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Dynamics of the restoration of physical trails in the grass-cutting ant *Atta capiguara* (Hymenoptera, Formicidae)

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ABSTRACT

Dynamics of the restoration of physical trails in the grass-cutting ant *Atta capiguara*. Leaf-cutting ants of the genus *Atta* build long physical trails by cutting the vegetation growing on the soil surface and removing the small objects they find across their path. Little is known on the dynamics of trail construction in these ants. How much time do they need to build a trail? To answer this question we selected six trails belonging to two different nests of *A. capiguara* and removed on each trail a block of soil of 20 cm × 15 cm that included a portion of the physical trail. This block was then replaced by a new block of the same size that was removed in the pasture near the trail and that was uniformly covered by the same type of vegetation as that found on the block of soil that was removed. The time required to restore the trail was then evaluated by the length of the grass blades found along the former location of the trail. The results show that ants rapidly restore the portion of the physical trail that was interrupted, which suggests that they could also do the same after their trails have been recolonized by the vegetation.

Introduction

Foraging in leaf-cutting ants involves the selection, cutting and transport of plant material to the nest (Della Lucia, 1993). It begins when a scout ant finds a plant to exploit and recruits its nestmates by laying trail pheromone on its way back to the nest (Jaffé and Howse, 1979; Shepherd, 1982; Roces, 1990). The main part of foraging however consists in cutting and transporting the plant material to the nest (Forti et al., 1987). The retrieval of the vegetation occurs along well-defined physical trails (Howard, 2001), which are an essential part of the foraging system of leaf-cutting ants (Shepherd, 1982; Hölldobler and Wilson, 2010).

In most species of leaf-cutting ants the physical trails form a dendritic network which consists of stable physical trails departing directly from the nest that branch successively in numerous relatively short and ephemeral trails which provide access to the resources (Wirth et al., 2003; Kost et al., 2005). The network of trails can be considered as a territory which delimits the foraging area of neighboring colonies and thus minimizes the frequency of agonistic encounters between alien foragers (Shepherd, 1982; Rockwood and Hubbell, 1987). Trail usage varies over time and ants use some trails more than others (Cherrett, 1968; Vasconcelos, 1990; Silva et al., 2013). In leaf-cutting ants of the genus *Atta* some foraging trails can be used for months or even years (Weber, 1972; Kost et al., 2005; Wirth et al., 2003). The combination of physical trails and of the trail pheromone signal laid down on the trail surface allows recruited ants to access easily the resources dispersed in their environment (Weber, 1972; Fowler and Robinson, 1979). The physical trails form corridors in the vegetation and they are used as physical guidelines by recruited workers to travel from the nest to the resources discovered by the scouts. They thus reduce the risks for naive recruited workers of losing their way while following the chemical trail. The construction and maintenance of physical trails involve energy and require time (Shepherd, 1982; Howard, 2001). Traveling on cleared trails however increases worker speed by 4–10 times compared to traveling on uncleared soil (Rockwood and Hubbell, 1987). In addition, it facilitates the transport of leaf fragments, thereby increasing the rate of return to the nest of the plant material.

Given their importance for the collection of plant material, one can hypothesize that physical trails should be rapidly restored by leaf-cutting ants whenever they are recolonized by the vegetation after they have been abandoned for some length of time. In this

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paper we present the results of a study investigating the dynamics of restoration of physical foraging trails in the leaf-cutting ant *Atta capiguara.*

Material and methods

The study was conducted on two nests of *A. capiguara* near the city of Botucatu, São Paulo state, Brazil (22° 50.833′ S and 48° 26.476′ W). The size of the nests, estimated by the area of loose soil over the nests, was 113.71 m^2 for nest 1 and 47.88 m^2 for nest 2. The nests were around 3–5 years old.

Foraging in *A. capiguara* is completely diurnal in the wet season and completely nocturnal during the dry season (Forti, 1985). Before the foraging activity began in the early morning, a 20 cm × 15 cm block of soil (thickness around 5 cm, preserving most of the root system of the plants) was removed from an active physical trail, at a distance of 3 m from the beginning of the trail.

This block was replaced by another block of exactly the same size (henceforth called experimental) which was removed in the same pasture in which the nests were located and which was uniformly covered by vegetation. We took care that the vegetation of the experimental block was the same as that found on the edges of the manipulated trail. In other words, if the manipulated trail was lined e.g. by *Paspallum*, the experimental block was covered by the same plant species.

We then removed a block of soil of the same size as that of the experimental block, at a distance of 2 m perpendicular to the manipulated trail, and replaced it by a block (henceforth called control) of the same dimension, which was removed at the same location as that of the block inserted on the manipulated trail. This allowed us to assess the vegetation growth in absence of ant traffic and to measure the background grazing and cutting activity of other animals in the pasture. To avoid the intrusion of big herbivores the experimental site was fenced during the evaluation period.

The two blocks of soil (experimental and control) were divided into twelve 5 cm × 5 cm quadrats by white nylon threads. Five centimeters corresponds to the average width of the physical trails of leaf-cutting ants in pastures (Lopes, unpublished results). They were checked every 12 h during 5 days and the length of the five longest grass blades in each of the three quadrats located along the median of the block, corresponding to the former location of the trail, was measured. Three trails from each of the two nests studied were manipulated during our study, yielding a total of 6 trails.

For each block of soil the mean length of the 15 grass blades measured was calculated. Since the initial state of the vegetation on the blocks varied among trails, in order to standardize the change in the vegetation over time for all blocks, we then calculated the percentage variation in the mean length of the grass blades between the first survey (at 12 h) and each successive survey for each block. We then tested with two-way within-subjects ANOVA whether the length of the grass blades varied differently over time in the control and experimental blocks for the 6 trails studied. Block type (with two levels: control vs. experimental) was entered as the first within-subjects factor, time of survey (with 8 levels) was entered as the second within-subjects factor, and trail as the random factor. If ants are actively cutting the grass to build their trail one should find a significant interaction between block type and time of survey: whereas the mean length of the grass blades in the experimental blocks should decrease over time, it should remain stable or slightly increase because of vegetation growth in the control blocks. The variation over time in the length of the grass blades was then tested for each block with a one-way within-subjects ANOVA with trail entered as a random factor. The software R 3.1.3 was used to analyze the data (R Core Team, 2015).

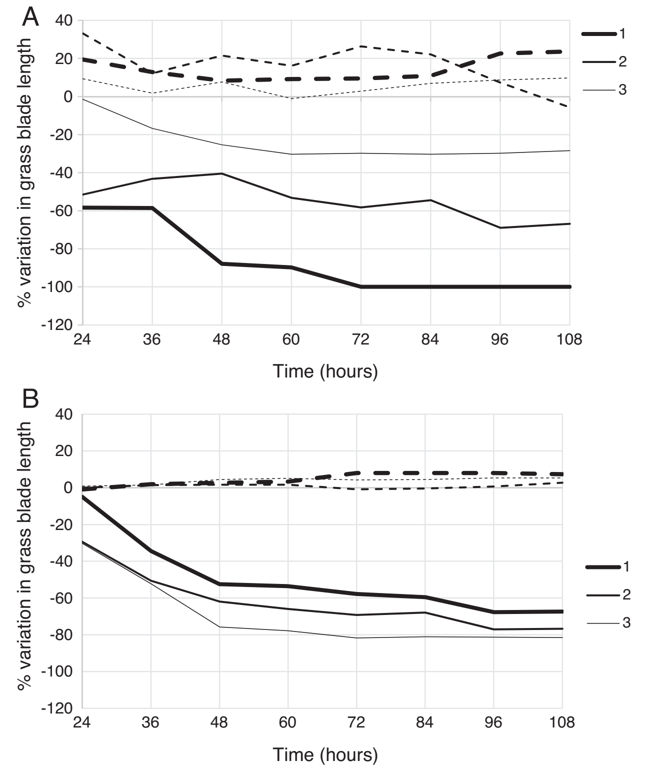

Fig. 1. Percentage variation in the mean length of grass blades for the experimental block (continuous lines) and control block (dashed lines) of each manipulated trail of Nest 1 (A) and 2 (B). The lines of same thickness correspond to the same trail.

Results

The percentage variation in the mean length of grass blades on the control and experimental blocks of each trail throughout the duration of the survey is shown in Fig. 1. The length of the grass blades varied differently between the control block and the experimental block for each trail (ANOVA, interaction block type × time of survey: $F_{7,35} = 9.931$, $p < 0.001$). Whereas the length of the grass blades did not vary over time in the control blocks (ANOVA: $F_{7,35} = 0.354$, $p = 0.923$), it decreased significantly in the experimental blocks (ANOVA: $F_{7,35} = 22.570$, $p < 0.001$). The vegetation disappeared completely for trail 1 of nest 1 (Figs. 2A and 3B) and was only partially cut for trail 3 of nest 1, probably because of the low traffic intensity recorded on this trail. The restoration of the physical trail can clearly be seen, even in absence of ant traffic. Only the layer of dry vegetation directly over the soil remained on the trail.

Discussion

Our results show that *A. capiguara* workers rapidly restore the portion of their physical trails that was interrupted and thus suggest that they could also do the same when their trails have been temporary abandoned and recolonized by the vegetation. The measure of the height of the grass blades on the control blocks shows that there was no cutting or grazing activity by other herbivores in the pasture during the time required for ants to restore their trail. For some control blocks (Nest 2: trail 1 and 3) a low growth of the vegetation was even registered, showing that the block transplantation did not affect the state of the vegetation.

Upon encountering the new block of soil placed across their trail, foraging ants stopped and formed a cluster around and on top of it.