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Herbivory Rate of Leaf-Cutting Ants in a Tropical Moist Forest in Panama at the Population and Ecosystem Scales

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ABSTRACT

Leaf-cutting ants are frequently characterized as the major herbivores in the Neotropics, but quantitative data to back up this assumption are scarce. In this study, the consumption and herbivory rates for the entire leaf-cutting ant (*Atta colombica*, Formicidae) population in an old secondary forest on Barro Colorado Island (BCI) in Panama were determined over 15 mo (on average 49 colonies). The number of harvested leaf fragments was calculated from monthly refuse deposition rates of the colonies and the regression between refuse deposition and harvesting rates. The inclusion of fragment characteristics (proportion of leaf fragments in the harvest, average fragment weight, and area) allowed us to calculate consumption and herbivory rates at colony, population, and ecosystem levels. The *A. colombica* population harvested 13.2 tons of biomass/yr and 13.1 ha of leaf area/yr, and deposited 9.4 tons of refuse material/yr. Rates varied considerably among colonies. At the ecosystem level, *i.e.*, per forest area, herbivory rates were 132 kg biomass/ha/yr and 1310 m^2 foliage/ha/yr. For the area on BCI where *A. colombica* occurs (100 ha), this is equivalent to 2.1 percent of the foliage area in the forest or 1.7 percent of the annual leaf-area production. This value is considerably lower than previously published estimates of leaf-cutting ant herbivory rates in tropical forests.

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

Key words: Atta colombica; Barro Colorado Island; consumption rate; folivory; insect herbivory; leaf area.

OWING TO THEIR CONSPICUOUS HERBIVOROUS ACTIVITIES, and the enormous economic damage they cause in plantations each year (Cramer 1967), leaf-cutting ants (*Atta* spp. and *Acromyrmex* spp., Formicidae, Hymenoptera) are regarded as the "prevalent herbivores" and the "dominant invertebrates" of the Neotropics (Wheeler 1907, Wilson 1982). Although cited frequently, these quotes lack a sound quantitative basis.

One reason for the paucity of quantitative assessments of consumption and herbivory rates of leaf-cutting ants is the enormous effort necessary to obtain quantitative data. Lugo *et al.* (1973) and Fowler *et al.* (1990) give overviews on consumption rates of colonies of numerous leaf-cutting ant species. However, most studies on leaf-cutting ant herbivory were conducted over short time periods and/or for only a few colonies, and are therefore neither temporally nor spatially representative. In addition, numerous untested assumptions possibly skewed the results (Fowler *et al.* 1990). Only one investigation determined the consumption rate of a leaf-cutting ant colony (*Atta colombica*) over an extended time span in a natural forest (Wirth *et al.* 1997).

A rapid method was recently developed to assess long-term *A. colombica* harvesting rates at multiple nests (Herz *et al.* 2007). Such assessments are required for comparing herbivory rates in different habitats, climatic conditions, and/or for recording temporal variation of leaf-cutting ant herbivory. Furthermore, they are important tools for understanding the flow of energy and matter in tropical forests since they allow investigations at the ecosystem scale. In this study, we assessed the long-term consumption and herbivory rates of *A. colombica* at the population and ecosystem level.

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 tropical moist forest (Leigh *et al.* 1996). BCI receives an annual rainfall of about 2600 mm with a pronounced dry-season from mid-December until mid-April (Windsor 1990). For details on climate and vegetation of the site, see Leigh *et al.* (1996) and Wirth *et al.* (2003).

STUDY SPECIES.—*A. colombica* Guérin (Formicidae) is distributed from Central America to northern South America, and is one of the dominant leaf-cutting ants in this region. It is highly polyphagous, consuming leaves, flowers, fruits, and other plant parts (Wirth *et al.* 1997, 2003). An extended trail system leads to the host plants up

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to 80 m away from the colony. In contrast to other *Atta* ants, this species typically disposes used plant material and other colony waste on an external refuse pile that is nearby the nest (Haines 1978, Hart & Ratnieks 2002). On BCI, *A. colombica* is the dominant leaf-cutting ant species. We studied nearly the entire population, which occupies an area of about 100 ha of late-successional forest (*ca* 100 yr old; Foster & Brokaw 1996) with a density of *ca* 0.5 colonies per hectare (Wirth *et al.* 2003); one colony that settled outside of the 100 ha was excluded. All nests on BCI are known and mapped (Wirth *et al.* 2003). Only one large colony of another *Atta* species (*A. cephalotes*) was recorded in that area during the study period. The concentration of *A. colombica* colonies on BCI in just 100 ha is not related to distinctive characteristics of the habitat, such as edaphic conditions or forest vegetation. Instead it may reflect colonization of the forest from the laboratory clearing (see Wirth *et al.* 2003).

CONSUMPTION AND HERBIVORY RATES.—The method for assessing long-term consumption and herbivory rates of *A. colombica* was based on the finding that 5-min counts of refuse deposition rates (RDR) are tightly correlated with 24-h harvesting rates (Herz *et al.* 2007). RDR, the rate at which workers leave the nest to deposit particles on a refuse pile, was determined monthly for all *A. colombica* colonies in the study area between July 1997 and October 1998. Incipient colonies younger than a year or small colonies, which did not yet have at least one established foraging trail, were excluded. Five-minute RDR counts were made as ants left the nest on the refuse trail without disturbing the ants. In a few cases, it was necessary to remove litter or other obstructions that blocked a view of the trail. Such alterations were done several hours or days before the actual count, so that ants were not disturbed during measurements. Counts were taken only under dry weather conditions (*i.e.*, at least 3 h after rain) to ensure that waste disposal activity resumed. Counts were postponed when a sunfleck directly illuminated and heated sections of the refuse trail, which can disturb the ants (H. Herz, pers. obs.).

Characteristics of the harvested plant fragments (average area and dry weight of the leaf fragments, proportion of leaves, and of several other nonleaf categories in the harvest, *i.e.*, flowers, fruits, and *Ficus* stipules), and average refuse particle weights were determined for the *A. colombica* population on BCI. They were assessed monthly between July 1997 and October 1998 at 10 randomly selected colonies.

For fragment characteristics, all fragments were collected for 2 min at each trail entrance during peak harvest activity (noon to late afternoon, see Wirth *et al.* 2003). All fragments (sometimes together with the ant) were grabbed with forceps or by hand and collected in a plastic container. Care was taken not to disturb other ants on the trail to minimize alarm reactions. Ants and fragments were separated, and the number of fragments in each category was counted in the field for each colony. On average, each colony yielded *ca* 260 fragments ($N = 126$ samples) for a total of 32,807 fragments. The fragments were stored in sealed plastic bags and brought to the laboratory for further processing. The total area of the leaf fragments in each sample was measured with a leaf-area meter (LI-3100 Area Meter, Li-COR, Lincoln, NE, U.S.A.). Dry weight was determined separately for leaf fragments and nonleaf fragments after drying in an oven for at least 48 h at 70°C (to 0.0001 g, Mettler AE200, Mettler Instrument Corp., Highstone, NJ, U.S.A.). Average leaf-fragment area and weight of a fragment in a category was calculated for each colony from the total value divided by the number of fragments.

For refuse particles, 100 ants and the refuse particles they carried were collected from each colony with a modified battery powered, hand-held vacuum cleaner on trail sections free of loose soil or litter. Ants and refuse material were separated, and the ants were released. Refuse material was dried for 48 h at 70°C, then weighed.

Number of harvested fragments for each colony each day (H_{24h}), and their confidence intervals, were calculated from the RDR based on the regression equation of H_{24h} on RDR ($H_{24h} = 964.4 \times \mathrm{RDR} + 20{,}472$), determined for the same population (Herz *et al.* 2007).

Calculations of H_{24h} were made for each census rather than using a single median value for the whole observation period, to account for possible temporal variation. H_{24h} values were integrated for each colony over the 15-mo study period assuming linear changes of H_{24h} between censuses, and then converted to annual rates. To assess colony consumption rates on a biomass or leaf area basis, the predicted number of annually harvested fragments was multiplied by the average biomass of harvested fragments, or by the proportion of leaf-fragments in the harvest and the average fragment area, respectively (Table 1). Harvesting rates were expressed as consumption rates per year at the population and colony levels, and at the ecosystem scale as annual herbivory rate per forest area.

The biomass of deposited refuse material was calculated by extrapolating the RDR counts to 24 h (Herz *et al.* 2007), and multiplying it by the overall average refuse particle weight. Annual

TABLE 1. *Overview of harvest and refuse characteristics, and additional parameters used to calculate the herbivory rate of the* Atta colombica*—population in the study area on BCI. Leaf-area index and annual leaf production are from data in Leigh (1999) and Wirth et al. (2003).*

Parameter	Mean ± SD	*N*
Population size and study area:		
Number visited colonies per month	48.8 ± 4.0	14
Study area [ha]	100	
Leaf area index [m^2 /m^2]	6.25	
Leaf area production [m^2 /m^2 /yr]	7.78	
Leaf biomass production [t /ha /yr]	6.55	
Harvest and refuse characteristics:		
Fragment weight [mg]	6.5 ± 1.8	126
Proportion of leaf fragments of all fragments [%]	76.1 ± 22.9	126
Leaf fragment weight [mg]	6.3 ± 1.6	124
Leaf fragment area [cm^2]	0.85 ± 0.16	123
Weight of a refuse particle [mg]	3.8 ± 1.1	115

rates were again calculated by integrating these extrapolations over the 15-mo study period and converting them to annual values.

Median values are given because RDRs within each census (and parameters calculated from RDRs) deviated from normal distributions (Shapiro-Wilks W-tests). Standard transformations did not result in normal distributions, so nonparametric statistics were used.

Herbivory rates were related to total standing leaf area in the forest (leaf area index [LAI]), and to total annual leaf production (area and biomass) in a stand in the center of the study area on BCI (Lutz catchment). In this stand, Leigh and Smythe (1978) determined an LAI of 7.25 by measuring the total area of shed leaves within a year, and Wirth *et al.* (2003) calculated an LAI of 5.25 using a light interception model. Values between 6 and 8 for LAI are typical for tropical moist and wet lowland forests (Leigh 1999). For the purpose of this study, a mean LAI of the two available studies was used (6.25; Table 1). Annual leaf production in the same area (Table 1) was based on Leigh (1999).

RESULTS

In the 15-mo study of the *A. colombica* population on BCI, 48.8 ± 4.0 (mean ± SD) colonies were present at each census. Variation in colony number over time was due to mortality, and recruitment of small colonies into the size class included in the study.

REFUSE DEPOSITION.—The *A. colombica* population on BCI deposited 9.4 tons/yr of refuse, ranging from 34.3 to 399.4 kg/yr/colony in colonies that were followed for at least 6 mo (Table 2). On average, the colonies deposited 95.7 ± 16.0 particles/min/colony ($N = 14$ censuses, average over census medians). Among censuses, the median RDR varied significantly (Friedman ANOVA, $\chi^2 = 92.71$, df = 13, $P < 0.001$), mainly due to lower RDRs in June, July, and August 1998 (Fig. 1; multiple Wilcoxon matched pairs tests, $P < 0.05$, Bonferroni corrected). Among colonies, RDR varied idiosyncratically during the study period: for many colonies RDR stayed relatively constant over time, but others showed continuous increases or decreases, or discontinuities during nest relocations (Fig. 2). The frequency distribution of the RDRs that were determined over the study period was skewed toward low values (Fig. 3), reflecting the size distribution of the colonies.

TABLE 2. *Calculated consumption and herbivory rates of* Atta colombica *on BCI.*

Integration level	Rate	± 95% confidence interval
Population		
Number of harvested fragments/yr	2.03×10^9	0.35×10^9
Harvested leaf area [ha /yr]	13.1	2.3
Harvested biomass [t /yr]	13.2	2.3
Deposited refuse [t /yr]	9.4	
Ecosystem		
Annual loss of		
Leaf area [m^2 /ha /yr]	1310	227
Biomass [kg/ ha /yr]	132.4	23.0
Standing leaf area [% /yr]	2.1	0.4
Leaf area production [% /yr]	1.7	0.3
Leaf biomass production [% /yr]	1.5	0.3

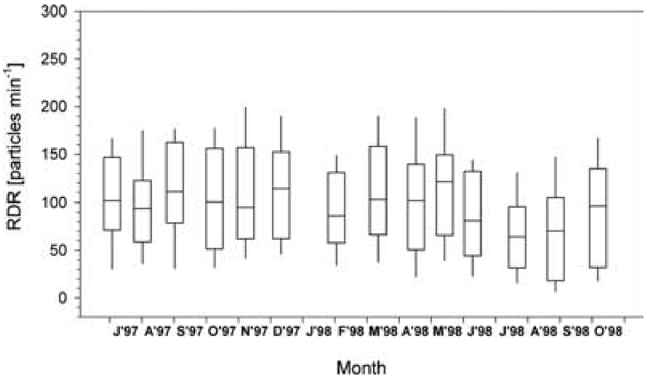

FIGURE 1. Refuse deposition rates (RDR) of *A. colombica*—colonies in 100 ha on BCI during the 15-mo study period. Box plot shows medians, 25th, 75th, 10th, and 90th percentiles. On average, 49 colonies were included in each census (Table 1).

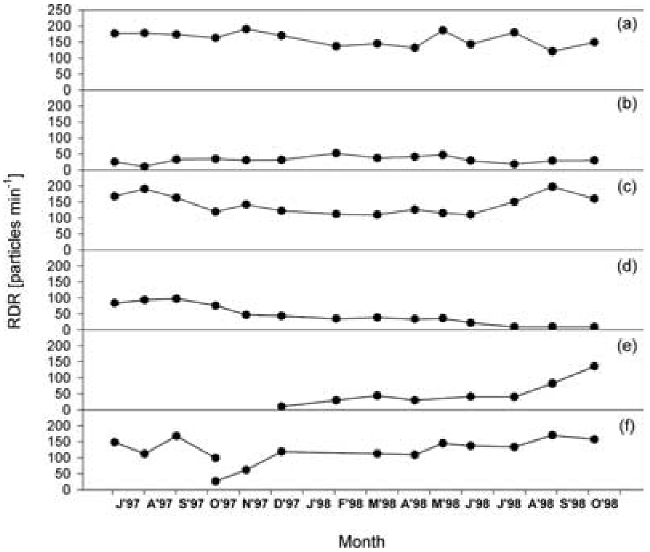

FIGURE 2. Examples of refuse deposition rates (RDR) of individual colonies of *A. colombica* during the observation period on BCI. Colonies in a, b, and c were present over the whole time and showed a relatively constant RDR for several months. The RDR of colony d decreased continuously until its demise in November 1998. The colony in e was newly founded and growing, and showed increasing RDR. The colony in f emigrated in October 1997, and, after several months at its new location, it showed a similar rate to that recorded preemigration.

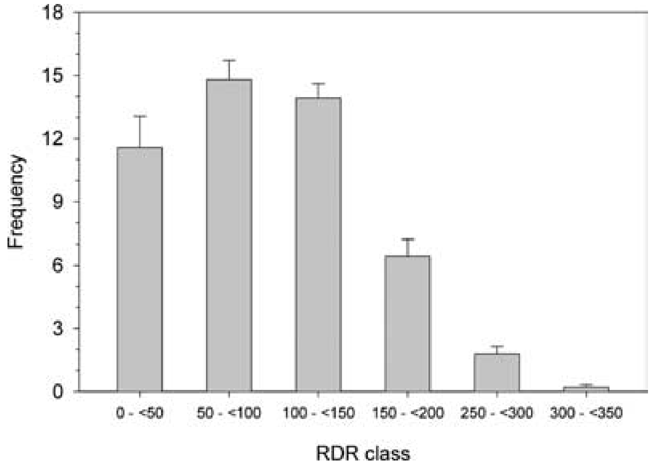

FIGURE 3. Frequency distribution of the refuse deposition rates (RDR, deposited particles/min) of *A. colombica*—colonies on BCI during the 15-mo study period. Values are means ± SE, $N = 14$ monthly censuses.

HARVEST OF FRAGMENTS AND THEIR CHARACTERISTICS.—At the population level, $2.03 \times 10^9 \pm 0.35 \times 10^9$ fragments/yr were harvested, *i.e.*, a median of 111,670 ± 15,940 fragments/d/colony (prediction ± 95% CI; Table 2). All patterns described earlier for RDRs also applied to the number of harvested fragments.

About three quarters of the harvested fragments were leaf fragments (Table 1). The remaining quarter consisted of nonleaf material, which included flowers, fruits, *Ficus*-stipules, and a small amount of leaf litter and other miscellaneous material (Herz 2001, Wirth *et al.* 2003). Average dry weight of harvested fragments, and dry weight and area of leaf fragments are given in Table 1.

CONSUMPTION AND HERBIVORY RATES.—Among colonies that were followed for at least 6 mo, harvested biomass and leaf area varied enormously, ranging from 88 ± 61 to 509 ± 66 kg/yr/colony and from 872 ± 607 to 5030 ± 657 m^2/yr/colony, respectively ($N = 25$ colonies). The whole population consumed a total of 13.2 tons of biomass and 13.1 ha of foliage/yr. At the ecosystem scale within the 100-ha study area, these ants cut about 2 percent of the available foliage area and the annual leaf production (Table 2).

On BCI, *A. colombica* is by far the most common leaf-cutting species and is almost entirely restricted to the 100-ha study area. The only other *Atta*-species, *A. cephalotes*, is very scarce and distributed over the entire 1600 ha of the island with approximately 12 colonies (H. Herz, pers. obs.). For the whole BCI forest, we therefore estimate that leaf-cutting ants consume about 0.13 percent of the available leaf area, and 0.1 percent of the annual leaf area and leaf biomass production.

DISCUSSION

Consumption rates varied about sixfold among the established colonies on BCI. This wide range covers almost the entire range of rates reported in other studies of consumption rates of leaf-cutting ant colonies harvesting dicotyledons (Table 3). Such variation

TABLE 3. *Colony consumption rates (dry weight unless indicated otherwise) of* Atta-*colonies compiled from literature. All values are for dicotyledon-cutting species. For grass-cutting species see Fowler* et al. *(1986). Question marks indicate lack of information in cited references.*

Consumption rate [kg biomass /col /yr]	Number of colonies	Nest size	Habitat	Method	Length of study	Reference
A. cephalotes						
68[a]	1	56 m^2	Rain forest in Guyana	Activity	1 d	Cherrett 1972
5.9 ± 1.0 (fresh weight)	1	In 8 yr on average 6.9 ± 2.2 liters fungus garden	Lab colony	Direct weighing	8 yr	Weber 1976
259.2	?	?	?	Activity	60 d	Harris 1969[b]
207.4	?	?	?	Activity	1 d	Markham 1966[b]
939.6	?	?	?	Activity	4 mo	Gara 1970[b]
55.7	1	?	?	Activity	60 d	Parsons 1968[b]
A. sexdens						
1.98	5	?	Lab colonies	Activity	10 d	Prado 1973
154.5	?	?	?	Conversion[d]	6.3 yr	Autuori 1947[b]
738	?	?	?	Conversion[d]	?	Amante 1967[b]
39.9	?	?	?	Activity	210 d	Vasconcelos 1987[b]
22.2	?	?	?	Activity	330 d	Schoereder 1985[b]
A. colombica						
183	1	3 trails	?	?	?	Emmel 1967[c]
416	1	44.8 m^2	Wet rain forest	Activity	50 h	Lugo *et al.* 1973
370	1	60 m^2	Moist rain forest	Activity	12 mo	Wirth *et al.* 1997
130 ± 60[a] (mean ± SD)	9	Diameter: 4.9 ± 1.1 m	Moist rain forest	Conversion[d]	4 mo	Haines 1978
266 ± 38 (pred. ± 95% conf.)	*ca.* 50	Mean: 22 m^2	Moist rain forest	Rate of refuse deposition	15 mo	This study

[a]Calculated from data in original publication; [b]cited in Fowler *et al.* (1990); [c]cited in Lugo *et al.* (1973); [d]a conversion factor from refuse to harvest biomass was used.

TABLE 4. *Consumption and herbivory rates of important herbivores on BCI (modified from Leigh 1999). Values in parentheses were used to calculate total folivory on BCI. Consumption of a sheep on a farm is shown for comparison (ARC 1965).*

Species or group	Consumption rate [kg dw /animal /yr]	Herbivory rate [kg /ha /yr]	Folivory rate [kg /ha /yr]
Alouatta palliatta (Mantled howler monkey)	110	88	35 (35)
Bradypus variegatus (Three-toed sloth)	22	110	110 (110)
Choloepus hoffmannii (Two-toed sloth)	22	22	22 (22)
Mazama americana (Red brocket deer)	282	≤ 60	? (60)
Tapirus bairdii (Baird's tapir)	2020	14	≤ 14 (14)
Coendou rothschildii (Rothschild's porcupine)	95	9–95	9–95 (10)
Iguana iguana (Green iguana)	5	7	7 (7)
Folivorous vertebrates (total)			< 300
Folivorous insects		476–624	476–624 (550)
Atta colombica[a]	266 ± 38 (per colony)	132.4 ± 23.0	96.6 ± 16.8 (97)
Frugivorous bats		*20*	
Frugivorous birds		*20*	
Total folivory rate on BCI (incl. *A. colombica*)			*ca* 900
Sheep (70 kg)	220		

[a] Calculated for the study area with high colony density on BCI, rate ± 95% confidence interval.

among colonies within a population can be attributed to age-related size differences, as well as to differences in the overall vitality of the colonies. In almost all studies of leaf-cutting ants to date, only single colonies were investigated (but see Haines 1978). Small sample sizes may help explain why the only other study based on several colonies (Haines) found a distinctly lower rate than in the present study, based on approximately 50 colonies (Table 3). Comparing results from the present study to published rates is of limited value since single colonies are not likely to be representative of a population.

Median consumption rates of *A. colombica* colonies on BCI were 266 kg/yr/colony. To put these consumption rates into a forest-wide perspective, this is about the same amount of biomass as the annual consumption by a single deer (*Mazama americana)*, which has the highest per capita consumption on BCI after the very rare tapirs (Terwilliger 1978, Leigh 1999; Table 4).

Our area-based herbivory rate of 132 kg biomass/ha forest/yr by *A. colombica* is at the lower end of the almost sevenfold range of reported herbivory rates by leaf-cutting ants in forest ecosystems (Table 5). At the ecosystem level, the estimates of 1.5 and 1.7 percent of the annual leaf area and biomass production, respectively, are considerably lower than the frequently cited values of 12–17 percent calculated by Cherrett (1989). The colony density in the study area was well within reported densities (Wirth *et al.* 2003), but colony densities can be as much as five times higher (*e.g.*, Rockwood 1973). This suggests that herbivory rates by leaf-cutting ants may indeed be higher in other forest systems, or may be higher in other species. However, the role of leaf-cutting ants as herbivores in other forests

TABLE 5. *Forest area based herbivory rates of leaf-cutting ants compiled from the literature.*

Herbivory rate [kg biomass /ha /yr]	Number of studied colonies	Size of study area	Habitat	Method	Duration of study	Reference
A. cephalotes						
653	3–4	0.15 ha	Experimental plots	Activity	5 mo	Blanton & Ewel 1985
A. colombica:						
517	1	0.13 ha	Moist rain forest	Activity	1 yr	Wirth 1996
297	1	1.4 ha	Wet rain forest	Activity	8 d	Lugo *et al.* 1973
98	9	28 ha	Moist rain forest	Conversion	4 mo	Haines 1978
132.4 ± 23.0[a]	*ca* 50	100 ha	Moist rain forest	RDR	15 mo	This study

[a] Calculated for the study area with high colony density on BCI, rate ± 95% confidence interval.

remains speculative as long as no quantitative data on colony sizes and consumption rates are available.

The great variation in consumption and herbivory rates reported for leaf-cutting ants (Tables 3 and 5) is probably due to numerous biological (a–c, below) and methodological (d–f) reasons: (a) *Species differences*: different species of leaf-cutting ants may have different consumption rates. The extent of any species differences is not known, since too few data are available (Table 3 and 5). (b) *Differences among habitats or host plant communities*: the highest herbivory rate of leaf-cutting ants detected so far was measured on relatively small plots that have been artificially altered by introducing exotic plant species (Blanton & Ewel 1985; Table 5). One plot even had a monoculture of manioc (*Manihot esculenta*), a species strongly preferred by *Atta*. (c) *Differences among spatial scales*: assessments of herbivory rates may depend strongly on scale. At the leaf level, herbivory can be much higher than on a whole plant level, or even larger landscape units. Individual host trees can experience a foliage loss of 5–50 percent and, in extreme cases, even total defoliation (Wirth *et al.* 2003, pers. obs.). Studies relating herbivory exclusively to the actual foraging area of a given colony obtained higher herbivory rates than studies on a landscape scale (Table 5). This difference emerges because leaf-cutting ants concentrate their activities to the 15–30 percent of the territory that is close to their persistent foraging trail system (Vasconcelos 1990, Wirth *et al.* 1997, 2003, Howard 2001). (d) *Selection of study colonies*: all investigations to date have included only a few colonies, which may not be representative for population or ecosystem scales. This is the first study to report the natural variability of consumption rates among colonies. Particularly large, "attractive" colonies have often been chosen for study, so that extrapolations to the whole population or larger landscapes units must lead to an overestimation of the herbivory rate (Fowler *et al.* 1990, Wirth 1996). (e) *Studies not representative at the temporal scale*: measurements of harvest activity were frequently obtained only over short periods of time (see Tables 3 and 5). Such short-term counts are susceptible to seasonally induced variability of harvesting activity (Wirth *et al.* 1997, 2003). (f) *Compiling disparate, nonrepresentative studies*: Cherrett (1989) compiled consumption rates of single colonies and colony densities in different areas from different studies. He obtained exceedingly high herbivory rates of 923 kg/ha/yr, or 12–17 percent of the annual leaf production, values which are in the same order of magnitude as the estimated *total* herbivory in Neotropical forests (see below and Leigh 1999).

The results from the current study allow us to reevaluate the contribution of leaf-cutting ants to folivory in tropical forests, and thereby their ecological role. On BCI, the total mass of available leaves is about 7360 kg/ha/yr (Leigh 1999) and total folivory is about 900 kg/ha/yr (Table 4; extended from Leigh 1999), which is equivalent to about 12 percent/yr of the available leaves (see Coley & Barone 1996 for comparison with other tropical forests). Thus, our determination of an herbivory rate of 2.1 percent of the available leaf area per year by *A. colombica* suggests that this one species causes about a sixth of the total folivory within the 100 ha area actually occupied by the population.

While BCI is an arbitrary area with respect to leaf-cutting ant biology, ecosystem studies often deal with landscape units unrelated to the distribution of certain species. At the landscape scale (*i.e.*, for the entire 1600 ha of BCI), *A. colombica* only consumes about 0.13 percent of the available leaf area, or about 0.7 percent of the total leaf consumption by all folivores. Since *A. colombica* is by far the most common leaf-cutting ant species on BCI, these estimates for *A. colombica* are only marginally lower than the herbivory rates of all leaf-cutting ants on BCI. This result shows that the overall effect of leaf-cutting ants on Neotropical forests can be considerably lower than estimates from focal study areas with high colony densities. Thus, animals such as sloths, howler monkeys, and deer cause a much higher proportion of the folivory on BCI (Table 4). Despite their conspicuous appearance in the fauna, leaf-cutting ants are clearly not the "dominant herbivores" on BCI.

The results from our study suggest that the impact of leaf-cutting ants as herbivores in natural tropical forests may be considerably lower than previously assumed, and highlight the surprising paucity of reliable information on this conspicuous and economically important organism. The population and ecosystem–level estimates of herbivory rates obtained in this study with a recently developed new method provide an important step toward comparative studies into the importance of leaf-cutting ants in various habitats, land-use, and disturbance regimes, or along geographic and climatic gradients.

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