# WHAT GOES IN MUST COME OUT: ASSIMILATION EFFICIENCIES OF *ATTA COLOMBICA* COLONIES IN PRIMARY AND SECONDARY FORESTS

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*Abstract:* Leaf cutter ants are responsible for an estimated 42% of herbivory in Corcovado National Park, Costa Rica. Given this and their unique habit of cultivating fungi to digest plant matter, it would be valuable to understand the efficiency with which they process energy. Secondary forest leaves are preferred by ants for fungus cultivation compared to primary forest leaves. We attempted to estimate assimilation efficiencies of two *Atta colombica* colonies in both primary and secondary forests. Two colonies carried organic waste out of the colonies into waste piles, while two colonies transported mineral dirt from underground and had no apparent organic waste piles. Only one colony yielded an estimate of assimilation efficiency that was potentially valid, and that estimate was unrealistically high (89%). Apparently these colonies are not in steady state, so calculations of assimilation efficiencies taken over two days are unlikely to be accurate.

*Key words: egestion, gut transit time, ingestion, leaf cutter ants*

## INTRODUCTION

As energy flows through trophic levels in an ecosystem, energy is lost during transfer (e.g., from producers to the consumers). The percent energy passed to the next level is related to the assimilation efficiency of the organisms that are consuming a lower trophic level. Assimilation efficiency is the percentage of food energy taken into the guts of the consumers which becomes available for incorporation into growth (Begon et al. 1986).

Mannan et al (1996) estimated that leaf cutter ants are responsible for 42% of the herbivory in Corcovado National Park. An estimation of the assimilation efficiency of these organisms would provide insight into how energy flows in this system. Secondary producers generally have low assimilation efficiencies (20 - 50%; Begon et al. 1986). Leaf cutter ants, however, have a unique method of digesting their diet. They harvest leaves and flowers for subterranean cultivation of fungus and then consume the hyphae and dispose of the waste material. *Atta colombica* dispose of this waste in piles outside their colonies (Stevens 1983). Because of this unique behavior, it may be possible to measure ingestion and egestion of individual colonies and therefore estimate their assimilation efficiency.

*A. colombica* occur in both primary and secondary forests. Nichol-Orians (1990, as cited in Bird et al. 1996) showed that because secondary forest leaves have fewer secondary metabolites, they are more suitable for fungus cultivation than primary forest leaves. Leaves from secondary forests may produce higher quality fungal food, which the ants will be able to assimilate at higher efficiencies. We therefore expected to see higher assimilation efficiencies in *A. colombica* colonies within the secondary forest.

## METHODS

We studied four leaf cutter ant colonies, two in secondary forest and two in primary forest, at Corcovado National Park, Costa Rica. We located all exit and entrance holes around the central colony nest by searching for any ant activity within a 10 m radius from the furthest entrance or exit to ensure that no entrances or exits were missed. We collected ingestion and egestion data on 4 - 5 February 2004. To measure

ingestion and egestion rate we counted the number of ants carrying plant or waste material in and out of the nest during 3 min observation bouts at each entrance and exit point. We measured all four colonies during five different time blocks (0800 - 0900, 1000 - 1100, 1200 - 1300, 1500 - 1700 and 2100 - 2300) over the two different days. We combined the two days of data to model diel patterns in ant activity.

To convert the counts per minute to ingested and egested biomass per minute, we measured the total dry mass of 15 - 20 leaf fragments and 50 - 75 clumps of waste particle egesta carried by the ants, then divided by the number of units to estimate approximate biomass for average particles of leaf or waste.

To determine total daily ingestion of each colony, we used a Fourier transformation (Veysey et al. 2000) to fit multiple regression models corresponding to sinusoidal functions with a period of one day (Appendix 1). We then calculated the area under the function using a Taylor approximation to obtain the daily ingestion rate (grams dry mass entering the nest per day). Because egestion rates did not exhibit diel patterns, we simply calculated the daily egestion rate of grams dry mass exiting the nest for each colony based upon the average rate per minute.

## RESULTS

We observed two different types of matter being carried out from the colonies. Ants in the primary forest (Colony $P_1$ and Colony $P_2$) carried material out of the colony from multiple holes in a large mound and deposited the material near the edge of the hole. Ants in the secondary forest (Colony $S_1$ and Colony $S_2$) carried material out of the colony from one hole and followed a trail away from the hole where they deposited the material onto a large mound. Microscopic examination revealed that the material from the secondary forest mounds was clearly organic (including leaf and stick remnants and mites), while the material from the primary forest mounds appeared to be entirely mineral soil, which was presumably the result of excavation activities rather than grooming fungus colonies.

The mass of leaf material from secondary and primary forest colonies did not differ greatly, while the mass of waste material did. The organic material from colonies $S_1$ and $S_2$ weighed less than the mineral soil from colonies $P_1$ and $P_2$ (Table 1). Colonies tended to have three to four active trails entering the nests, while there were six to nine active exits for the primary forest colonies and only one for each secondary forest colony (Tables 2 - 5).

The ingestion rates over one day followed a sinusoidal curve for Colony $P_1$ ($r^2$ = 0.89, $F_{2,4}$ = 8.45, P = 0.12), $S_1$ ($r^2$ = 0.95, $F_{2,4}$ = 18.57, P = 0.05) and $S_2$ ($r^2$= 0.96, $F_{2,4}$ = 29.43, P = 0.03), but not for Colony $P_2$ ($r^2$= 0.04, $F_{2,4}$ = 0.04, P = 0.96). Colonies differed in the timing of peak ant activity: Colony $P_1$ at 0130, $P_2$ had no peak, Colony $S_1$ at 1500 and Colony $S_2$ at 2130 (Fig 1). Average rates of material exiting the colony (± SE) were 1.26 ± 0.29, 10.51 ± 1.11, 1.39 ± 0.21 and 0.32 ± 0.06 g / min for Colonies $P_1$, $P_2$, $S_1$, and $S_2$ respectively (Fig 1). The colonies in primary forest did not have trails of ants carrying organic waste material, and the colonies in secondary forest showed no excavation.

Table 1. Approximate dry mass of individual leaf fragments and egesta for each colony, as used to calculate total biomass flux.

| Colony | Individual leaf mass (g) | Individual exiting mass (g) |
|---|---|---|
| $P_1$ | 0.022 | 0.017 |
| $P_2$ | 0.015 | 0.028 |
| $S_1$ | 0.023 | 0.013 |
| $S_2$ | 0.014 | 0.008 |

Table 2. Colony $P_1$ ingestion rate and excavation rate data recorded on 4 - 5 February 2004. Rates came from the sum of the rates from each trail. There was no evidence of organic waste exiting the nest.

| Time of day | # active trails | Total ingestion / min | # active waste piles | Total excavation / min |
|---|---|---|---|---|
| 0800 | 3 | 173.0 | 9 | 116.7 |
| 1045 | 3 | 30.0 | 9 | 123.0 |
| 1300 | 4 | 194.3 | 6 | 72.7 |
| 1600 | 4 | 250.7 | 6 | 95.0 |
| 2130 | 4 | 228.7 | 9 | 77.0 |

Table 3. Colony $P_2$ ingestion rate and excavation rate data recorded on 4 - 5 February 2004. Rates came from the sum of the rates from each trail. There was no evidence of organic waste exiting the nest.

| Time of day | # active trails | Total ingestion / min | # active waste piles | Total excavation / min |
|---|---|---|---|---|
| 0900 | 3 | 17.7 | 9 | 372.7 |
| 1120 | 3 | 51.7 | 9 | 306.7 |
| 1240 | 2 | 66.7 | 9 | 372.3 |
| 1645 | 3 | 36.7 | 8 | 405.3 |
| 2130 | 3 | 173.0 | 9 | 400.7 |

Table 4. Colony $S_1$ ingestion rate and egestion rate data recorded on 4 - 5 February 2004. Rates came from the sum of the rates from each trail. There was no evidence of excavation activity.

| Time of day | # active trails | Total ingestion / min | # active waste piles | Total egestion / min |
|---|---|---|---|---|
| 0900 | 4 | 17.7 | 1 | 99.3 |
| 1000 | 4 | 26.7 | 1 | 78.0 |
| 1230 | 4 | 50.7 | 1 | 84.0 |
| 1645 | 4 | 83.0 | 1 | 83.3 |
| 2200 | 3 | 48.7 | 1 | 65.0 |

Table 5. Colony $S_2$ ingestion rate and egestion rate data recorded on 4 - 5 February 2004. Rates came from the sum of the rates from each trail. There was no evidence of excavation activity.

| Time of day | # active trails | Total ingestion / min | # active waste piles | Total egestion / min |
|---|---|---|---|---|
| 0800 | 1 | 1.7 | 1 | 43.3 |
| 1100 | 2 | 69.7 | 1 | 38.3 |
| 1245 | 4 | 55.3 | 1 | 30.3 |
| 1600 | 3 | 86.7 | 1 | 38.3 |
| 2100 | 2 | 1.3 | 1 | 51.0 |

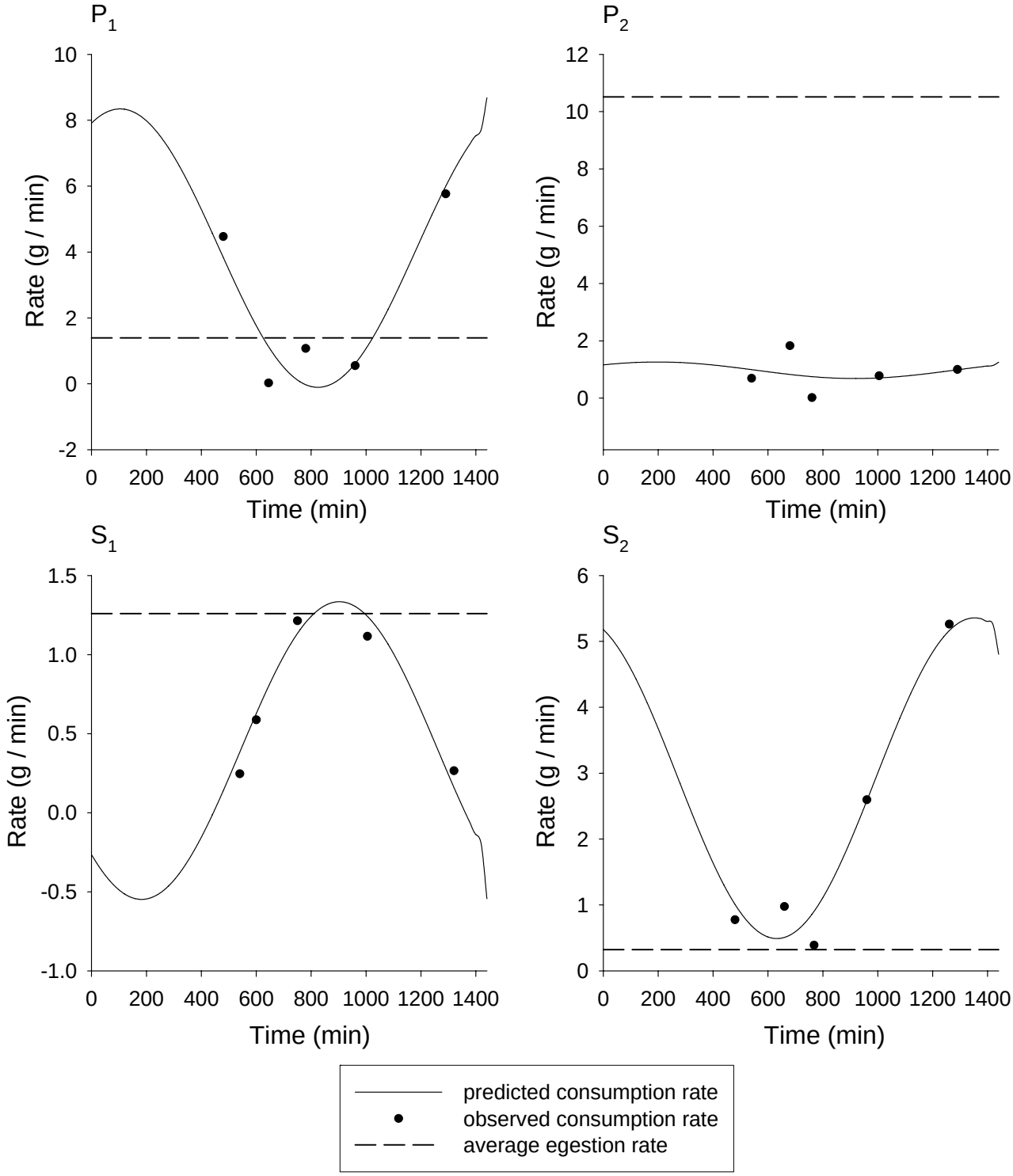


Fig. 1. Consumption rates (with best fit sinusoidal functions) and egestion rates over one day (1440 minutes) for colonies in primary forest ($P_1$ and $P_2$) and secondary forest ($S_1$ and $S_2$).

Assimilation rates could not be calculated for colonies $P_1$ and $P_2$ because we lacked estimates for egestion (Table 6). Calculated assimilation rate for $S_1$ was negative (and therefore impossible). For colony $S_2$, assimilation rate was estimated as 3.84 kg per day, and assimilation efficiency was estimated at 89%, which, if true, would be higher than for any other herbivore that has been studied.

Table 6. Calculated daily rates of ingestion, egestion, and excavation, along with corresponding estimates of assimilation rate (ingestion - egestion), and assimilation efficiency (assimilation / ingestion) for *A. colombica* in primary forest (Colony $P_1$and Colony $P_2$) and secondary forest (Colony $S_1$and Colony $S_2$).

| Colony | Ingestion (kg/day) | Egestion (kg/day) | Excavation (kg/day) | Assimilation rate (kg/day) | Assimilation efficiency (%) |
|---|---|---|---|---|---|
| $P_1$ | 6.1 | -- | 1.8 | -- | -- |
| $P_2$ | 1.4 | -- | 15.1 | -- | -- |
| $S_1$ | 0.75 | 2.0 | 0 | -1.25 | -- |
| $S_2$ | 4.3 | 0.46 | 0 | 3.84 | 89.2 |

## DISCUSSION

Assimilation efficiencies were difficult to calculate over a two day time period. For one of the colonies, the calculated assimilation rate was negative, which is biologically impossible, and for another it was unrealistically high. One possible explanation is that it is not valid to assume that the system was in a steady state. *A. columbica* are selective foragers and may discover more preferred leaf types some days than others. A pulse in ingestion would presumably yield a subsequent pulse in egestion, so egestion could temporarily be greater than ingestion. Departures from steady state introduce particularly large errors in assimilation efficiency when the measurement period is brief compared to retention time in the system. We guess that the mean retention time for undigested material in an *A. colombica* colony is considerably more than two days.

Another difficulty in calculating assimilation for *A. colombica* colonies was that we could not locate egestion piles for two of the colonies. One possible explanation is that *A. colombica* stores some egested fecal matter underground. In fact, we were unable to find even inactive waste piles for the two colonies in primary forest.

Although we could not calculate assimilation efficiencies, we did observe some interesting behavioral patterns of the ants. Trails exposed to direct sunlight often have reduced ant activity during the hottest hours of the day, perhaps to reduce the risk of desiccation. Because sun exposure varied over the trails, this may explain the differences in timing of peak ant activity between colonies. Future studies should take into account trail exposure when making comparisons in ant activity.

Our study indicates that it is not easy to estimate assimilation efficiencies for *A. colombica* colonies. Nevertheless, an enormous volume of primary productivity passes into the underground chambers of leaf cutter ants throughout the Neotropics (4.8 tons / ha / year; Mannan et al. 1996). The efficiency with which biomass is processed has consequences for energy flux through the rest of the ecosystem. The habit of *A. colombica* of creating above-ground waste piles seems to create possibilities for further studies of how leaf cutter ants influence tropical ecosystems.

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Appendix 1. Fourier transformations to fit ingestion rates to a sinusoidal function.

Time was transformed twice with these equations:

SINE TIME = [1 + sin[$\pi$/2 + (time (min)) *2$\pi$/24]]/2

COSINE TIME = [1 + cos[$\pi$/2 + (time (min)) *2$\pi$/24]]/2

Multiple regressions were run with observed ingestion rate for each colony vs. sine time and cosine time to yield the three parameters b, $m_1$, $m_2$ , for the equation:

INGESTION RATE = b + $m_1$* [1 + SINE TIME] + $m_2$ * [1 + COSINE TIME]

This equation was used to interpolate ingestion rates for times in 20 minute intervals throughout the day, starting from 0000 to 2400.

Parameters for equation derived from a multiple regression of observed ingestion rate versus sine time and cosine time:

| Colony | b | $m_1$ | $m_2$ |
|---|---|---|---|
| A | 2.3581 | 7.2606 | -3.7389 |
| B | 1.0244 | 0.3375 | -0.4391 |
| C | 0.3166 | -1.1985 | 1.351 |
| D | -0.3261 | 4.6749 | 1.823 |