

COMUNICACIONES

Distribution of attacked plants along trails in leaf-cutting ants (Hymenoptera: Formicidae): consequences in territorial strategies

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Abstract: Leaf-cutting ants generally abandon plants before they are completely defoliated, following the intraspecific leaf quality variation among and within plants. One *Atta cephalotes* nest was studied to determine the trail rotation consequences in the territorial defense development. We supposed that, as a result of changes in the harvest activity and trail use, leafcutting ants obtain a good and unpredictable coverage of the foraging area. The study was conducted in Barro Colorado Island, Panamá, in October, 1989. During seven sampling days we registered number, distance and orientation of attacked/abandoned trees and new/abandoned trails. The results suggest a large and unpredictable covering of the foraging area as a consequence of rotational harvest activity. Since both, plants and colony are sessile, advantages of dominating a large foraging area are discussed.

Key words: Leaf-cutting ants, territoriality, trail system, angular statistics

Leaf-cutting ants (*Formiciade, Attini*) are considered one of the most destructive herbivorous insects in the Neotropics. Ants visit many plant species within their foraging areas, but are apparently selective. Although they sometimes defoliate entire trees, partial defoliation seems more common (Cherrett 1968, Rockwood 1977). Of 120 attacked plants, just 6 were attacked more than six days, and 30 just for a day (Cherrett 1968). Cherrett (1968) and Rockwood (1977) suggested that leafcutters abandon some resources before completely harvesting since each colony is sedentary, and there are only limited resources within their foraging range. A conservative foraging strategy could be positively selected to prevent overgrazing. Fowler and Stiles (1980) critically reviewed this idea, and proposed that the spatial and temporal variability of palatable patches in the

vegetation more easily explains this behavior. Howard's (1990) demonstration of a lack of induced defenses by grazing, and intraspecific variation of leaf quality both among and within the same plants support this hypothesis. Intraspecific variation in leaf quality is one of the causes of partial defoliation. The ants would be exploiting the most palatable patches at their maximum development, thus following them in space and time. It is well known that leaf cutting ants show ability to discriminate among small variations in the quality of foraged material (Rockwood 1977, Hubbel & Wiemer 1983, Howard 1990). On the other hand, leafcutters have well established trail systems (Hölldobler & Lumsden 1980). Spatial and temporal heterogeneity of patch harvest within a colony's neighborhood may produce changes in trail direction, changes in the use of trails, and modifications in the geometry of

cations in the geometry of foraging territories (Fowler & Stiles 1980). Much has been written about why trail systems exist in leaf-cutting ants, but almost nothing about their consequences in relation to territorial defense. Even though trails are constructed to harvest palatable patches, it seems probable that they also have an "inertial" defensive function in protecting the potential and restricted vegetation patches from possible competitors. It is known that leaf-cutting ants do frequently defend their territory, especially against other *Atta* species (Vilela & Howse 1986). Spatial distribution between colonies is an effective measure to reduce the aggression between some ant species (Hölldobler & Lumsden 1980). Intraspecific attacks in *Atta* include attacks on founding queens from other nests, on smaller colonies, and battles between columns of workers from different nests (Fowler 1977, Jutsum 1979, and personal field observation).

This study presents preliminary evidence that supports the hypothesis that rotation in harvest activity and trail results in a general and unpredictable covering of the area around the nest. This characteristic could be selectively advantageous to leaf-cutting ants as an "inertial" defense strategy.

The research was conducted on Barro Colorado Island (BCI), Panamá, during the late rainy season, October 1989. BCI, in Gatun Lake, is covered with tropical deciduous and semi-evergreen seasonal forest, estimated to be from 75 to 200 years old, and *Atta* spp. are common. We selected one adult *Atta cephalotes* (L.) nest (5 m aprox. of ratio) near the Shannon-Snyder Molino trail, and for seven consecutive days (except for one rainy day without ant activity) revisited it each morning. Each day we mapped: (a) number, distance and orientation (angle respect to the north) of the attacked/abandoned trees, and (b) number, length, and orientation of new/abandoned trails. Angular data were analyzed with angular statistics (Batschelet 1981).

Attacked plants per trail show a clustering in their angular disposition with regard to the main trail orientations (Fig. 1 and 2). The distribution of trail orientations can not be distinguished from random (Rayleigh test, $P > .55$, Bastchelet 1981, Fig. 2). A random distribution of the location of the abandoned trees (with 1, 2, 3 and 4 consecutive days of attack), also cannot be

rejected (Rayleigh test, $P = .25$, Bastchelet 1981) (Fig. 3). Data of attacked and abandoned trees is presented in Appendix 1, and its detail per day and trail in Table 1.

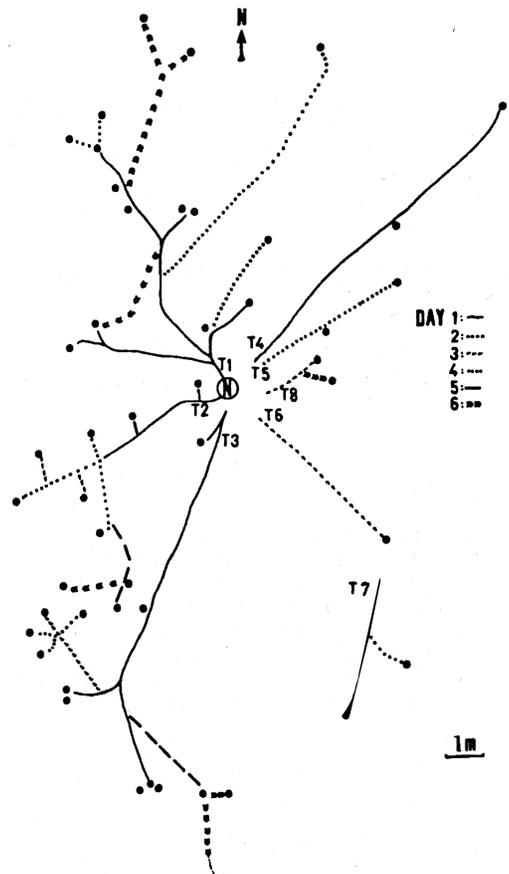


Fig. 1. Map of one adult *Atta cephalotes* nest (N) with the physical trails (T) (lines) and attacked trees (circles) during seven sampling days. The different lines utilized represent the day of the "trail inauguration".

We found two kinds of indirect evidence that could support the hypothesis of territorial defense: (a) the distribution of trails angularly covering a large area (Fig. 1 and 2), and (b) the angular orientation of abandoned trees could not be distinguished from random distribution (Table 1 and Fig. 3). Even though we sampled only seven days, the probability of ant presence was great in a wide foraging area. A visible consequence of the rotation in the attack of trees and in the use of trails is an unexpected presence of ants within the nest area, and a general covering of the foraging territory (Fig. 1 and 3).

TABLE 1

Newly attacked (left) and newly abandoned (right) trees per day and per trail

Trail									
Day	1	2	3	4	5	6	7	8	Total
1	8/0	0/0	4/0	2/0	0/0	0/0	1/0	0/0	15/0
2	4/1	1/0	3/0	0/1	2/0	0/0	0/0	0/0	10/2
3	0/2	3/0	1/2	0/0	0/0	1/0	0/0	1/0	6/4
4	1/2	2/2	3/2	0/0	0/0	0/0	0/0	0/0	7/6
5	0/2	2/2	1/3	0/0	0/0	0/0	0/0	0/0	3/7
6	3/0	2/1	5/0	0/0	0/2	0/1	0/0	1/1	11/5
Total	16/7	10/5	17/7	2/1	2/2	1/1	2/0	2/1	52/24

Number of attacked trees/number of abandoned trees. More than 46% of the total harvested trees were abandoned.

Since ant colonies are sessile it is an obvious advantage to dominate a wide foraging area, and to possess a maximize harvest pattern that also minimizes competition (Traniello 1989). There are many demonstrations of aggression between ant colonies (Fowler 1977, Jutsum 1979, Vilela & Howse 1986). Therefore, we suspect that the defense of the foraging area

plays an important role in the nests development and maintenance in ecological and evolutionary time. The foraging effort is centered on trails (Sheperd 1982) and the majority of these are conspicuous even though they are inactive during long periods (Gamboa 1975). For the nest studied, the attacked trees are highly angularly associated with the main trails (Fig 2).

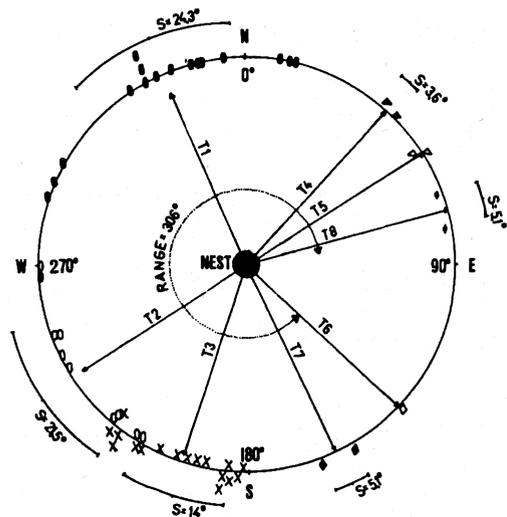


Fig. 2. Angular distribution (S) of attacked trees per trail (T). Attacked trees associated with each trail have different symbols, show a clustering in their angular disposition with regard to the main trail direction. Considering the mean vectors (T1, T2, etc.) as a trails direction, a regular (random) distribution cannot be rejected (Rayleigh test $P > .55$, Batschelet 1981).

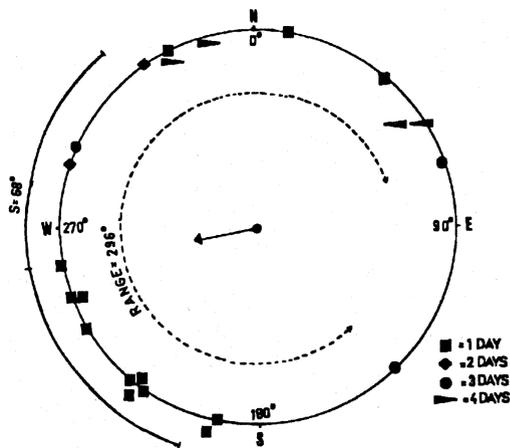


Fig. 3. Angular distribution of trees abandoned before they were defoliated during the study period. Different symbols represent trees with different numbers of continuous days being attacked. A regular (random) distribution can not be rejected (Rayleigh test $P = .25$, Batschelet 1981).

TABLE 2

Angular distribution of trails in some leaf-cutting ants nests

Autor	Lugo <i>et al.</i> (1973)	Gamboa (1975)	Cherrett (1968)
Ant specie	<i>Atta colombica</i>	<i>Acromyrmex versicolor</i>	<i>Atta cephalotes</i>
number of trails	5	4	4
mean trail	75.3	76.8	147.2
r	0.40	0.18	0.34
Angular desviation	62.8	73.8	65.6
Rayleigh test (random distribution)	P= 0.475	0.86 < P < 0.89	0.55 < P < 0.58

Data were obtained from nest maps of the papers cited. In all the cases regular distribution (randomnes) can not be rejected (Rayleigh test, Batschelet 1982).

Since both plants and colonies are sessile, the permanent trails would be acting as a "physical memory" showing the spatial location of patches that will be palatable in some period of the year. The temporal variations in their use would be following the qualitative variations of the resources. In this way we could explain the permanence of trails that apparently are not being used, but would be in some period of the year. This pattern of apparent "spatial stasis" and "temporal dynamism" associated with a permanent search for new plants, would have important consequences related to the defense of the foraging territory. The leafcutters' activity depends not only on a number of parameters of the "food resources" (quality, quantity, chemical defenses), but also on either the presence or the absence of alien foragers within the discovered patches (Hölldobler & Lumsden 1980). The resources previously occupied by competitors are clearly less attractive than the non visited ones (Hölldobler & Lumsden 1980). Therefore, the unpredictable presence of ants covering a large foraging area is obviously advantageous.

On the other hand, our data about the angular rotation of attacked trees during the sampling period do not show a systematic movement. There are no studies about the existence of a systematic rotation in the use of trails and in the foraging cycles of leaf-cutting ants, and a few antecedents of rotation in ant foraging columns (but see Franks & Fletcher

1983). Since the leafcutter foraging area is seen as a nest centered sector system (Hölldobler & Lumsden 1980), activity on each trail could possibly be independent of the others over a short time period. Ant trails have more than one function (Traniello 1989), and their existence is strong physical and chemical signs of an active colony. Generally, the disposition of trails covers the greatest part of the area around the leaf-cutting ant nest. This pattern can be seen in nests on other *Attini* species (Table 2), which could indicate a general pattern in leaf-cutting ants.

In conclusion, a consequence of the partial defoliation of trees is the temporary abandonment of trails and the establishment of "new" ones, with a general and unpredictable ant presence in the foraging area. Therefore, we suggest that this rotation in the trail use may have an indirect but important role in the territorial defense.

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Appendix 1: Trail utilized, nest distance, attack day, abandon day, and angular orientation of harvested trees by one adult *Atta cephalotes* nest during six activity days.

Trail	R1	R2	Thetha	T1	T2	total trees	
1-1	6	8	340	1	-	1	
	10	12	10	1	2	2	
	15	20	15	2	-	3	
1-2a	23	27	347	1	5	4	
	23	28	348	2	-	5	
1-2B	25	27	332	1	-	6	
	26	30	332	1	-	7	
	34	35	332	1	5	8	
	36	38	335	2	3	9	
	37	38	328	2	4	10	
	42	50	355	6	-	11	
	47	53	346	6	-	12	
	1-2c	42	47	14	4	-	13
		17	29	300	6	-	14
1-3	18	19	295	1	-	15	
	19	20	290	1	3	16	
2	2	4	270	3	-	17	
	11	12	260	5	6	18	
	28	30	244	2	-	19	
	24	26	250	3	4	20	
	21	23	240	3	4	21	
	15	17	250	4	5	22	
	24	40	220	4	5	23	
	29	50	210	5	-	24	
	29	51	211	6	-	25	
	3	32	57	220	6	-	26
4		4	205	1	-	27	
3-a	27	27	200	1	-	28	
	40	41	210	1	-	29	
	40	42	209	2	4	30	
	30	46	220	3	4	31	
	32	41	215	4	5	32	
	27	41	215	4	5	33	
	32	42	216	4	5	34	
3-b	45	46	192	1	-	35	
	45	46	191	2	3	36	
	45	46	193	2	3	37	
	50	51	184	5	-	38	
	83	86	180	6	-	39	
	63	66	185	6	-	40	
	83	86	182	6	-	41	
	83	87	185	6	-	42	
	50	52	183	6	-	43	
	4	25	25	45	1	-	44
40		42	40	1	2	45	

5	9	9	58	2	6	46
	17	19	58	2	6	47
6	24	24	134	3	6	48
7	16	16	160	1	-	49
	10	13	150	4	-	50
8	7	7	70	3	6	51
	5	5	80	6	-	52

R1 is the direct tree distance to the ant nest, and R2 the real distance in the field following the trail. Theta is the angle respect to the north for each tree. T1 is the first attack day, T2 the abandon day, and (-) with ant harvest activity at the day 7.