

Forager size of the leaf-cutting ant *Atta sexdens* (Hymenoptera: Formicidae) in a mature eucalyptus forest in Brazil

Athayde Tonhasca Jr.¹ and Marcos Antonio Lima Bragança

Centro de Ciências e Tecnologias Agropecuárias, Universidade Estadual do Norte Fluminense, Av. Alberto Lamego, 2000, Campos dos Goytacazes, RJ 28015-620, Brazil.

¹ Corresponding author. Athayde Tonhasca Jr. UENF-CCTA. Av. Alberto Lamego, 2000, Campos dos Goytacazes, RJ 28015-620, Brazil. Fax: +55-24-726-3746. E-mail: tonhasca@uenf.br

Received 2-XI-1999. Corrected 2-VI-2000. Accepted 16-VI-2000.

Abstract: We determined the size characteristics of foragers of the leaf-cutting ant *Atta sexdens* in a mature eucalyptus forest in Campos dos Goytacazes, Rio de Janeiro State, Brazil, at daytime (7: 30 to 10: 00 hr) and nighttime (19: 00 to 23: 00 hr). There were no significant differences between daytime and nighttime ant mass (M_a), but leaf fragment mass (M_l) and burden ($B = [M_a + M_l]/M_a$), which indicates relative load capacity, were significantly greater at daytime. There was a positive linear relationship between M_a and M_l for the combined daytime and nighttime data, and increases in M_a resulted in lower B . We compared *A. sexdens* characteristics with published results for *Atta cephalotes*, a closely related species. *A. sexdens* is larger and therefore able to carry heavier loads, but its burden is about 72% of the average value for *A. cephalotes*. We suggest that the lower load capacity of *A. sexdens* in comparison to *A. cephalotes* is related to its relatively larger size.

Key words: *Atta sexdens*, *Atta cephalotes*, ecology, foraging, leaf-cutting ants.

The leaf-cutting ant *Atta sexdens* (L., 1758) is common in primary forest throughout most of South America, but it readily invades new areas of agriculture or forestry, where it may become a serious pest (Cherrett 1986). The range and economical importance of *A. sexdens* have been increasing, probably because of the decline of native forests (Fowler 1983). Foraging of *A. sexdens* is predominantly nocturnal, although daytime foraging may occur sparsely throughout the day or during short periods of intense activity (personal observation). During daytime foraging, *A. sexdens* is exposed to harsh climatic conditions such as high temperatures and low humidity (Pereira da Silva 1975, Fowler and Robinson 1979), as well as parasitism from several species of phorid flies (Feener and Moss 1990).

Because of the high degree of polymorphism of *Atta* spp. (Wilson 1980a), it could be expected that *A. sexdens* colonies undergo a reduction in the average size of foragers from nighttime to daytime to cope with higher risks of desiccation (Wetterer 1990) and phorid parasitism (Orr 1992). This study was conducted to determine the size characteristics of *A. sexdens* foragers and whether there were significant differences on mass and load capacity between diurnal and nocturnal foragers. We also compared *A. sexdens* and *Atta cephalotes* (L., 1758) regarding the sizes of foragers and their loads. Research on the ecology of *Atta* spp. has focused mainly on *A. cephalotes* in natural forests, with considerably less available information on *A. sexdens* in disturbed habitats.

Because both species have the widest distributions of *Atta* spp. in South America (Fowler *et al.* 1989), we considered these comparisons worthwhile.

MATERIALS AND METHODS

The study was conducted from August 1995 to February 1996 in a forest of eucalyptus (*Eucalyptus* spp.) of approximately 1,300 ha located 35 km from Campos dos Goytacazes (21°48'S, 41°20'W), Rio de Janeiro State, Brazil. The forest undergrowth was composed mostly of grasses, which are rarely harvested by *A. sexdens*. Foraging trails of adult *A. sexdens* colonies were selected according to the ants' foraging activity, which was determined by the presence of fresh pieces of eucalyptus leaves along trails and around tunnel entrances. Because foraging activity varies among colonies and among trails within colonies, the location of observed trails varied during the study period, but at least five trails from five nests were used at each sampling date.

Leaf-cutting ants were sampled on three pairs of daytime (from 7: 30 to 10: 00 hr) and nighttime (from 19: 00 to 23: 00 hr) sampling dates: August 29 (n = 51) and 31 (n = 107), September 6 (n = 88) and 5 (n = 80), and February 7 (n = 47) and 6 (n = 107). Additional, non-paired samples were obtained at daytime on August 25 (n = 51), September 27 (n = 38), and February 16 (n = 125), and at nighttime on September 19 (n = 114). Each sample consisted of loaded ants collected randomly at approximately equal numbers from each foraging trail. The same trails were used on each pair of dates. Ants and their loads were placed individually in glass vials, which were held in an ice chest to reduce loss of water of the leaf fragments. In the laboratory, ants and leaf fragments were weighed to the nearest 0.1 mg on a precision balance. The ants' relative load capacity was evaluated with burden (B): $B = (M_a + M_l) / M_a$, where M_a and M_l are ant and leaf fragment masses, respectively (Rissing 1982).

To compare day and night results of M_a , M_l and B, we used mixed-model ANOVA's on the paired data only. Periods (day and night) were considered fixed effects and dates were considered blocks of random effects. Thus, F tests for period effects were calculated with the interaction between period and date. When interactions were not significant at a probability level of at least 0.25, interaction and residual mean squares were pooled (Sokal and Rohlf 1995). Analyses of M_a and M_l were done after a $\log(x)$ transformation to correct heterogeneity of variances. In the results, means are followed by ± 1 standard deviation.

Because division of labor is associated with polymorphism of *Atta* spp., head size is a good indicator of the workers' foraging capability (Wilson 1980a, 1980b). Head size of 161 ants selected at random from our samples was measured by the standard head width, which is the greatest width of the head viewed face on (Wilson 1980a). Measurements were taken to the nearest 0.1 mm with a dissecting microscope equipped with an ocular micrometer. The values of head size were correlated with mass for determination of an allometric relationship.

RESULTS

The ANOVA's indicated that the effects of dates were not statistically significant for M_a , M_l or B, but there was a significant interaction period x date for M_a ($F_{2,474} = 6.71$, $P = 0.001$). As the interactions period x date for M_l ($P = 0.44$) and B ($P = 0.93$) were not significant, residual and interaction mean squares for those variables were pooled. Daytime M_a was not significantly different from nighttime M_a , but M_l and B were significantly higher during the day (Table 1).

Similar to other leaf-cutting ant species (Burd 1995 and references therein), there was a positive linear relationship between mass of *A. sexdens* foragers and their loads (Fig. 1). The least-squares method was not adequate to describe the association between B and M_a because regression diagnostics demonstrated

TABLE 1

Comparison of forager and fragment mass (mg) and burden of daytime and nighttime *A. sexdens* foragers. Means are followed by ± 1 standard deviation.

Period	M_a	M_f	B
Daytime	21.8 \pm 15.1	40.8 \pm 34.5	3.3 \pm 1.7
Nighttime	21.4 \pm 15.1	31.6 \pm 22.2	2.7 \pm 1.1
ANOVA	$F_{1,2}=0.02, P=0.9$	$F_{2,476}=4.60, P=0.03$	$F_{2,476}=8.60, P=0.004$

M_a = forager mass, M_f = fragment mass, B = burden = $(M_a + M_f)/M_a$.

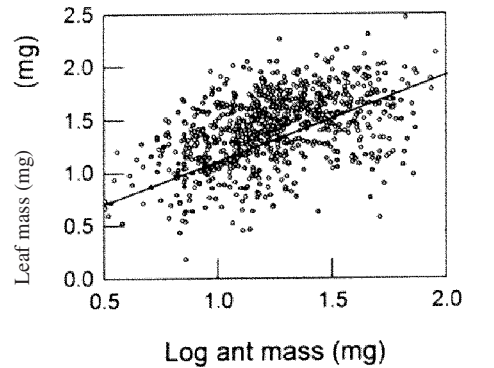
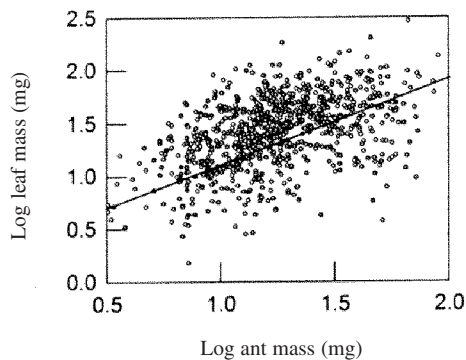


Fig. 1. The association between *A. sexdens* forager mass (M_a) and leaf fragment mass (M_f) for the combined daytime and nighttime data in a \log_{10} scale. The least-square model is: $\log M_f = 0.708 + 0.565 \log M_a$ ($r^2 = 0.217, P < 0.001, n = 808$).

that the assumption of homogeneity of variances did not hold despite transformations. However, histograms of M_a data divided in 10-mg intervals clearly demonstrated that an increase in M_a resulted in higher M_f and lower B (Fig. 2). The frequency of the mass-class distribution of all ants indicates that most foragers are in the 10-20 mg interval (Fig. 3). The allometric relationship between head size (HS) and M_a for *A. sexdens* can be expressed as $HS = 0.70 + 0.53 M_a^{1/2}$ ($r^2 = 0.983, P < 0.001, n = 161$). By converting mass values to head sizes, we determined that less than 20% of foragers have head widths between 2.2 and 2.6 mm, which was proposed by Wilson (1980b) as the most efficient size for *A. sexdens* foragers.

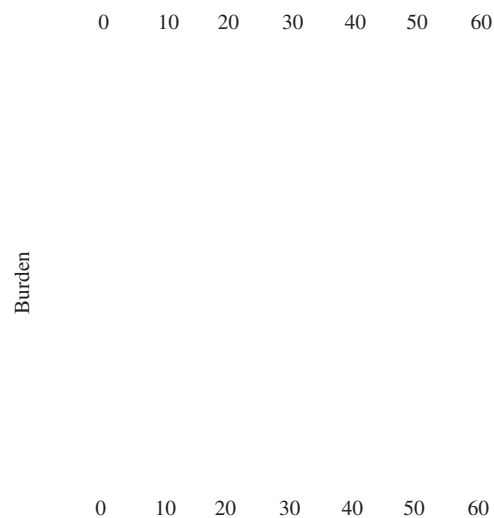


Fig. 2. The association between ant mass divided in 10-mg intervals and leaf mass (A) and burden (B). Number of observations are given for each interval; bars represent standard errors. Values of ant mass greater than 60 mg (2.4% of the data) were not considered because of their high variability.

TABLE 2

Comparison of forager and fragment mass (mg) and burden of *A. cephalotes* and *A. sexdens*. Means are followed by ± 1 standard deviation.

Species	M_a	Range	M_f	B	n
<i>A. cephalotes</i>	7.3 \pm 4.1	1.4 - 32.1	21.9 ^a	4.0 \pm 1.4	900
<i>A. sexdens</i>	21.5 \pm 14.6	2.3 - 90.0	33.9 \pm 26.4	2.9 \pm 1.4	808

M_a = forager mass, M_f = fragment mass, B = burden = $(M_a + M_f)/M_a$.
^a value estimated from Table 1 in Wetterer (1994).

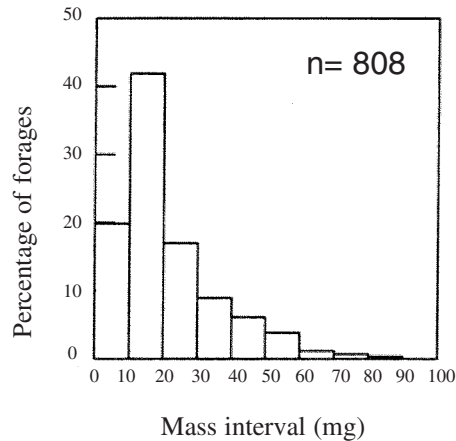


Fig. 3. The relative mass-class distribution of all *A. sexdens* foragers.

Both *A. sexdens* and *A. cephalotes* have reduced transport efficiency with increasing forager size (Fig. 2; Wetterer 1994). However, while *A. sexdens* foragers carry loads about 50% heavier than *A. cephalotes*, the average burden of *A. sexdens* is about 72% of the average value for *A. cephalotes* (Table 2). Additionally, while more than 80% of *A. cephalotes* foragers carry burdens larger than 1.5 times their body sizes (Rudolph and Loudon 1986, Wetterer 1994), almost half of all *A. sexdens* foragers (47.2%) had loads smaller than 1.5 times their body sizes, which corresponds to B = 2.5 (Fig. 2).

DISCUSSION

The traffic of *A. sexdens* foragers at daytime was very light and generally stopped abruptly when the temperature approached 30°C, a characteristic already described by Fowler and Robinson (1979). Despite their low numbers, daytime foragers were not significantly smaller than nighttime foragers. An earlier study in the same area (Tonhasca 1996) also failed to detect any meaningful diel differences for *A. sexdens* on trails, foragers or not.

Wetterer (1990) and Orr (1992) have proposed that the significant reduction on the average daytime mass of *A. cephalotes* foragers could be a strategy to escape parasitism from phorid flies, which prefer larger ants. Although we expect a greater impact of phorids on *A. sexdens* during daytime (Bragança *et al.* 1998), the effect of these parasitoids in response to diel differences has to be better evaluated, as we have observed strong phorid activity at nighttime (unpublished). The similarity between day and night foragers size may be related to the two-stage foraging system deployed by *A. sexdens*. While arboreal workers cut the petioles and drop the leaves, other workers cut leaf fragments on the ground and transport them to the nest (Fowler and Robinson 1979). Thus, efficient foraging either at daytime or nighttime require workers of a minimum size for cutting

the hard tissue of petioles, and this should be particularly important in homogeneous, mature commercial forests. Nonetheless, if foraging during the day is a riskier activity than at night because of greater chances of desiccation or parasitism, it could be expected that foragers optimize their daytime excursions by carrying greater loads. In fact, leaf fragment weight and burden of *A. sexdens* was heavier for daytime foragers.

Despite the significant relationship between ant and fragment masses, the linear model was a poor predictor of this relationship, even with a large number of observations and the log scale used. Equivalent results were obtained for *A. cephalotes* and *Atta colombica* (Guérin-Méneville, 1844)(e.g., Wetterer 1990, Shutler and Mullie 1991, Wetterer 1994, Burd 1995). It is clear from field observations that foraging of *A. sexdens* is subject to a great deal of "noise" from the environment. Ants drop their loads when they are disturbed by high wind speed, other arthropods and by hovering phorid flies (Bragança *et al.* 1998). Abandoned fragments may be picked up by other ants, and in these cases there is no apparent load size selection. Fragments also are abandoned when they become stuck in obstacles along trails, although occasionally foragers remove pieces of these fragments and resume their trips. As traffic along trails is routinely impaired by litter, larger fragments are more likely to be dropped because of obstacles. It has been demonstrated that leaf-cutting ants carry loads below their capacity, possibly because of a trade off between load mass and ant velocity (Rudolph and Loudon 1986, Lighton *et al.* 1987) or an overall gain of efficiency at the colony level (Burd 1996). Transport difficulties may be another factor that contribute to the relatively lower burden of larger workers of *A. sexdens* and *A. cephalotes* (Lighton *et al.* 1987) and the lower burden of *A. sexdens* in relationship to *A. cephalotes*. If that is the case, the lower foraging capacity of *A. sexdens* in comparison with *A. cephalotes* is associated with the larger size of *A. sexdens* foragers.

ACKNOWLEDGEMENTS

Thanks are expressed to Milton Erthal Jr. for helping with the field work. Jackie Blackmer, Gilberto Albuquerque and Og de Souza made important contributions on early drafts of this manuscript. A. Tonhasca Jr. was supported by a grant from the International Foundation for Science.

RESUMEN

Nós determinamos as características de tamanho de forrageiras da saúva *Atta sexdens* em uma floresta adulta de eucalipto em Campos dos Goytacazes, estado do Rio de Janeiro, Brasil, nos períodos diurno (7: 30 a 10: 00 hr) e noturno (19: 00 to 23: 00 hr). Não houve diferença significativa entre o dia e a noite para a massa das formigas (M_a), mas a massa dos fragmentos de folhas (M_f) e o esforço ($(M_a + M_f)/M_a$), o qual indica a capacidade relativa de carga, foram significativamente maiores durante o dia. Houve uma correlação linear positiva entre M_a e M_f para os dados diurnos e noturnos combinados, e o aumento em M_a resultou em esforço menor. Nós comparamos as características de *A. sexdens* com resultados publicados para *Atta cephalotes*, uma espécie correlata. *A. sexdens* é maior e portanto capaz de carregar cargas mais pesadas, mas seu esforço é cerca de 72% do valor médio obtido para *A. cephalotes*. Nós sugerimos que a menor capacidade de carga de *A. sexdens* em relação a *A. cephalotes* é devida ao seu tamanho relativamente maior.

REFERENCES

- Bragança, M. A. L., A. Tonhasca Jr. & T. M. C. Della Lucia. 1998. Reduction in the foraging activity of the leaf-cutting ant *Atta sexdens* caused by the phorid *Neodohrniphora* sp. Entomol. Exp. Appl. 89: 305-311.
- Burd, M. 1995. Variable load size-ant size matching in leaf-cutting ants, *Atta colombica* (Hymenoptera: Formicidae). J. Insect Behav. 8: 715-722.
- Burd, M. 1996. Server system and queuing models of leaf harvesting by leaf-cutting ants. Amer. Natur. 148: 613-629.
- Cherrett, J. M. 1986. History of the leaf-cutting ant problem, p. 10-17. In C. S. Lofgren & R. K. Vander Meer (eds.). Fire ants and leaf-cutting ants: biology and management. Westview, Boulder, Colorado.

- Feener, D. H., Jr. & K. A. G. Moss. 1990. Defense against parasites by hitchhikers in leaf-cutting ants: a quantitative assessment. *Behav. Ecol. Sociobiol.* 26: 17-29.
- Fowler, H. G. 1983. Distribution patterns of Paraguayan leaf-cutting ants (*Atta* and *Acromyrmex*) (Formicidae: Attini). *Stud. Neotrop. Fauna Env.* 18: 121-138.
- Fowler, H. G. & S. W. Robinson. 1979. Foraging by *Atta sexdens* (Formicidae: Attini): seasonal patterns, caste and efficiency. *Ecol. Entomol.* 4: 239-247.
- Fowler, H. G., M. I. Pagani, O. A. Silva, L. C. Forti, V. Pereira da Silva & H. L. Vasconcelos. 1989. A pest is a pest is a pest? The dilemma of Neotropical leaf-cutting ants: keystone taxa of natural ecosystems. *Environmental Manage.* 13: 671-675.
- Lighton, J. B. R., G. A. Bartholomew & D. H. Feener, Jr. 1987. Energetics of locomotion and load carriage and a model of the energy cost of foraging in the leaf-cutting ant *Atta colombica* Guer. *Physiol. Zool.* 60: 524-537.
- Orr, M. R. 1992. Parasitic flies (Diptera: Phoridae) influence foraging rhythms and caste division of labor in the leaf-cutter ant, *Atta cephalotes* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 30: 395-402.
- Pereira da Silva, V. 1975. Contribuição ao estudo das populações de *Atta sexdens rubropilosa* Forel, e *Atta laevigata* (Fr. Smith) no Estado de São Paulo (Hym.: Formicidae). *Stud. Entomol.* 18: 201-250.
- Rissing, S. W. 1982. Foraging velocity of seed-harvester ants, *Veromessor pergandei* (Hymenoptera: Formicidae). *Environ. Entomol.* 11: 905-907.
- Rudolph, S. G. & C. Loudon. 1986. Load size selection by foraging leaf-cutter ants (*Atta cephalotes*). *Ecol. Entomol.* 11: 401-410.
- Shutler, D. & A. Mullie. 1991. Size-related foraging behaviour of the leaf-cutting ant *Atta colombica*. *Can. J. Zool.* 69: 1530-1533.
- Sokal, R. R. & F. J. Rohlf. 1995. *Biometry*. Freeman, New York. 887 p.
- Tonhasca Jr., A. 1996. Interactions between a parasitic fly, *Neodohrniphora declinata* (Diptera: Phoridae), and its host, the leaf-cutting ant *Atta sexdens rubropilosa*. *Ecotropica* 2: 157-164.
- Wetterer, J. K. 1990. Diel changes in forager size, activity, and load selectivity in a tropical leaf-cutting ant, *Atta cephalotes*. *Ecol. Entomol.* 15: 97-104.
- Wetterer, J. K. 1994. Forager polymorphism, size-matching, and load delivery in the leaf-cutting ant, *Atta cephalotes*. *Ecol. Entomol.* 19: 57-64.
- Wilson, E. O. 1980a. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). I. The overall pattern in *A. sexdens*. *Behav. Ecol. Sociobiol.* 7: 143-156.
- Wilson, E. O. 1980b. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). II. The ergonomic optimization of leaf cutting. *Behav. Ecol. Sociobiol.* 7: 157-165.