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Fast Food Delivery: Is There a Way for Foraging Success in Leaf-Cutting Ants?

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Abstract
Walking long distances through a trail system is an intrinsic feature of the leaf-cutting ants. Workers travel hundreds of meters to forage by using well-defined physical routes that are cleared of vegetation or obstacles. Despite the costs of construction and maintenance, cleared trails should promote more benefits than non-physical ones, especially related to the leaf supply for the colony. Here, the leaf delivery rate in constructed and non-constructed trails was compared by counting the foraging flow and travel time of workers. In addition, we measured the length and width of trails. The leaf delivery rate was almost 70% higher for foragers who were walking along physical trails. The forager walking speed on physical trails was 86.10% higher. These significant increments might be related to the truly narrow corridor present inside physical trails that are leaf litter-free, and thereby chemically stronger and smoother than non-physical ones. The speed improvement could induce the construction of longer trails, which guide the workers more efficiently to the foraging patch. Thus, physical trails have an important role in foraging efficiency as they allow workers to go quickly and further to forage, since they limit a path and congregate more individuals, raising the leaf delivery rate. This study provides additional information about foraging trails of leaf-cutting ants.

Introduction

One of the most important aptitudes of life involves motility. From intracellular molecular transport to flight of birds, movement is one of life's central attributes (Chowdhury et al., 2005). This assumption is strikingly evident for leaf-cutting ants who travel along trails hundreds of meters long (Lewis et al., 2008). Walking long distances through a trail system is an intrinsic feature of leaf-cutting ants. The main function of this trail system is to guide foragers between the nest and the resource patch (Shepherd, 1982; Fowler & Stiles, 1980).

Foraging trails arise from the recruitment process, which involves outbound scouts, who are the first workers to leave the nest seeking food. Once they find it, the scouts return to the nest laying chemical cues, which leads forager workers to the resource (Jaffe & Howse, 1979). After collecting leaves, foragers return to the nest also laying the trail pheromone. As a result, a positive feedback occurs, in which the more intense the pheromone trails, the more ants that are recruited and so on (Sumpter, 2006). This huge flow of individuals can assure a greater food supply to the colony, since more forager workers are directly related to increase of material collection. However, the forager flow along a trail can be established in various environments with different physical characteristics, such as rugosity (Moll et al., 2010), and in the presence of leaf litter (Bruce & Burd, 2012), which may or may not facilitate the forager traveling (Bollazzi & Roces, 2011).

Some ant species, such as those which belong to the genera *Atta,* are able to construct true corridors by cleaning vegetation and debris from the trails. Ant-constructed trails (from now on "physical trails") have inherent costs, such as the construction effort (Lugo et al., 1973; Shepherd, 1982) and reduction of the foraging flow due to increase of head-on collisions among foragers traveling on the same path (Burd & Aranwela, 2003). On the other hand, the intrinsic benefits of physical trails involve increased velocity, improved trail-laying properties (Shepherd, 1982) and even physical memory of foraging (Lewis et al., 1974; Shepherd, 1982; Farji-Brener & Sierra, 1998). Another extremely profitable circumstance to workers is that physical trails may remain inactive in the field

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up to eight months without regrowth of vegetation (Rockwood & Hubbell, 1987) and it can be reactivated with almost no cost. Thus, considering the advantages and disadvantages of constructed trails it is probable that the benefits of physical trails are greater than non-physical trails, especially related to the leaf supply of the colony.

Here, we compared in the field the leaf delivery rate and travel time of forager workers in physical and non-physical trails of *Atta sexdens* (Linnaeus, 1758) colonies, as well as some physical features of the trails such as length and width. The investment in physical trail construction and maintenance is offset by worker walking speed improvement (Johnson & Hubbell unpublished data, cited in Rockwood & Hubbell, 1987), thus it has been argued if the leaf delivery rate in physical trails may also be higher than when physical trails are not present. Also, physical trails may be longer and narrower since their construction is actively modulated by workers.

Material and Methods

The study was carried out in Rio Preto State Park, Minas Gerais, Brazil (18°9'15"S 43°20'50"W), located in the Cerrado biome. This park is a conservation unit with approximately 12 ha. Data was taken in August 2014, during four days between 7:00 and 11:00 PM, with assistance of a white flashlight filtered with red cellophane paper.

We selected three physical and three non-physical trails located at least 100-m apart from each other. Physical trails were those free of debris and/or litter and visible soil surface (Fig 1), while non-physical trails were those in which it was not possible to see the soil surface, but leaf transport by workers was observed. In each trail, we established a 20 cm-trail section 2m apart from the foraging hole. At this section, we also established a fixed point for foraging flow register.

To assess the foraging flow we counted loaded and unloaded inbound foragers at three consecutive 1-minute intervals every 5 minutes for 20 minutes. Thus, it was possible to obtain 12 replicates of 1-min foraging flow/trail/day. We repeated this procedure for four days in all six selected trails. Therefore, there are 144 replicates for physical trails and 144 for non-physical trails. Flow data was used to calculate leaf delivery rate (LD)/minute by the formula (Dussutour et al., 2007): LD= LI/(LI+UI), where: LI= loaded inbound foragers; UI = unloaded inbound foragers.

We registered the travel time of 20 loaded inbound medium workers along the 20cm-trail section in each one of the six trails during the same four days. Medium workers were selected due to this size class being likely to act as foragers (Wetterer, 1999). In addition, as they belong to the same size class, it is possible to infer that they were probably carrying leaf fragments of the same size (Weber, 1972).

In order to compare trail features, we measured the length of the trails from the nest entrance to the foraging patch while width was taken every 50 cm, beginning from the foraging patch. We repeated this procedure daily for non-physical trails, as they were not marked over the soil surface.

The ANOVA test was used to analyse the response of leaf delivery rate under effect of the categorical variable - type of trail (physical and non-physical) and the influence of type of trail in the continuous variable travel time. Trail width variances were not homogeneous (Bartlett's K-squared: T = 236.00, df = 1, p <0.001), thus this variable was compared with the Mann-Whitney-Wilcoxon test. In the same way, the trail length variance homogeneity was tested (Bartlett's K-squared: T = 2.95, df = 1, p = 0.085) and now the *t* test was more appropriate to compare physical and non-physical trail length. Statistical analyses were performed and graphs generated in the R environment (R Core Team 2013).

Fig 1. *Atta sexdens* physical trail. Parque Estadual do Rio Preto - MG, Brazil.

Results

Leaf delivery rate was higher in physical trails than in non-physical ones ($F = 87.33$, $df = 1$ and 474, $p < 0.001$) (Fig 2) (physical: $\bar{x} = 0.39 \pm 0.22$un/min, maximum value = 1.00, minimum value = 0.03; non-physical: $\bar{x} = 0.23 \pm 0.17$, maximum value = 0.75, minimum value = 0.02). Leaf delivery rate also represents the proportion of laden foragers in relation of the total flow of inbound foragers, so it indicates that there were proportionally more laden foragers in physical trails than in non-physical ones. Travel time of forager workers was shorter on physical trails than along non-physical ones ($F = 206.41$, $df = 1$ and 474, $p < 0.001$) (Fig3), indicating that foragers walked faster in these trails and thus physical trails facilitate the foragers' travel. In other words, across the 20cm observed, the travel time of laden foragers on clean paths were 48.33% lower than for workers on non-physical trails (physical: $\bar{x} = 20.14 \pm 7.32$s, non-physical: $\bar{x} = 38.98 \pm 19.10$s). In other words, the forager walking speed raised in average 86.10% in physical trails.

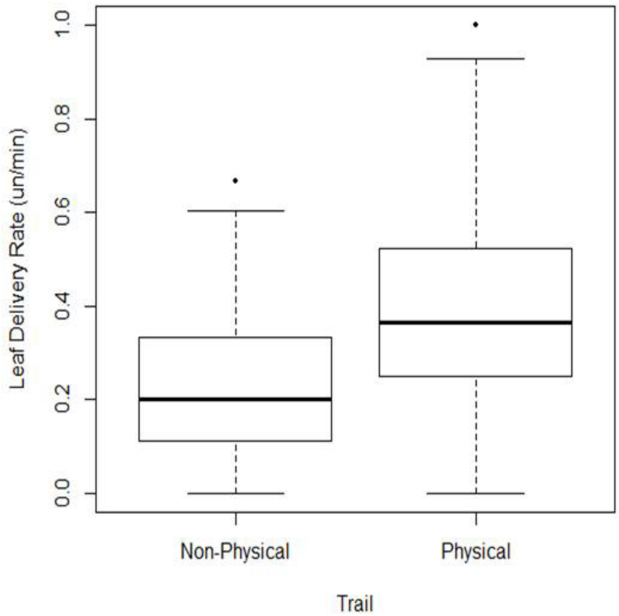

Fig 2. Relationship between leaf delivery rate and the two types of trails - physical and non-physical.

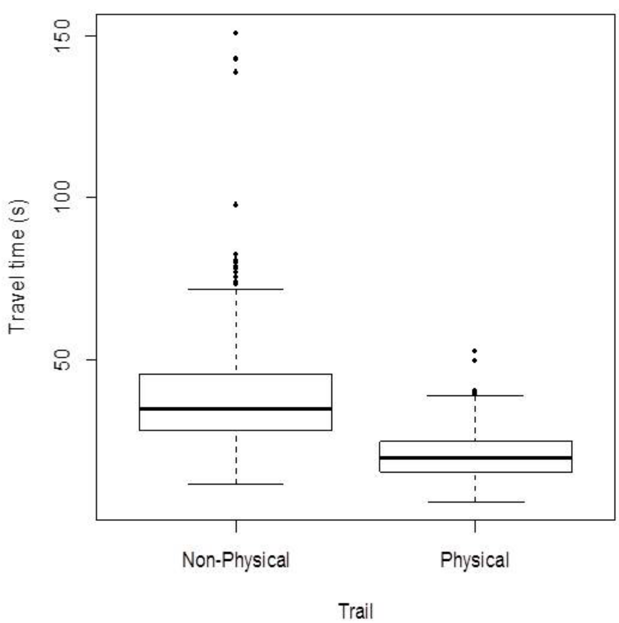

Fig 3. Relationship between travel time of forager workers and the two types of trails - physical and non-physical.

Physical trails were longer than non-physical ones (t = -5.444, df = 2.242, p = 0.025), which allow workers to explore resources farther from the nest (Fig 4A). The average length of physical trails was 21m (maximum value = 24.3m, minimum value = 16.2m) and for non-physical trails was 8m (maximum value = 10.4m, minimum value = 5.4m). Furthermore, physical trails were narrower than non-physical ones (W = 7127, p < 0.001), promoting a directed flow as workers travel along a delimited path (Fig 4B). The average width of physical trails was 6.72 cm (maximum value = 10cm, minimum value = 3cm) while for non-physical trails was 11.11 cm (maximum value = 75cm, minimum value = 3cm).

Discussion

The present study has indicated that the leaf delivery rate was on average 69.56% higher in physical trails when compared with non-physical ones. Inbound laden workers walking in these trails took less time to travel up to the nest compared with those traveling in non-physical ones, which could explain the construction of longer and narrower trails.

Several works have well documented the widespread feature of ant species with regards to physical trails and their benefits in terms of foraging efficiency (Shepherd, 1982; Hölldobler & Wilson, 1990; Anderson & McShea, 2001) and the impact of rough surfaces on walking speed (Seidl & Wehner, 2008; Bernadou et al., 2011). Clear trails enable workers to forage in a straight line, almost without obstacles, increasing their walking speed. Physical trails seems to be an important attribute to leaf-cutting ants (Rudolph & Loudon 1986; Wetterer, 1990; Roces & Hölldobler, 1994; Burd, 1996), since it increases the leaf delivery rate of the colony. Nevertheless, the presence of leaf litter along the path could make the traffic flow of forager ants difficult, resulting in a lower leaf delivery rate on non-physical trails. Even in physical trails, there is an edge-trail effect provoked by the vegetation on trail edges that disturb the forager flow (Bruce & Burd, 2012). Once non-physical trails are formed over leaf litter, forager workers must be under this edge-trail effect all along the trail path. In this way, a higher disturbance on the traffic flow in non-physical trails would be expected when compared with physical ones.

Physical trails were the narrow ones and those with high leaf delivery rate, inferring that narrow trails improve leaf delivery rate. A similar negative relationship between trail width and foraging efficiency has already been identified for *Atta colombica* (Guérin-Méneville, 1844) (Dussutour et al., 2007).

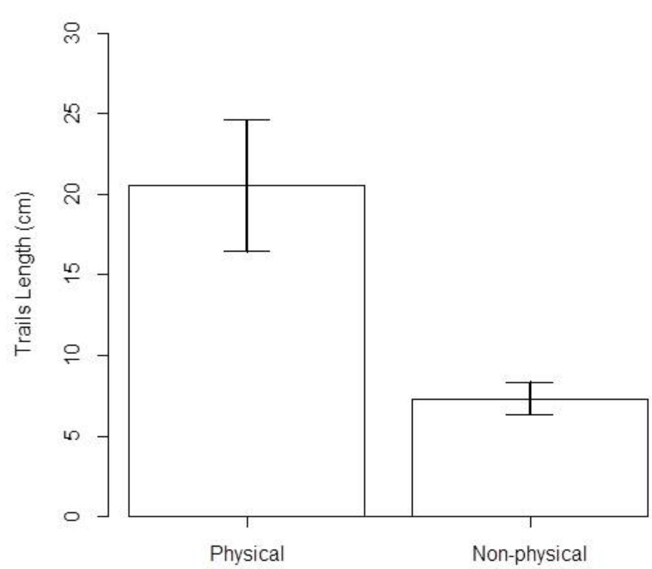

Fig 4A. Comparison of foraging trail features - physical and non-physical. A) Average and standard deviation of physical and non-physical trail length.

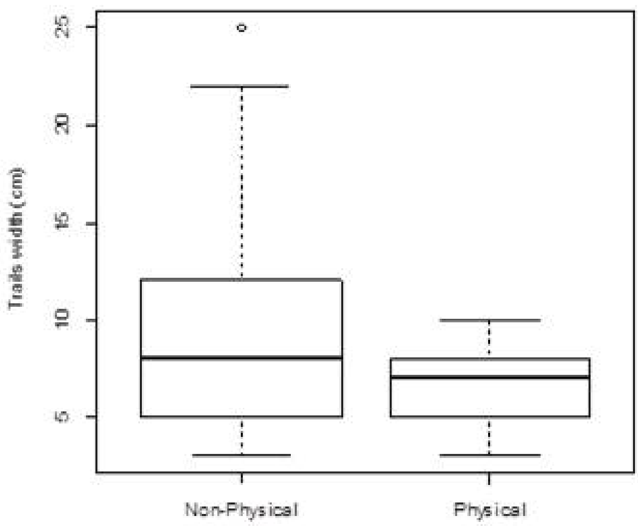

Fig 4B. Minimum, medium and maximum width of non-physical and physical trails.

This relationship can be explained by the ontogeny of physical trails. Since non-physical trails are predecessors of the physical ones, they are chemically weak, confused and the pheromone marking is dispersed, whilst the physical ones become chemically stronger (Edelstein-Keshet et al., 1995) through a positive feedback mechanism (Sumpter, 2006), in which several forager workers will follow and reinforce the pheromone cues. In the case of intense flow persistence, these trails now chemically stronger will delineate straight lines over time (Edelstein-Keshet et al., 1995). This process allied to path clearing by workers molds physical trails. Physical trails are narrower and more attractive to the ants due the high pheromone concentration (Edelstein-Keshet et al., 1995).

Undisputed is the fact that the construction and maintenance of physical trails incur costs (Lugo et al., 1973; Shepherd, 1982; Howard, 2001). These costs can be variable depending on environmental conditions as the potential gains differ according with distance, quality and availability of different food sources. In this way, some features that influence the workers travel time, like wind and surface rugosity (Lewis et al., 2008; Seidl & Wehner, 2008), could also be considered here. Cleared trails create barriers unintentionally at both sides of the trail. One can therefore assume that foragers may be protected from some abiotic factors, for instance the wind. High wind speed could unbalance the laden foragers by tilting them laterally and making them slower. Inside the trail, however, workers may be less affected by this force. Likewise, physical trails are leaf litter-free and thereby are smoother than non-physical ones. This evident difference at soil surface rugosity leads a striking improvement in travel speed of workers in these type of trails. Data showed that the walking speed was 86.10% higher in physical trails when comparing with non-physical ones. In a field study comparing cleared soil trails and foraging trails over fallen branches, Farji-Brener et al. (2007) found that due to lower rugosity, foragers have higher speed over fallen branches than those walking along cleared trails on the forest floor. This intrinsic feature of physical trails leads to a shorter travel time and a higher leaf delivery rate beyond the workers having a physical foraging trail memory (Lewis et al., 1974; Shepherd, 1982; Farji-Brener & Sierra, 1998).

Our results highlight one more advantage to physical trail construction that surpasses their costs, because when foragers travel along longer trails they spend much time traveling from the nest to the foraging patch. The additional time needed for this round trip causes a delay of laden workers arriving to the nests (Bruce & Burd, 2012). Here we verified that physical trails, which are longer than the non-physical ones, had a higher leaf delivery rate due to being cleared and thus reducing the travel time. The travel speed of forager workers seems to be an important attribute of the foraging process (Wetterer, 1990; Roces & Hölldobler, 1994; Burd, 1996; Farji-Brener et al., 2007). Furthermore, long physical trails allow workers to enlarge their foraging area (Howard, 2001). The same occurs for *Camponotus sericeiventris*. For this species, lianas and plant branches can function as physical trails, increasing their life area (Yamamoto & Del-Claro, 2008). Physical trails allow workers to move faster and, as they become longer and narrower, the foraging flow becomes greater, allowing both the discovery of new and more distant unexplored food sources as well as the maintenance of stable routes to permanent and already known food sources.

We showed that physical trails are more profitable to the colony than non-physical ones as they decrease the time travel of laden inbound workers and thus increase leaf delivery rate to the colony even for more distant food sources. Moreover, physical trails are narrower, mobilizing a huge quantity of workers rapidly through chemical recruitment. Physical trails have such a great role in foraging efficiency as they (i) enlarge colony foraging territory; (ii) speed-up forager workers along their trip; (iii) limit a path in the external environment and so focus more individuals; and finally (iv) raise the leaf delivery rate, making the foraging even more efficient. This study contributes to explain the investment in physical trail construction, filling gaps for the comprehension of the complex and successful foraging system of leaf-cutting ants.

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References

Anderson, C. & McShea, D.W. (2001). Intermediate-level parts in insect societies: adaptive structures that ants build away from the nest. Insectes Sociaux, 48: 291-301. doi: 10.1007/PL00001781.

Bernadou, A., Espadaler, X., Dos-Reis, V. & Fourcassié, V. (2011). Effect of substrate roughness on load selection in the seed-harvester ant *Messor barbarus* L. (Hymenoptera: Formicidae). Behavioral Ecology and Sociobiology, 65: 1763-1771. doi: 10.1007/s00265-011-1184-4

Bollazzi, M. & Roces, F. (2011). Information needs at the beginning of foraging: grass-cutting ants trade off load size for a faster return to the nest. PLoS ONE, 6.(3): e17667. doi:10.1371/journal.pone.0017667.

Bruce, A.I. & Burd, M. (2012). Allometric scaling of foraging rate with trail dimensions in leaf-cutting ants. Proceedings of the Royal Society of London-Series B, 279: 2442–2447. doi: 10.1098/rspb.2011.2583

Burd, M. (1996). Foraging performance by *Atta colombica*, a leaf-cutting ant. American Naturalist, 148: 597-612.

Burd, M. & Aranwela, N. (2003). Head-on encounter rates and walking speed of foragers in leaf-cutting ant traffic. Insectes Sociaux, 50: 3-8. doi: 10.1007/s000400300001

Chowdhury, D., Schadschneider, A. & Nishinari, K. (2005). Physics of transport and traffic phenomena in biology: from molecular motors and cells to organisms. Physics of Life Reviews, 2: 318-352. doi: 10.1016/j.plrev.2005.09.001

Dussutour, A., Beshers, S., Deneubourg, J.L. & Fourcassié, V. (2007). Crowding increases foraging efficiency in the leaf-cutting ant *Atta colombica*. Insectes Sociuax, 54: 158-165. doi:10.1007/s00040-007-0926-9.

Edelstein-Keshet, L., Watmough, J. & Grunbaum, D. (1995). Do travelling band solutions describe cohesive swarms? An investigation for migratory locusts. Journal of Mathematical Biology, 36: 515-549.

Farji-Brener, A.G. & Sierra, C. (1998). The role of trunk trails in the scouting activity of the leaf-cutting ant *Atta cephalotes*. Ecoscience, 5: 271-274.

Farji-Brener, A.G., Barrantes, G., Laverde, O., Fierro-Calderon, K., Bascope, F. & Lopez, A. (2007). Fallen branches as part of leaf-cutting ant trails: their role in resource discovery and leaf transport rates in *Atta cephalotes*. Biotropica, 39: 211–215 2007. doi: 10.1111/j.1744-7429.2006.00256.x

Fowler, H.G. & Stiles, E.W. (1980). Conservative resource management by leaf-cutting ants? The role of foraging territories and trails, and environmental patchiness. Sociobiology, 5: 25-41.

Hölldobler, B. & Wilson, E.O. (1990). The Ants. Belknap Press of Harvard University Cambridge, 796 p.

Howard, J.J. (2001). Costs of trail construction and maintenance in the leaf-cutting ant Atta columbica. Behavioral Ecology and Sociobiology, 49: 348-356. doi: 10.1007/s002650000314.

Jaffe, K. & Howse, P.E. (1979). The mass recruitment system of the leaf-cutting ant, *Atta cephalotes* (L). Animal Behavior, 27: 930-939. doi: doi: 10.1016/0003-3472(79)90031-9.

Lewis, O.T., Pollard, G. & Dibley, G. (1974). Rhythmic foraging in the leaf-cutting ant *Atta cephalotes* L. (Formicidae, Attini). Journal of Animal Ecology, 43: 129-141. doi:10.2307/3162.

Lewis, O.T., Martin, M. & Czaczkes, T.J. (2008). Effects of trail gradient on leaf tissue transport and load size selection in leaf-cutter ants. Behavioral Ecology, 19: 805-809. doi: 10.1093/beheco/arn032.

Lugo, A.E., Farnworth, E.G., Pool, D. Jerez, P. & Kaufman, G. (1973). The impact of the leaf cutter ant *Atta colombica* on the energy flow of a tropical wet forest. Ecology, 54: 1292-1301. doi: 10.2307/1934191.

Moll, K., Roces, F. & Federle, W. (2010). Foraging grass-cutting ants (*Atta vollenweideri*) maintain stability by balancing their loads with controlled head movements. Journal of Comparative Physiology A, 196: 471-480. doi: 10.1007/s00359-010-0535-3.

R Development Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org. Acesssed in 12 September 2013.

Roces, F. & Hölldobler, B. (1994). Leaf density and a trade-off between load-size behavior in the ant *Atta cephalotes*. Oecologia, 97: 1-8. doi: 10.1007/BF00317902.

Rockwood, L.L. & Hubbell, S.P. (1987). Host-plant selection, diet diversity, and optimal foraging in a tropical leafcutting ant. Oecologia, 74: 55-61.

Rudolph, S.G. & Loudon, C. (1986). Load size selection by foraging leaf-cutter ants (*Atta cephalotes*). Ecological Entomology, 11: 401-410.

Seidl, T. & Wehner, R. (2008). Walking on inclines: how do desert ants monitor slope and step length. Frontiers in Zoology, 5: 8. doi:10.1186/1742-9994-5-8.

Shepherd, J.D. (1982). Trunk trails and the searching strategy of a leaf-cutter ant, *Atta colombica*. Behavioral Ecology and Sociobiology, 11: 77-84. doi: 10.1007/BF00300095

Sumpter, D.J.T. (2006). The principles of collective animal behavior. Philosophical Transactions of the Royal Society B, 361: 5-22. doi: 10.1098/rstb.2005.1733./

Weber, N. (1972). Gardening ants, the Attines. Philadelphia: American Philosophical Society, 146 p.

Wetterer, J.K. (1990). Load-size determination in the leaf-cutting ant, *Atta cephalotes*. Behavioral Ecology, 1: 95-101. doi: 10.1093/beheco/1.2.95.

Wetterer, J.K. (1999). The ecology and evolution of worker size-distribution in leaf-cutting ants (Hymenoptera: Formicidae). Sociobiology, 34: 119-144.

Yamamoto, M. & Del-Claro, K. (2008). Natural history and foraging behavior of the carpenter ant *Camponotus sericeiventris* Guérin, 1838 (Formicinae, Campotonini) in the Brazilian tropical savanna. Acta Ethologica 11:55-65. doi:10.1007/s10211-008-0041-6.