BIOTROPICA 39(4): 476–481 2007 10.1111/j.1744-7429.2007.00283.x

# Assessing Herbivory Rates of Leaf-Cutting Ant (*Atta colombica*) Colonies Through Short-Term Refuse Deposition Counts

**Hubert Herz**[1]

Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Ancón, Republic of Panamá

**Wolfram Beyschlag**

Department of Experimental and Systems Ecology, University of Bielefeld, Universitätsstraße 25,
33615 Bielefeld, Germany

and

**Berthold Hölldobler**

Department of Behavioral Physiology and Sociobiology, University of Würzburg, Am Hubland, 97074 Würzburg, Germany;
and School of Life Sciences - LSC 274, Arizona State University, Tempe, AZ 85287-4501, U.S.A.

## ABSTRACT

Leaf-cutting ants (genera *Atta* and *Acromyrmex*) are considered dominant herbivores of Neotropical forests. However, so far quantitative, long-term, and large-scale assessments of their impact on these ecosystems are rare, because the available assessment methods were laborious and/or destructive. We describe a rapid, nondestructive, and inexpensive method to estimate the long-term harvest of *Atta colombica* colonies. Workers of *A. colombica* dump the colony refuse (exhausted fungal substrate) outside the nest. A single trail connects the refuse pile and the nest. In contrast to the foraging activity, the refuse deposition rate (the number of deposited refuse particles per minute) is diurnally constant and varies little on subsequent days. The number of refuse particles deposited per day was tightly correlated with the number of harvested fragments in nests of differing sizes ($R^2 = 0.77$, $P < 0.0001$). Therefore, the daily harvest of a particular colony can be calculated from short-term counts (5 min) of the refuse deposition rate at any time of the day. Combining these data with information on average fragment size (weight and/or area) allows the calculation of the total daily amount of biomass and/or foliage area harvested by the colony. This new method facilitates quantifying *A. colombica* herbivory on scales of populations and ecosystems, or over long-term scales.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

*Key words:* Barro Colorado Island; consumption rate; foraging activity; Formicidae; method; refuse production; tropical moist forest.

LEAF-CUTTING ANTS (ATTA SPP. AND *ACROMYRMEX* SPP., FORMICIDAE) ARE CONSPICUOUS AND WELL-KNOWN INSECTS OF THE NEOTROPICS, due to their remarkable activity as herbivores and the huge economic damage they cause in plantations. The foragers of these ants cut fragments of leaves and other plant parts from a large variety of host plant species and carry them to their large subterranean nests, where a mutualistic fungus (*Leucocoprinus gongylophorus*, Basidiomycetes) is cultured on these fragments (Weber 1972, Hölldobler & Wilson 1990). The fungus produces carbohydrate- and protein-rich food bodies (gongylidia) at the hyphal tips, which the ants feed to their larvae.

Leaf-cutting ants are perceived as the "prevalent herbivores" and "dominant invertebrates" of the Neotropics (Wheeler 1907, Wilson 1982). Although these quotes are cited frequently, they lack a sound quantitative base. Of the numerous publications on the harvest activity of leaf-cutting ants, only a few explicitly aim to quantify colony consumption or herbivory rate (for overviews see Lugo *et al.* 1973 and Fowler *et al.* 1990, but see Haines 1978, Wirth *et al.* 1997). Usually, only one or two colonies were studied and data were collected for a few days or weeks. The results, therefore, are unlikely to be representative for the population, habitat, or ecosystem level.

One reason for these shortcomings is the great effort required for data collection. Although the consumption rate for most herbivores can be concluded relatively easily from their biomass (*e.g.*, Schowalter *et al.* 1981 [insects], Nagy 1987 [vertebrates]), the huge subterranean colonies of leaf-cutting ants elude this approach (Cherrett 1989). For leaf-cutting ants, two main approaches have been used in the past. The harvested biomass is extrapolated from the amount of exhausted vegetable substrate deposited as waste in the subterranean chambers using a conversion factor (Autuori 1947, Amante 1967, Jonkman 1977, Fowler *et al.* 1994). This method requires the destruction of the nest (and therefore the colony), and the excavation procedure is extremely laborious. Therefore, most researchers apply the activity method where counts of fragment laden ants entering the nest and average fragment weights are used to calculate the colony consumption rate (Fowler *et al.* 1990). Because of the diurnal fluctuation of the harvesting activity (*e.g.*, Hodgson 1955, Lewis *et al.* 1974, Waller 1986, Wirth *et al.* 1997), such counts have to be conducted at short and regular intervals. Furthermore, they have to be performed simultaneously at all harvesting trails leading to the nest, which are often numerous. This method requires a considerable amount of effort, because data

Received 19 September 2005; revision accepted 1 September 2006.

---

[1] Corresponding author; e-mail: herzh@si.edu

collected automatically with photoelectric counters are not very reliable (Fowler *et al.* 1990).

To determine herbivory rates at the population or ecosystem level, indirect methods like exclusion experiments, transect methods, or remote sensing may be considered. Naturally, these are only practical in areas with a relatively thin and low canopy such as in studies of grass-cutting ant species (Fowler *et al.* 1986, 1990).

Lugo *et al.* (1973) and Fowler *et al.* (1990) published colony consumption rates for numerous leaf-cutting ant species. However, untested assumptions concerning fragment weights and the duration of annual activity were used for the calculations. In addition, single colonies may not be representative for the entire population. Quite often studies were conducted only on particularly big, "attractive" colonies, but the collected data were subsequently used for estimates at population or even at the landscape level, which could lead to erroneous overestimations (Fowler *et al.* 1990).

In this paper, we describe a simple and effective method for determining the consumption and herbivory rate of one of the most important leaf-cutting ant species of the Neotropics, *Atta colombica*. The method is based on the external refuse-dumping behavior of this species. Using this method, one can assess consumption and herbivory rates directly at the population level. We will describe this in a following paper (Herz *et al.* 2007). This enables comparisons among colonies, habitats, climatic conditions, and/or recordings of temporal variation.

## METHODS

STUDY SITE AND CLIMATE.—The study was conducted on Barro Colorado Island (BCI), Panama (9°09′ N, 79°51′ W), which is covered by a diverse lowland tropical moist forest (Leigh *et al.* 1996). In the focal area of this study, the forest is in a late-successional status of *ca* 100 years of age (Foster & Brokaw 1996). BCI receives an annual precipitation of *ca* 2600 mm with a pronounced dry season from mid December until mid April (Windsor 1990). For details on the study area and its vegetation see Leigh *et al.* (1996).

STUDY SPECIES.—*Atta colombica* Guérin (Formicidae) is distributed from Central America to Northern South America and is one of the dominant leaf-cutting ant species in that region. On BCI, it is the most abundant leaf-cutting ant species, occurring in about a 100-ha area at a density of 0.5 colonies/ha (Wirth *et al.* 2003). It is highly polyphagous, harvesting leaves, flowers, fruits, and other plant parts (Wirth *et al.* 1997, Herz 2001). Typical for this species is an external refuse pile directly outside the nest where the exhausted plant material is dumped (Haines 1978). Workers remove shredded and exhausted substrate from the fungus culture, form little pellets, and transport them to the waste heap on a single trail (Hart & Ratnieks 2002, pers. obs.).

REFUSE DEPOSITION RATE.—The refuse deposition rate (RDR) was assessed by counting the number of ants carrying refuse particles at the exit hole of the refuse trail. Ants carrying only a minute fragment (parts of disintegrated refuse particles) or dead ants were not included. Temporal variability of RDR was assessed at the scale of minutes, single and multiple days: For 10 colonies RDR was continuously counted for 10 min, recording individual values for each minute. Diurnal courses of RDR were measured for 20 colonies of a wide range of sizes: 5-min counts of RDR were taken at 1–1.5 h intervals for 24 h on selected days between June 1996 and December 1997. Nine diurnal courses were measured during the dry season and 11 during the wet season. Two additional diurnal courses of RDR of *A. colombica* on BCI were included from another study (Hodgson 1955: due to the characteristic refuse deposition behavior, the species he investigated can be re-identified as *A. colombica*). The total number of refuse particles carried within 24 h was calculated by integrating the curve of the diurnal course of RDR. Variation of RDR over several days was assessed for five colonies by taking 5-min counts at the same time of the day for each colony for 8 to 11 days.

HARVESTING RATE.—Diurnal courses of foraging activity were obtained in parallel with the measurements of diurnal courses of RDR for the 20 colonies (see above). Immediately after the measurement of the RDR, the foraging activity of the colony was recorded by counting the number of ants carrying plant material on each foraging trail for 3 min (Wirth *et al.* 1997). Again, two additional diurnal courses for *A. colombica* on BCI were included from Hodgson (1955). The total amount of fragments harvested by each colony in 24 h was calculated by summing up the foraging rates of all trails at the respective nest, and integrating the curve of the diurnal course of total foraging activity. The regression equation between the number of refuse particles deposited and the number of fragments harvested was calculated for the 22 diurnal courses.

TEST OF THE PREDICTIVE VALUE OF REFUSE DEPOSITION RATE FOR ESTIMATING THE DAILY HARVEST OF A POPULATION OF COLONIES.—The predictive value of a single RDR count for estimating the daily harvest (*i.e.*, total amount of harvested fragments) of *A. colombica* colonies was tested by comparing *predicted* values of daily harvest with *counted* values. Predicted values were obtained by selecting a single RDR count from each of the 22 diurnal courses in the different colonies at random. From these single RDR counts, the total number of deposited refuse particles in 24 h was calculated for each colony assuming a constant RDR for the entire 24 h. Subsequently, these values and the empirically derived linear equation of the correlation (Fig. 4) were used to calculate the total amount of harvested fragments for each of the available 22 diurnal courses. The *predicted* number of fragments was then compared with the *counted* number of fragments with linear regressions. This procedure was repeated 10 times to determine the variance of the goodness of the fit.

## RESULTS AND DISCUSSION

Refuse deposition rates (RDR) varied little throughout 24 h (Fig. 1), with an average coefficient of variation (CV) of 9.3 ± 6.1 percent (± SD, $N = 22$). Even throughout several subsequent days, RDR remained rather constant (CV of 7.1 ± 1.9%, $N = 5$; Fig. 2). In contrast, the rate of harvested plant fragments changed markedly

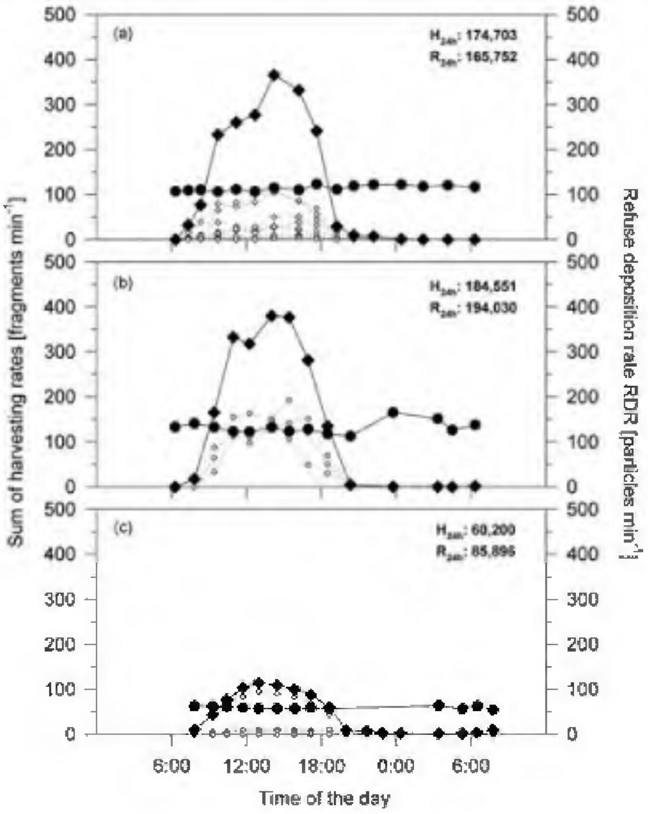

FIGURE 1. Examples for diurnal courses of harvesting and refuse deposition rates (RDR) for three different *Atta colombica* colonies on BCI. Shown are harvesting rate (number of plant fragments per time carried into the nest) on the individual trunk trails (open diamonds), the sum of these rates from all trunk trails (closed diamonds), and the deposition rate of refuse particles (closed circles). Further, the integrated total daily numbers of harvested plant fragments ($H_{24h}$) and deposited refuse particles ($R_{24h}$) are given for each diurnal course (see text).

during a diurnal course (Fig. 1) and had a CV of nearly 100 percent (98.3 ± 30.9%, $N = 22$). Diurnally fluctuating harvest activity in leaf-cutting ants is well known and has been ascribed to avoidance of parasitic phorids, avoidance of unsuitable environmental conditions, and/or exploitation of leaves with a higher energy content, with photoperiod and/or temperature serving as proximate cues (Hodgson 1955, Waller 1986, Orr 1992, Braganca *et al.* 1998). Diurnal constancy of refuse worker activity in *A. colombica* carrying waste particles has also been observed before (Hodgson 1955, Herz 2001, Hart & Ratnieks 2002). The causes for the lack of periodicity in refuse-dumping activity, and especially the contrast with harvest activity, remain unclear (Hart & Ratnieks 2002).

At the scale of minutes, refuse-carrying ants left the nest at varying rates. RDR counts over a single minute deviated on average 9.2 ± 8.2 percent from counts over 10 min (Fig. 3), with a maximum difference of 42 percent. In contrast, RDR based on 5-min counts deviated only by 3.62 ± 2.65 percent (range: 0.49–7.37%, $N = 10$) from the 10-min counts. Therefore, 5-min counts of the refuse deposition rates are well suited for assessing the diurnal as well as the long-term deposition rate of *A. colombica* colonies.

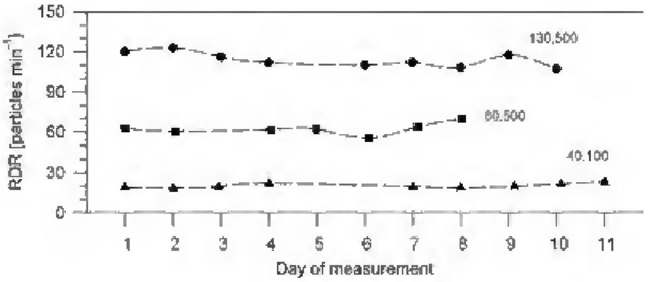

FIGURE 2. Examples of refuse deposition rates (RDR) of three *A. colombica* colonies of different sizes on consecutive days (different symbols for each colony). Averaged daily number of harvested plant fragments (calculated according to eq. (1)) are also given for the three colonies. Missing counts are due to rainfall events at the time of scheduled measurement when counts were omitted.

Across 22 colonies investigated, the number of refuse particles deposited on the external refuse pile in 24 h and the number of harvested fragments in 24 h were tightly and highly significantly correlated (Fig. 4). The harvested plant fragments constitute the original source for the refuse material. Ants process the fragments in the nest and implant them into the fungus culture, the mutualistic fungus digests the substrate, and the ants then remove degraded material from the garden and carry it to the refuse heap. Hence, the refuse consists mainly of digested remains of the plant fragments and possibly some adhering fungal hyphae (H. Herz, pers. obs.). A tight correlation between the number and the biomass of imported and exported fragments is therefore not surprising. Such a physiological relation, expressed as a conversion factor, has been used previously to

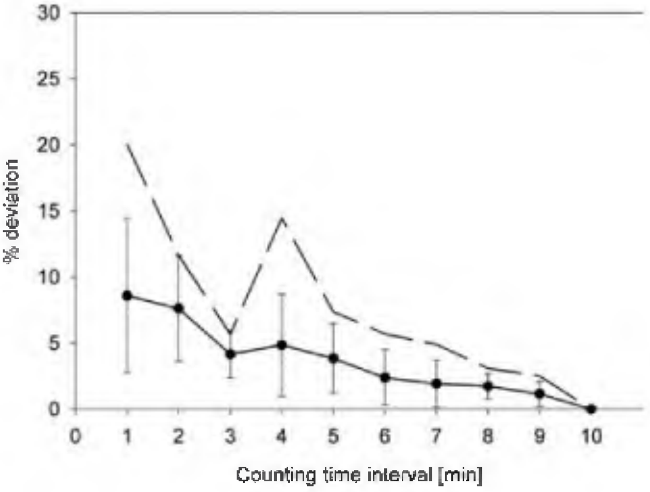

FIGURE 3. Effect of counting time interval on the quality of the results. The curves show average (±SD; $N = 10$; continuous line) and maximum (broken line) deviation of the measured refuse deposition rate (RDR) relative to a 10-min counting time interval.

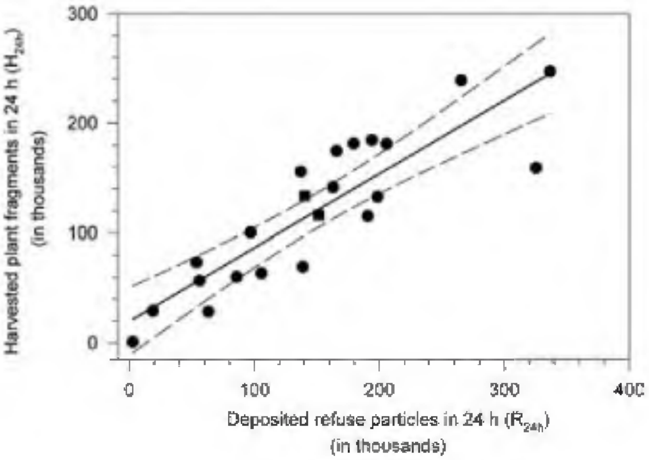

FIGURE 4. Correlation between the integrated total daily number of harvested plant fragments and deposited refuse particles for 22 *A. colombica* colonies on BCI. Also included are literature data for two colonies from Hodgson (1955) (squares). The regression equation is $H_{24h} = 0.6697 \times R_{24h} + 20472$, $R^2 = 0.767$, $P < 0.0001$, $N = 22$. Upper and lower 95 percent confidence limits (dashed lines) are described by the equations $H_{24h} = 0.4779 \times R_{24h}{}^2 + 6.2579 \times 10^{-7} \times R_{24h} + 50591$ and $H_{24h} = 0.8615 \times R_{24h}{}^2 + 6.2579 \times 10^{-7} \times R_{24h} - 9647$, respectively.

assess the amount of harvested biomass from the refuse biomass for leaf-cutting ant species with internal refuse chambers (see overview in Fowler *et al.* 1990).

The diurnal constancy of RDR (Fig. 1) and its tight linear relationship with harvesting activity (Fig. 4) can be employed to estimate the amount of colony harvest from its RDR. The equation for calculating the amount of diurnally harvested fragments ($H_{24h}$; fragments/24 h) from short-term determinations of the RDR (particles/min) can be derived from the regression equation in Figure 4 as

$$H_{24h} = 964.4 \times \mathrm{RDR} + 20472. \qquad (1)$$

Upper ($H_{24h-uc}$) and lower ($H_{24h-lc}$) 95 percent confidence limits for predicted $H_{24h}$ can be calculated with equations (2) and (3),

$$H_{24h-uc} = 1.2976 \times \mathrm{RDR}^2 + 688.2 \times \mathrm{RDR} + 50591 \qquad (2)$$

$$H_{24h-lc} = -1.2976 \times \mathrm{RDR}^2 + 1240.6 \times \mathrm{RDR} - 9647. \qquad (3)$$

When the number of fragments harvested by a colony in 24 h was calculated based on an RDR count randomly selected among the counts during a diurnal sampling period using this regression equation, the *predicted* values correlated highly significantly with the number of actually *counted* harvested fragments (Fig. 5). In 10 random draws, the average $R^2$ of the correlations was 0.74 ± 0.03 (minimum: 0.67, maximum 0.79), and all correlations were highly significant ($P < 0.0001$). Thus a short-term count of RDR at any time of the day can be used for the prediction of the diurnal harvesting rate.

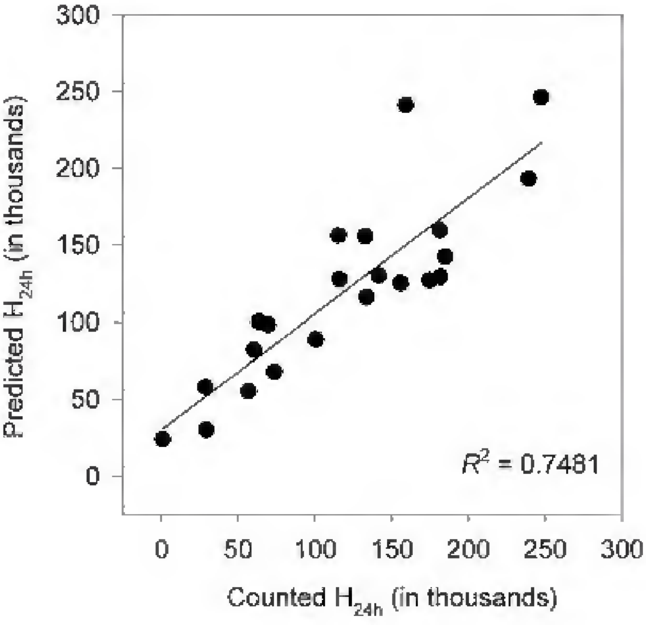

FIGURE 5. Example for the correlations between predicted and directly counted daily number of harvested fragments ($H_{24h}$). For each of the 22 colonies, one refuse deposition rate (RDR) was randomly selected among the RDR counts during the 24-h sampling interval, and used for the prediction according to eq. (1). ($P < 0.0001$, $N = 22$).

Combining the harvesting activity predicted from RDRs and characteristics of the harvested fragments, such as fragment weight and/or area, and the percentage of fragments that are leaves, allows one to calculate the long-term biomass and leaf area consumption and/or herbivory rate of *A. colombica* at a colony, population, or ecosystem level (Herz *et al.* 2007).

To estimate the daily biomass harvested by an *A. colombica* colony, the presented method requires four parameters: (1) average weight of a fragment; (2) RDR; (3) slope of the regression line; and (4) the *y*-intercept of the regression line. The accuracy of these parameters influences the quality of the result at different degrees. A sensitivity analysis showed that changes of the *y*-axis intercept had relatively little influence, in contrast to changes in the other three parameters (Table 1).

The method presented here has the advantage that short-term harvesting activity fluctuations, caused by rain or a predominance of exceptionally light or heavy loads (Wirth *et al.* 1997), are balanced by the temporal buffer effect of the fungus gardens (Kaspari & Vargo 1995, Fowler & Louzada 1996). Counts of the refuse particles, therefore, may reflect the overall herbivorial activity of a colony better than short-term counts of the harvesting rate (Wirth *et al.* 1997).

The method relies on the capacity to determine the refuse deposition rate, which is possible to do nondestructively in leaf-cutting ant species that dump their refuse externally (so far known from *Atta colombica, A. mexicana, A. laevigata, Acromyrmex landolti, Ac. lobicornis, Ac. lundi*; Haines 1978, Marquez-Luna &

TABLE 1. *Sensitivity analysis of the parameters of the proposed method to assess the amount of harvest of* Atta colombica. *The relative changes of the predicted daily harvested biomass in response to various relative changes of the four parameters necessary for the calculation (average fragment weight, refuse deposition rate, slope, and y-intercept of the regression line, compare eq. (1)) are shown.*

| Parameter changes (%) | Change in calculated harvested biomass (%) |
|---|---|
| (a) 5% increase of all parameters | +14.8% |
| (b) 5% reduction of all parameters: | −13.5% |
| (c) 100% increase of a single parameter: | |
| Fragment weight | +100% |
| Refuse deposition rate (RDR) | +82.3% |
| Slope of regression line | +82.3% |
| *y*-Intercept of the regression line | +17.7% |

Navarrete-Heredia 1995, Farji-Brener & Silva 1996, Jonkman 1977, Claver 1990, Bucher & Marchesini 2004). However, the diurnal rhythm of refuse deposition has not yet been studied for any species other than *A. colombica*.

The method presented in this paper allows assessment of the consumption rates of many colonies of *A. colombica* in a relatively short time and at low cost. It thus allows reliable assessment the herbivory rate of this important Neotropical herbivore at the scale of populations, habitats, or ecosystems.

## ACKNOWLEDGMENTS

We thank Boris Leymann, Andreas Meier, Antje Siegel, and Dorkas Kaiser for their help in the field. Rainer Wirth, Bettina Engelbrecht, and Damond Kyllo contributed to this project through valuable discussions or comments on the manuscript. We thank the Smithsonian Tropical Research Institute for providing field sites and facilities. The study was supported by the Deutsche Forschungsgemeinschaft SFB 251 and SFB 567, University of Würzburg, Germany.

## LITERATURE CITED

AMANTE, E. 1967. Prejuizos causados pela formiga saúva em plantações de Eucalyptus e Pinus no Estado de São Paulo. Silvicult. S. Paulo. 6: 355–363.

AUTUORI, M. 1947. Contribuição para o conhecimento da saúva (*Atta* spp. IV). O sauveiro depois da primeira revoada (*Atta sexdens rubropilosa* Forel, 1908). Arch. Inst. Biol. Sao Paulo 18: 39–70.

BRAGANCA, M. A. L., A. TONHASCA, AND 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.

BUCHER, E. H., AND V. MARCHESINI. 2004. Herbivory by leaf-cutting ants: nutrient balance between harvested and refuse material. Biotropica 36: 327–332.

CHERRETT, J. M. 1989. Leaf-cutting ants. *In* H. Lieth and M. J. A. Werger (Eds.). Ecosystems of the world 14B, pp. 473–488. Elsevier, Amsterdam, The Netherlands.

CLAVER, S. 1990. Methods for estimating the population density of leaf-cutting ant colonies. *In* R. K. Vander Meer, K. Jaffe, and A. Cedeno (Eds.). Applied myrmecology: A world perspective, pp. 220–227. Westview Press, Boulder, Colorado.

FARJI-BRENER, A. G., AND J. F. SILVA. 1996. Leaf-cutter ants' (*Atta laevigata*) aid to the establishment success of *Tapirira velutinifolia* (Anacardiaceae) seedlings in a parkland savanna. J. Trop. Ecol. 12: 163–168.

FOSTER, R. B., AND N. V. L. BROKAW. 1996. Structure and history of the vegetation of Barro Colorado Island. *In* E. G. Leigh, A. S. Rand, and D. M. Windsor (Eds.). The ecology of a tropical forest: Seasonal rhythms and long-term changes, 2nd edition, pp. 67–81. Smithsonian Institution Press, Washington, DC.

FOWLER, H. G., L. C. FORTI, V. PEREIRA-DA-SILVA, AND N. B. SAES. 1986. Economics of grass-cutting ants. *In* C. S. Lofgren and R. K. Vander Meer (Eds.). Fire ants and leaf-cutting ants: Biology and management, pp. 18–35. Westview Press, Boulder, Colorado.

FOWLER, H. G., L. C. FORTI, AND L. F. T. DI ROMAGNANO. 1990. Methods for the evaluation of leaf-cutting ant harvest. *In* R. K. Vander Meer, K. Jaffe, and A. Cedeno (Eds.). Applied myrmecology—a world perspective, pp. 228–241. Westview Press, Boulder, Colorado.

FOWLER, H. G., AND J. LOUZADA. 1996. Refuse production in leaf-cutting ants (Hymenoptera: Formicidae) and its relationship with leaf harvest. Biol. Rhythm. Res. 27: 148–152.

FOWLER, H. G., M. N. SCHLINDWEIN, AND L. C. FORTI. 1994. Decomposition rates of spent fungal refuse of *Atta sexdens* (Hymenoptera: Formicidae) and implications for estimating forage intake by leaf-cuttings ants. Pedobiologia 38: 266–268.

HAINES, B. 1978. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. Biotropica 10: 270–277.

HART, A. G., AND F. L. W. RATNIEKS. 2002. Waste management in the leaf-cutting ant *Atta colombica*. Behav. Ecol. 13: 224–231.

HERZ, H. 2001. Blattschneiderameisen im tropischen Regenwald: Freilanduntersuchungen zur Populationsdynamik sowie zu trophischen und nicht-trophischen Effekten von *Atta colombica* in Panama. Ph.D. Thesis, University of Bielefeld, Bielefeld, Germany.

HERZ, H., W. BEYSCHLAG, AND B. HÖLLDOBLER. 2007. Herbivory rate of leaf-cutting ants in a tropical moist forest in Panama at the population and ecosystem scales. Biotropica.

HODGSON, E. S. 1955. An ecological study of the behavior of the leaf-cutting ant *Atta cephalotes*. Ecology 36: 293–304.

HÖLLDOBLER, B., AND E. O. WILSON. 1990. The ants. Harvard University Press, Cambridge, Massachusetts.

JONKMAN, J. C. M. 1977. Determination of the vegetative material intake and refuse production ratio in two species of grass-cutting ants. Z. angew. Entomol. 84: 440–443.

KASPARI, M., AND E. L. VARGO. 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. Am. Nat. 145: 610–632.

LEIGH, E. G., A. S. RAND, AND D. M. WINDSOR (Eds.). 1996. The ecology of a tropical forest: Seasonal rhythms and long-term changes, 2nd edition. Smithsonian Institution Press, Washington, DC.

LEWIS, T., G. V. POLLARD, AND G. C. DIBLEY. 1974. Rhythmic foraging in the leaf-cutting ant *Atta cephalotes* (L.) (Formicidae: Attini). J. Anim. Ecol. 43: 129–141.

LUGO, A. E., E. G. FARNWORTH, D. POOL, P. JEREZ, AND G. KAUFMANN. 1973. The impact of the leaf-cutter ant *Atta colombica* on the energy flow of a tropical wet forest. Ecology 54: 1292–1301.

MARQUEZ-LUNA, J., AND J. L. NAVARRETE-HEREDIA. 1995. Biological notes on *Oosternum attacomis* (Coleoptera, Hydrophilidae), from Morelos State, Mexico. Entomol. News 106: 203–208.

NAGY, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111–128.

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.

SCHOWALTER, T. D., J. W. WEBB, AND D. A. CROSSLEY. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. Ecology 62: 1010–1019.

WALLER, D. A. 1986. The foraging ecology of *Atta texana* in Texas. *In* C. S. Lofgren and R. K. Vander Meer (Eds.). Fire ants and leaf-cutting ants: biology and management, pp. 146–158. Westview Press, Boulder, Colorado.

WEBER, N. A. 1972. Gardening ants: The attines. Am. Philos. Soc., Philadelphia, Pennsylvania.

WHEELER, W. M. 1907. The fungus-growing ants of North America. Bull. Am. Mus. Nat. History 23: 669–807.

WILSON, E. O. 1982. Of insect and man. *In* M. D. Breed, C. D. Michener, and H. E. Evans (Eds.). The biology of social insects, pp. 1–3. Proceedings of the 9th Congress of the International Union for the Study of Social Insects. Westview Press, Boulder, Colorado.

WINDSOR, D. M. 1990. Climate and moisture variability in a tropical forest: Long-term records from Barro Colorado Island, Panama. Smithson. Contrib. Earth Sci. 29: 1–145.

WIRTH, R., W. BEYSCHLAG, R. J. RYEL, AND B. HÖLLDOBLER. 1997. Annual foraging of the leaf-cutting ant *Atta colombica* in a semideciduous rain forest in Panama. J. Trop. Ecol. 13: 741–757.

WIRTH, R., H. HERZ, R. J. RYEL, W. BEYSCHLAG, AND B. HÖLLDOBLER. 2003. Herbivory of leaf-cutting ants: A case study on *Atta colombica* in the tropical rainforest of Panama. Springer, Berlin Heidelberg, Germany/New York, New York.