branches and on cleared tracks of trunk trails. We randomly selected 100 returning laden ants (20 per nest in five nests), and measured the time needed by the same ant to walk along 20 cm of a trunk trail and along the next 20 cm of a fallen branch. These measurements were taken without disturbing the ants, and compared using a paired *t*-test. With these data we also calculated the change in speed for each ant when walking on fallen branches.

To determine the role of fallen branches in discovering new food sources, we performed the following field experiment. Two groups of corn flakes were presented simultaneously to the ants at opposite sides of a main trunk trail, one of them at 20 cm away in the leaf litter, and the other at the end of a 20 cm fallen branch perpendicular to the trail. Fallen branches were placed horizontally on the forest floor, like a dead stick, and used only once per trial. We registered where the corn flakes were first discovered by a scouting ant. The treatments were reassigned to different sides of the trunk-trail after each test, and both treatments were located at the same distant from the nest entrance (between 2 and 10 m). A discovery was considered successful when an ant colleted a corn flake and returned to the nest. We used corn flakes as food resources because they are highly preferred by leaf-cutting ants, and successfully used in several food preferences studies (see Farji-Brener 2001 and references therein). We completed 34 tests using 16 trails of six different nests, 15 tests in the morning at the beginning of the foraging activity, and 19 in the afternoon, at the peak of foraging activity.

RESULTS

Fallen branches were a common component of the trail system of nests in *A. cephalotes*. Fallen branches were present in all the nests ($N = 6$), and in the majority of the trunk trails sampled (13/16). The mean length ($\pm$ 1 SD) of a trunk trail was 22 ± 2 m ($N = 16$), and 30 percent of their length was composed of fallen branches (6.5 ± 1 m). The mean angle ($\pm$ SD) between the trail built on the forest floor and a fallen branch used as a trail was significantly different from zero ($38 \pm 4°$, $r = 0.94$, $P < 0.001$, $N = 30$). In addition, laden ants were faster when they walked along 20 cm of a fallen branch than in the same length of a cleared trunk trail (8.2 ± 0.3 vs. 12.08 ± 0.5 sec, $N = 100$ ants, paired *t*-test = 11.1, $P < 0.0001$). This increment in speed when using fallen branches was higher in slow-walking ants (*e.g.*, with larger loads) than in fast-walking ants (*e.g.*, with smaller loads) ($r = -0.52$, $P < 0.05$, $N = 100$ ants, Fig. 1).

Leaf-cutting ants showed a tendency to discover the resources at the end of fallen branches earlier than those in the leaf litter,
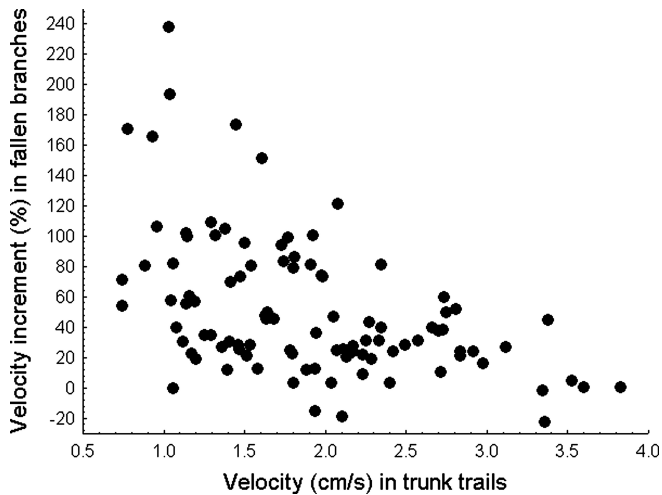
FIGURE 1.   Increment in velocity of laden ants walking along a 20 cm segment of fallen branches relative to the walking velocity on a 20 cm section of a cleared trunk trail {[(velocity along fallen branch − velocity along trail)/velocity along trail] × 100}. Each point represents the same ant in both situations. Note that slow-walking ants (*e.g.*, with larger loads) have a higher increment in speed on fallen branches than fast-walking ants (*e.g.*, with smaller loads) ($r = -0.52$, $P < 0.05$, $N = 100$).

but only at the beginning of their foraging activity. Early in the morning the ants first discovered the corn flakes located at the end of branches in 11 of 15 trials (Binomial test, $P = 0.06$), while in the afternoon only in 9 of 19 tests (Binomial test, $P = 0.50$). When the ants first discovered the corn flakes at the end of fallen branches, the corn flakes located on the forest floor were not discovered during the sampling period; in a few cases the corn flakes were discovered several hours later.

DISCUSSION

Fallen branches were a common component of the trail system in *A. cephalotes* nests. This study suggests that fallen branches play an important role in foraging and affect the chance of discovering food. At the beginning of foraging activity, when scouting is more common (Howard *et al.* 1996, Farji-Brener & Sierra 1998), leaf-cutting ants showed a tendency to explore more frequently along fallen branches than on the forest floor. Moreover, laden ants traveled significantly faster on fallen branches than on cleared sections of trunk trails, and this increment in speed was much higher (up to 200%) in slow-walking ants (*e.g.*, heavily loaded). Therefore, the presence of fallen branches seems to affect the searching effort of leaf-cutters and increase the foraging speed of laden ants when they are part of the trunk-trail system.

Several works have shown that reducing the absolute time for transporting a leaf fragment is an important aspect of the leaf-cutting ant foraging (Rudolph & Loudon 1986, Wetterer 1990, Roces & Hölldobler 1994, Burd 1996). For example, workers can discriminate among leaf fragments of different size, rejecting loads that increase traveling times. This is especially true in *Atta* species that have large, complex trunk-trail systems, where a foraging trip is time-consuming (Roschard & Roces 2002). Thus, the rugosity of a foraging trail possibly has an important effect on the rate of material transported to the nest. This work suggests that the use of fallen branches as part of the trail system is adaptive because walking along fallen branches greatly reduces travel times (especially for ants carrying large loads), probably because fallen branches have a smooth surface even compared with a cleared soil track of a trunk trail (A.G. Farji-Brener, pers. obs.).

We showed that a laden ant reduced, on average, 4 sec per 20 cm walked on a fallen branch when compared with the same distance walked on a cleared trail on the forest floor. A typical trunk trail of 22 m length is composed of 7 m of fallen branches (see results). This represents 140 sec of time reduction for a laden ant in a single trip. Considering that a large *Atta* nest has at least four main foraging trails (Wirth *et al.* 2003) and a population of approximately 50,000 forager ants (Howard 2001), the presence of fallen branches on the trail system may reduce the travel time by 7778 h (324 d) per nest per day, considering only one trip per foraging ant. Thus, the use of fallen branches represents a huge reduction in foraging time at the colony level, with the concomitant increment in the transport rate of garden material.

Shorter travel time has other possible adaptive advantages, besides the obvious increment in plant material transported to the nest. A rapid return to the nest may (1) reduce desiccation of leaf fragments, since humidity may become important for fungal growth (Bowers & Porter 1981); (2) increase the rate of information transfer and therefore the intensity of recruitment (Roces & Nuñez 1993, Roschard & Roces 2002); and (3) reduce the time of exposure to attacks of parasitoid phorid flies and to other foraging risks (Feener & Moss 1990). In addition, fallen branches do not have the cost of construction and maintenance that trunk trails have because they do not accumulate leaf litter (Howard 2001 and A. G. Farji-Brener, pers. obs.). These advantages seem to be an indirect consequence of the ants' scouting behavior, which will determine if fallen branches are incorporated into the design of a new foraging trail.

We consider that the inclusion of fallen branches in the foraging trails occurs during the scouting process, as suggested by some lines of evidence in this study. Despite the fact that ants generally show a marked preference to continue walking in the direction that the trail runs (described as "behavioral inertia"; see Rosengren 1971, Denny *et al.* 2001), fallen branches often showed a deviation from the orientation of the foregoing main trail. This supports the idea that fallen branches direct ant movement rather than being a simple continuation of a preceding trunk trail. In addition, our results suggest that ants explored the length of fallen branches more frequently than they did the forest floor. Consequently, a food resource may have a higher probability of being discovered when it is located at the end of a fallen branch. Once discovered, the fallen branch used by the scout can be incorporated as part of the trail that connects the resource with the nest. However, fallen branches could also be incorporated to the trunk-trail system after discovering a resource, when a scout ant returns to her nest. In this case, fallen

branches would play a more important role in the foraging activity than in the discovery process. Nevertheless, our results suggest that the use of fallen branches as part of foraging trails results from their initial role in directing the search for plant material.

Although the use of fallen branches saves energy and time because it increases the walking speed of ants without the costs of trail construction and maintenance, there are other possible reasons that explain why ants often explore along fallen branches. First, ants may be attracted to novel materials placed near the trails. Thus, a faster rate of bait discovery at the end of experimental fallen branches should be simply due to the fact that experimental fallen branches were considered as novel materials. However, the evidence that leaf-cutters prefer new materials is contradictory (Littledyke & Cherrett 1975, Howard *et al.* 1996). Moreover, fallen branches are common elements of rain forest floor for the ants. Therefore, we believe that exploring through the leaf litter represents the same novelty than exploring along a fallen branch. Second, to discover and forage on fresh leaves in tropical forests, leaf-cutting ants often walk along living tree branches, and the presence of similar structures in the forest floor may stimulate ants to use them when exploring for new resources. In other words, leaf-cutters tend to walk on fallen branches because at the end of branches is where they expect to find fresh leaves. Comparative studies with leaf-cutting ant species that forage entirely on grasses (*e.g.*, *Atta vollenweideri*, and some *Acromyrmex* species) could be used to test this idea.

Whatever was the cause of this behavior, the tendency to follow fallen branches may explain some unusual foraging patterns in leaf-cutting ants, as the infrequent use of vegetation immediately surrounding their nest. For example, Cherrett (1968) described that *A. cephalotes* foraged on leaves of a *Terminalia amazonica* tree located 65.4 m from their nest in Guyana's tropical rain forest, whereas at least seven other trees of the same species were nearer to the nest but were not cut. In another study, Rockwood and Hubbell (1987) calculated that *A. cephalotes* colonies in Costa Rica could increase the quantity of leaves cut by 40 percent and reduce the foraging distance by 20 percent just by visiting the trees near the nest. If, as suggested by our results, scouting ants mainly explore along fallen branches, the spatial orientation of these fallen branches on the forest floor certainly determines the location of the resources exploited, since resource patches connected by (or near to) fallen branches to an existing trail will have a higher chance of being discovered. Thus, the spatial and temporal distribution of exploited trees may be, at least partially, determined by the random location of fallen branches in space and time. Our results also indicate that fallen branches reduce the foraging costs of leaf-cutters by minimizing the foraging time. It is possible that a plant distant from but connected to the nest may provide a higher reward that an unconnected plant of the same species near the nest. Thus, the distance between a palatable tree and the nest is not necessarily a good predictor of the foraging pattern of leaf-cutting ants (Rockwood & Hubbell 1987, Howard 1991).

In sum, the use of fallen branches in leaf-cutting ants that inhabit tropical forests may play a role in scouting, and appear to have a vital function in the foraging processes. First, fallen branches largely reduce exploring and foraging time and/or energy. Secondly,

if a resource is discovered, the fallen branch used for exploration can be incorporated as an extension of an existing foraging trail, or form part of a new one without the cost of trail construction and maintenance, incrementing the ant foraging speed. The evidence presented here can help to explain why fallen branches are a very common feature in the trunk trails system of some leaf-cutting ant species.

ACKNOWLEDGMENTS

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