Load Capacity of Workers of *Atta robusta* During Foraging (Hymenoptera: Formicidae)

by

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ABSTRACT

Worker ants are highly polymorphic in the genus *Atta* and they are usually classified into castes according to the specific functions they perform in a colony. Minor workers (head width ≤ 2.0 mm) help to maintain and grow the symbiotic fungus whereas larger workers (head width > 2.0 mm) cut and transport plant fragments. This study investigated the roles in the cutting and transporting of different plant resources of different *Atta robusta* worker classes that were classified based on the size of their head capsule. Experiments were conducted in the restinga of Grussaí/Iquipari, São João da Barra, Rio de Janeiro State, Brazil. In each month between October 2009 and September 2010, we collected 100 ants and their respective loads from the trails of four nests of *Atta robusta*. The samples were individually transported to the laboratory, where the ants and their loads were weighed and the head capsules of the ants were measured. Large ants transported heavier loads. These ants usually transported more fruit and seeds than smaller ants.

Keywords: leaf-cutting ants, *Atta robusta*, restinga, load transport, polymorphism

INTRODUCTION

In the genus *Atta*, individual ants display a high degree of polymorphism and they are classified into castes according to the specific functions they perform within a colony (Wilson 1971). In *Atta sexdens*, the gardener ants have a head capsule of 0.8 to 1.0 mm and they perform tasks such as the care of the fungus and the offspring, as well as the final treatment of the fungal

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substrate. Generalist ants have a head capsule that measures about 1.4 mm in width and they perform various tasks such as the processing of plant material, attending the offspring during ecdysis, queen care, waste disposal, and rebuilding the fungus. The foragers have a head capsule width that varies from 2.0 to 2.2 mm and they explore, cut, and transport vegetable material that is destined for the nest. The guards or soldier ants are the largest and they have head capsules that measure 3.0 mm on average. They defend the nest, but they also forage because they possess large mandibles that facilitate the task of cutting leaves (Wilson 1980). This division of castes has also been described in the genus *Acromyrmex*, although polymorphism is not as conspicuous in this genus as it is in *Atta* (Forti *et al.* 2004; Moreira *et al.* 2010).

The performance of a specific task that is a function of worker body size is referred to as alloethic (Wilson 1980). This can be considered as a quantitative relationship for characterizing polyethism. Foraging and fungus cultivation have a strong alloethic correlation because of the gradual change in the skills with the reduction in worker body size (Forti *et al.* 2004).

The ant *Atta robusta* transports large amounts of fruit and seeds to the nest throughout the year, which belong to various plant species (Teixeira 2007). In general, *Atta* workers carry loads that are appropriate to their body capacity as observed in *Atta colombica* (Lighton *et al.* 1987); *Atta cephalotes* (Wetterer 1990) and *Atta vollenweideri* (Kleineidam *et al.* 2007). However, the seed freight capacity of *Atta robusta* might possibly be increased due to the cooperation and participation of soldiers in the transport of larger seeds (Teixeira 2007).

This study aimed to clarify how distinct classes of *Atta robusta* workers participate in the transport of resources. We tested whether the size of the ant influenced the size of the load carried and whether there was specialization in the transport of specific resources in different forager size classes.

MATERIALS AND METHODS

Study area

The study was conducted at the restinga ecosystem from Grussaí/Iquipari complex, located in São João da Barra (21 44'S; 41 02'O), north of Rio de Janeiro State, Brazil.

Establishment of worker size classes

The foragers were separated into classes based on the size of the head capsule, using a scale of 1 mm per class. The workers with a head width less than 1 mm were not considered in the tests because they were not abundant. We obtained five classes of foragers with the following head capsule sizes: Class 1 (1 to 2 mm); Class 2 (2.1 to 3 mm); Class 3 (3.1 to 4 mm); Class 4 (4.1 to 5 mm) and Class 5 (≥ 5.1 mm).

Relationship of the transported resource with the workers size of the *Atta robusta*

Each month, ants were collected from trails as they carried resources to four nests located in physiognomic units that were defined as Beach Grass and Shrub Formations. We collected 100 ants and their loads at 30 cm from the entrance of each nest. The ants and their loads were individually placed in glass vials.

Samples were collected after 5:00 pm, when the major foraging flow was established. The collected material was stored in a refrigerator to reduce any mass loss by the evaporation of water. The mass of the material collected was measured using a precision balance (Marte, Ay 220. 0,0001g). Measurements of the head capsules of ants were made using a digital caliper (Digimess, resolution of 0,005mm/0,002"). The reliability of these measurements were assessed by comparing them with measurements made using a binocular stereoscopic microscope and an ocular micrometric (WILSON 1980). There was no difference so we preferred to make the measurements using a caliper because it was faster and it made the handling easy. The loads carried by workers were classified as leaf, dry leaf, flower, cladode, fruit, seed, stem, bud, or other.

Data analysis

To compare the load mass with the size of the head capsule of ants we used an Analysis of Variance (ANOVA) to compare the means with a Tukey test at a $p < 0.01$ significance level.

To test whether there was specialization in the transportation of specific resources according to the class of workers, we made comparisons using the chi-square test at a $p < 0.01$ significance level. To determine whether there was any specialization in the worker in the transport of specific resources such as cladodes, fruit, and seeds, we analyzed samples from nests when these resources were being foraged. We counted the total fruit and seeds that were foraged and the total of other resources and we compared them using a chi-square test for each class of foraged fruit, seeds, and other resources. The same comparison was made for the cladode resource.

RESULTS

Atta robusta foragers were classified into five classes based on the size of their head capsule which ranged from 0.95 mm to 5.62 mm. It was verified that the average mass of load carried by the foragers was 0.0365g and the maximum load was 0.450 g.

Most foragers present on the trails were in classes 1 and 2, and these two classes combined constituted 95% of all ants collected from the trails (Fig. 1).

We showed that there was a significant difference in the mass of the loads transported by the different classes of workers (ANOVA, $F = 243.26$, $p < 0.01$).

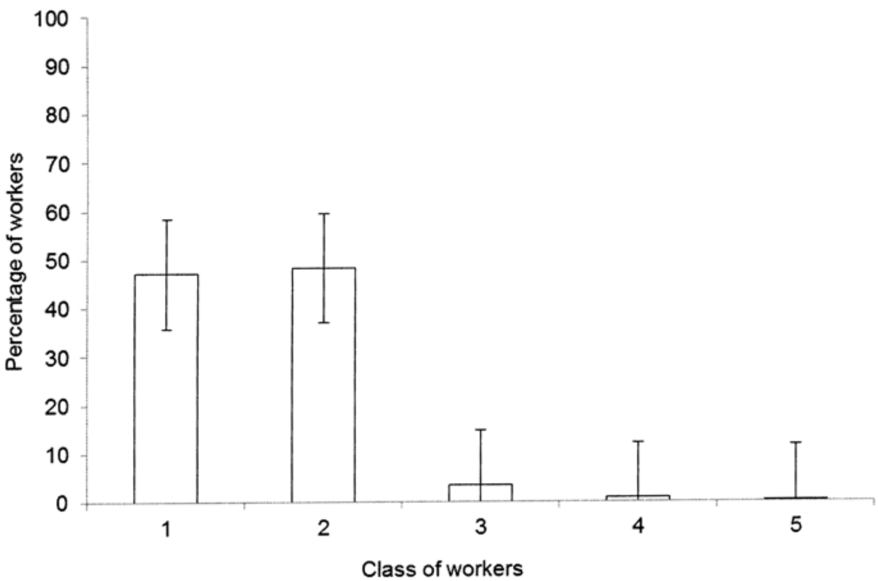

Fig. 1. Percentage (± SE) of workers of *Atta robusta* of different size classes that foraged during one year in restinga ecosystem from Grussaí/Iquipari complex. Class 1 (head capsule 1 to 2 mm), class 2 (head capsule 2.1 to 3 mm), class 3 (head capsule 3.1 to 4 mm), class 4 (head capsule 4.1 to 5 mm) and class 5 (head capsule (≥ 5.1 mm).

Ants with a larger head capsule transported the plant fragments with the highest mass ($p < 0.01$). Classes 3 and 4 did not differ in the mass of the load they transported ($p = 0.69$) (Fig. 2).

All classes transported all the different types of plant material, i.e., leaf, flower, fruit, seed, cladodes, and other. In nests ($n = 4$) that foraged for fruit and seeds, this corresponded to 8% of all the resources foraged. It was shown that workers in class 3 ($\chi2 = 75.13$; $p < 0.0001$), class 4 ($\chi2 = 5.44$; $p < 0.0197$), and class 5 ($\chi2 = 44.78$; $p < 0.0001$) transported more fruit and seeds than other resources. Thus, it was shown that when a colony exploited a substrate source producing fruit or seeds, the larger workers (class 3, 4 and 5) transported these resources preferentially (Fig. 3).

In nests where the ants collected cladodes, these constituted approximately 30% of all the resources foraged. Workers in class 4 transported significantly more cladodes than other resources (Fig. 4).

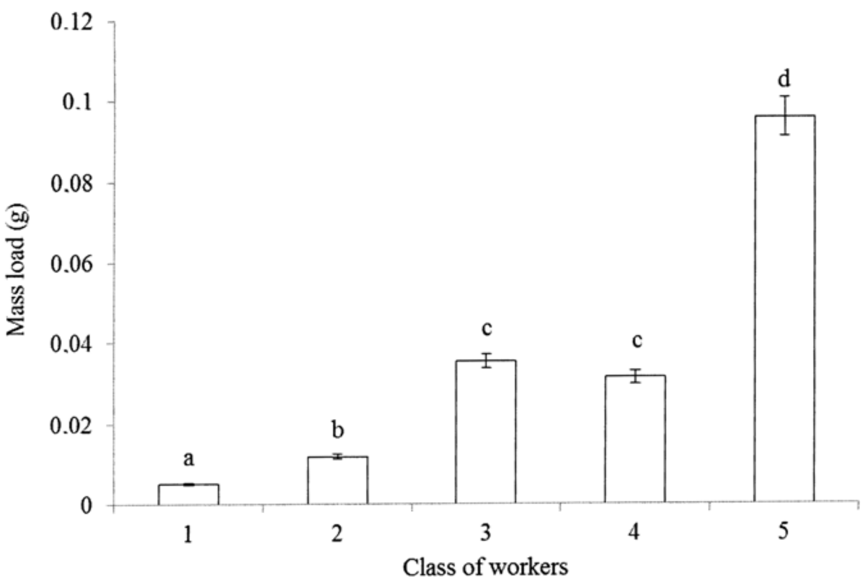

Fig. 2. Mass (g) (mean ± SE) of load transported by different classes of workers of *Atta robusta* in restinga ecosystem from Grussaí/Iquipari complex. Class 1 (head capsule 1 to 2 mm), class 2 (head capsule 2.1 to 3 mm), class 3 (head capsule 3.1 to 4 mm), class 4 (head capsule 4.1 to 5 mm) and class 5 (head capsule (≥ 5.1 mm5 to 6 mm). Different letters indicate significant difference by Tukey test, $p < 0.01$.

DISCUSSION

Atta robusta has foragers with the same pattern of caste distribution of the other attines. This was demonstrated by the large amount of workers in class 1 and 2 (head width from 1 to 3 mm) on trails sampled throughout a year of sampling. Colonies of the genus *Atta* contain a small number of larger foraging individuals, whereas most workers are of a medium size (Wilson 1985; Helanterä & Ratnieks 2008). The division of tasks inside a colony may be related to age polyethism, where young workers execute tasks inside the nest whereas older workers come out to forage (Hölldobler & Wilson 1990). Other factors, such as colony size and the worker size distribution, can also affect the division of tasks in the nest (Roces & Hölldobler 1994).

Larger *A. robusta* workers belonging to class 5 (head capsule width greater than or equal to 5 mm) transported loads that weighed significantly more than

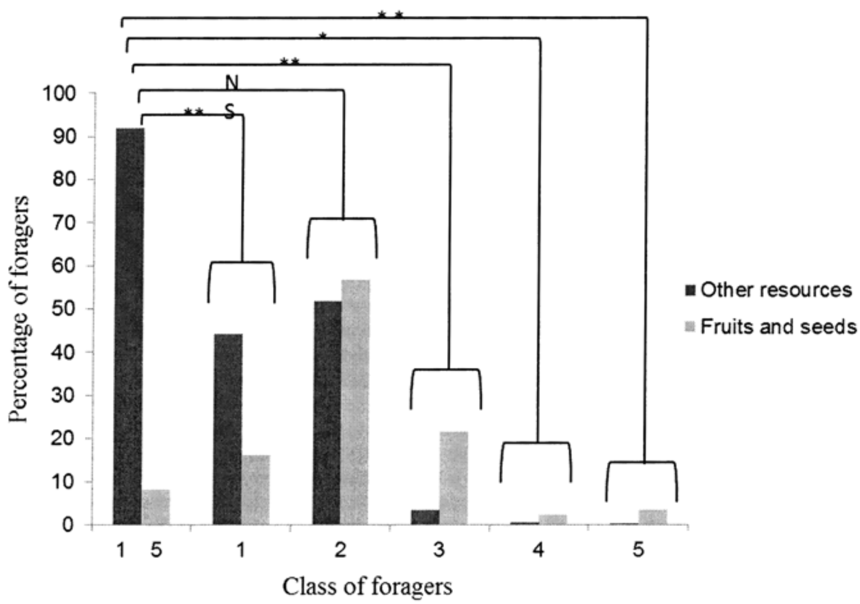

Fig. 3. Percentage of foragers of *Atta robusta* that transported fruits and seeds compared with that transporting other resources. NS = no significant difference by test $\chi 2$, * significant difference, $p \leq 0.0197$ and ** significant difference, $p < 0.0001$. Class 1 ($\chi 2 = 21.13$ and $p < 0.0001$), class 2 ($\chi 2 = 0.39$ and $p = 0.53$), class 3 ($\chi 2 = 75.13$ and $p < 0.0001$), class 4 ($\chi 2 = 5.44$ and $p < 0.0197$) and class 5 ($\chi 2 = 44.78$ and $p < 0.0001$).

those of other classes. According to Kleineidam *et al.* (2007), larger workers of *A. vollenweideri* transport heavier loads. The high degree of polymorphism in the genus *Atta* means that larger workers are proportionally more efficient in terms of energy returns, which compensates for the increased expenditure on their production (Hölldobler & Wilson 1990). Large *Atta cephalotes* workers specialize on leaves with a different thickness and hardness when exploiting leaves from a great diversity of plants. However, the foragers of *Acromyrmex octospinosus* are small in size so they cut a lower range of plants (Wetterer 1992). The foraging of leaves by *Atta vollenweideri* was divided into at least two phases, where the larger ants cut the leaves while the smaller ants carry the fragments to the nest (Röschard & Roces 2003).

In *Atta*, larger workers are responsible for the defense of the colony, but can also cut leaves. They have well-developed head capsules and mandibles (Evison 2007). In *Atta robusta*, the larger workers in class 4 participated in the cutting of cladodes from *Cereus fernambucensis* Lem. (Cactaceae) and they

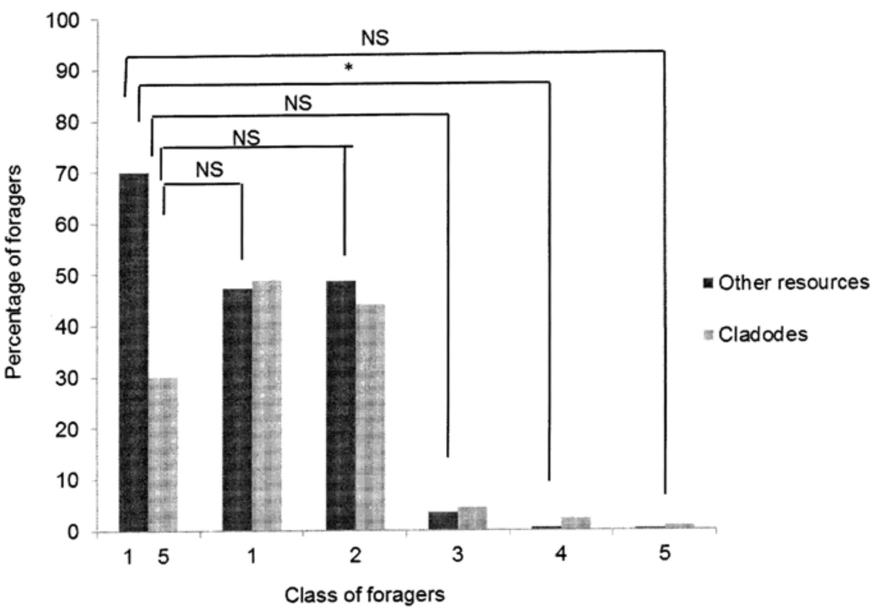

Fig. 4. Percentage of foragers of *Atta robusta* that transported cladodes compared with those that transported other resources. NS = no significant difference by test $\chi 2$, * significant difference, $p < 0.0171$. Class 1 ($\chi 2 = 0.07$ and $p = 0.79$), class 2 ($\chi 2 = 0.60$ and $p = 0.43$), class 3 ($\chi 2 = 0.44$ and $p = 0.50$), class 4 ($\chi 2 = 5.69$ and $p < 0.0171$) and class 5 ($\chi 2 = 0.76$ and $p = 0.38$).

collected proportionally more cladodes than other resources. The cladodes have a hard exterior, so workers with larger mandibles are required to cut this type of resource. During the cutting of *C. fernambucensis*, it was shown that larger workers cut the exterior surface of the cladodes, which is the hardest, whereas medium foragers in classes 1 and 2 collected the internal plant material that was easier to remove. These results reinforce the concept that colony polymorphism is an important factor that allows colonies to exploit a greater diversity of resources. Furthermore, it allows the colony to respond more efficiently to changes in the quality of available resources. Furthermore, Dussutour et al. 2009 also demonstrated the flexibility of foraging behavior in the leaf-cutting ant *Atta colombica*. The size and shape of the fragments of foraging material brought back to the nest were significantly modified when a constraint was placed on the trail, independent of their size, forager ants cut smaller and rounder fragments in the presence of a height constraint than in its absence.

In general, the *Atta* carry loads that are below their body capacity (Lighton *et al.* 1987; Wetterer 1990; Kleineidam *et al.* 2007). However, the seed load capacity of *Atta robusta* is increased, which is possibly due to cooperation and the participation of larger workers in the transport of larger seeds (Teixeira 2007). When larger workers were foraging, we found that classes 3, 4, and 5 preferentially transported heavier loads such as fruit and seeds rather than other resources. According to Evison (2007), larger *Atta laevigata* and *Atta sexdens* workers also transport fruit. In *Atta laevigata* colonies, only a small proportion of larger workers forage and they preferentially cut large pieces of fruit using their long mandibles (Evison 2007; Helanterä & Ratnieks 2008).

In the restinga of Grussaí/Iquipari, *Atta robusta* workers with significantly larger head capsules carried fruit and seeds. The transport of fruit and seeds by workers in classes 3, 4, and 5 supports the hypothesis of Teixeira (2007), which suggests that larger *Atta robusta* workers are responsible for the transport of larger seeds from several species of plants in the restinga, in addition to their defensive role in the colony. Thus, they have an important role in the ecosystem, because they may help the dispersal of seeds in the restinga. Several studies have shown that most of the fallen fruit from plants was removed by species of leaf-cutting ants, which played a relatively important role in terms of the amount of dispersed seeds, especially for plants with small fruit (Leal

& Oliveira 1998; 2000; Christianini & Oliveira 2009). Thus, leaf-cutting ants may disperse seeds found beneath plants or that were not dispersed by other animals (Christianini & Oliveira 2009).

This study demonstrated that larger *A. robusta* workers preferentially transported fruit and seeds. This behavior indicates the importance of larger workers, although they are present in smaller quantities on the foraging trail, in the exploitation of heavier resources such as fruit and seeds and their potential role in seed dispersal. Thus, this study contributes to the available evidence on the importance of *A. robusta* in the restinga ecosystem and this species should be considered in future management programs aimed at the conservation of these areas.

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