INTRODUCTION

Organisms use the space available to them in diverse ways. Thus, it should come as no surprise that "social animals" share in this diversity. In what areas do these differences appear? Unfortunately, compared to the amount of data compiled on solitary or subsocial animals, the territorial behavior of social animals has yet to be extensively studied. Ants are no exception, though some important laboratory studies have been completed.

Hölldobler and Wilson (1980) showed that the shape of the territory of three different ant species strongly depended on each species' foraging strategy: the weaver ant (Oecophylla longinoda) permanently occupies an "absolute territory" ranging up to 1600 m² including no more than 17 trees. A colony specific territorial pheromone acts as a repellent to foreign conspecifics, protecting the territory against invasions, even in the absence of residents. The harvester ants (Pogonomyrmex barbatus and P. rugosus) also have stable territories, but their territory is defined by trunk trails used by workers to collect seeds. Thus, Hölldobler and Wilson claim that the territory only consists of the trail system and the ant nests. Trails from different colonies never cross; rather, they tend to be oriented toward opposite directions. Accidental convergence of trails from different colonies causes aggressive confrontations lasting until the trails no longer intersect. Thus, the layout of a colony's trail system depends on that of its neighbor. The honey ant (Myrmecocystus mimicus) has a variable territory, which changes depending on the foraging activity and availability of termites. Hölldobler and Wilson (1980) claim that termites are a changing resource which make a stable territory inefficient and contact between workers from different colonies more frequent. This justifies the existence of ritualized confrontations that eliminate worker injury. Such a system also allows different colonies to exploit the same resource or use the same geographical area, thanks to separate spatio-temporal foraging patterns. If an area or resource is used simultaneously, neighboring colonies battle until one gives up. The winning colony takes over the loser's nest, killing the queen and taking larvae, pupae and replates to their nest.

Most of what is known of ant territorial behavior is based on descriptions from laboratory studies (Hölldobler and Wilson 1976, 1977;
Cammaerts et al. 1977; Fresneau 1980; Jaffe and Puche 1984) but little is
known about territorial behavior in the field (Wilson et al. 1971; Skinner
1980; Hölldobler 1981; Hölldobler 1983). The present work is part of a series
which will exhaustively study territorial behavior of Atta colonies in the field.
Attla laevigata, the most common Attla species in Venezuela and
Colombia, is normally found in savannas or disturbed habitats, where it forms
gigantic nests, possibly the largest Attini colonies. Little is known about its
territorial behavior, whereas for other Attini, territorial behavior of laboratory
colonies has been repeatedly observed (Jaffe et al. 1979; Vilela 1983;
Hölldobler and Wilson 1986). Despite these studies, not much can be inferred
about territorial behavior in a natural environment, since the habitat offered
to captive colonies is not comparable to the nest areas available in the field.
The present work studies the dynamics and territorial strategy of Attla
laevigata colonies in the field. In the process, some insight into the
significance of Attla colony territorial behavior should be gained.

MATERIALS AND METHODS

The study was performed on four neighboring Attla laevigata colonies
in commercial pine tree plantations (Pinus caribea) at Estado Monagas,
Venezuela. The site had 15 year-old pines and showed an A. laevigata density
of over 30 mature nests per hectare. To study the topographic distribution of
the territorial mark, a series of test were performed along a trunk trail. An
arena consisting of a bottomless plastic cylinder (9 cm diameter, 8 cm high)
was placed on the ground either at a nest mound where workers were
excavating earth, at the beginning of an active trail (0-1 m from a nest
mound), or at the middle or end of the trail (cutting area). The resident
workers were taken from the site where the experiment was performed and
were chosen from among the workers walking from the nest to the foraging
area. The intruders were collected from among the workers exiting their
nests, at the beginning of the trail. The experiment introduced either the
resident or the intruder to the arena, followed five minutes later by the other
ant. After introducing the second ant to the arena, the behavior of both ants
was observed for five minutes.

Each time, the cylinder was placed on a different site, avoiding bias
produced by a possible site-dependency. The cylinder was covered with Fluon
(ICl), avoiding the escape of test ants or the passage of ants from the outside.

Controls consisted of confrontations between ants of two neighboring
colonies on virgin territory. The cylinder was placed outside trails in sites
where no ant activity was observed.

The four test nests were observed for 19 months. The experimental area
(1500 m²) was drawn on a chart and the trunk trails, mounds, etc. replotted
approximately every four months; i.e. in March 1987 (middle of the dry
season), June 1987 (beginning of the rain period), November 1987 (end of the
wet season) and March, April and September of 1988. Such maps allowed a
study of the nests' temporal dynamics and the ants' foraging trails.

The identification of each nest mound was performed progressively by
observing chronological appearance, connection with common active trails,
synchronous foraging activities with the nearest central nest, the results of
experimental confrontations of workers from different mounds and
observation of spontaneous conflicts.
RESULTS

Geographical distribution of the territorial mark

At nest mounds and the beginning of the trail, the tests showed a clear dominance of the resident over an intruder (Table I), regardless of which ant first entered the arena. The presence of a territorial mark is also shown when the resident was observed transporting the intruder. At the middle of an active trail, the resident worker demonstrated reduced aggressiveness if entering the arena after the intruder, but was always the only biting ant. No transport of the intruder was observed in this case. At the end of a trail, the first ant to enter the arena always had an advantage in aggressive encounters, suggesting the absence of a territorial mark. As expected, confrontations on virgin territory revealed an advantage for the first ant entering the area, independent of its origin. Transport of the vanquished was never observed in this case.

TABLE I. Frequencies of aggressive behavior shown (in % of tests performed, n= 40) by the first (1) to the second (2) introduced workers when either the intruder (I) was introduced into the arena with a 5 min delay respect to the resident (R) or vice-versa (R-I or I-R, respectively).

<table>
<thead>
<tr>
<th>Activity</th>
<th>R-I</th>
<th>I-R</th>
<th>X²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Active nest mound without trails or foraging activity:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bitings 1-2</td>
<td>55</td>
<td>5</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Transport of I</td>
<td>5</td>
<td>5</td>
<td>---</td>
</tr>
<tr>
<td>Beginning of the trail:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bitings 1-2</td>
<td>57,5</td>
<td>10</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Transport of I</td>
<td>10</td>
<td>10</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td>Middle of the trail:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bitings 1-2</td>
<td>30</td>
<td>0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Transport of I</td>
<td>0</td>
<td>0</td>
<td>---</td>
</tr>
<tr>
<td>End of the trail:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bitings 1-2</td>
<td>12,5</td>
<td>7,5</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td>Transport of I</td>
<td>0</td>
<td>0</td>
<td>---</td>
</tr>
<tr>
<td>Virgin territory (workers from societies A and B):</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bitings 1-2</td>
<td>A-B</td>
<td>B-A</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td>Transport</td>
<td>0</td>
<td>0</td>
<td>---</td>
</tr>
</tbody>
</table>
Figure 1 shows the topographic layout of nests, mounds and pines during the observation period, whereas Figure 2 shows the annual dynamics of some important features. The following observations merit special comment:

MARCH 1987: Twenty three per cent of the pine trees on the study site were connected to foraging mounds through trails. Worker activity was essentially nocturnal.

JUNE 1987: The foraging activity stopped and the trails were neglected. Only 4% of the trees were connected to clean but apparently inactive trails. The reduction in nest mounds was significant, ranging between -26% to -66% per nest, compared to the number of mounds counted in March. Ants' activity concentrated on excavations below some of the central nest area mounds. On June the 7th, at sun rise, nests displayed intense preswarming activity (another had been observed 10 days before). Sexual forms emerged only from nests two and three, but intense activity was also observed on nests one and four. In all cases, workers and soldiers were found outside the mounds near the nest center walking in all directions. At 10 a.m., the nuptial flights ended. III-formed females which did not fly and males resting on the ground were exterminated, even by their nestmates. After the flight, inseminated queens dug a vertical gallery, 20 to 30 cm deep, ending in a circular chamber, five to 10 cm in diameter. During this time, workers from nests which did not produce sexual forms were walking in all directions, killing any queen they met. Young nests were carefully excavated and queens, if present, killed. The next day, small mounds with characteristic pellets of sand indicated the success of 65 founding queens.

NOVEMBER 1987: Thirty two percent of the trees were connected with active clean trails and an increase in the number of foraging mounds was observed (+145%). Ants were collecting leaves, particularly during the night and the early morning. Nest three had 71 m of active trails. This strong activity helped to discover incipient colonies: only 15 newly-founded nests were now present, 77% of the founding queens had disappeared and some of the empty nests were now colonized by Camponotus sp. and a solitary wasp.

MARCH 1988: We recorded the maximum foraging activity (Figure 2). A total of 175 m of active trails were measured at this point. These were active during day and night. Workers stopped foraging only during the warmest hours of the day (between 11 a.m. and 7 p.m.). Only three mature nests survived the dry season and more than 95% of the incipient colonies had disappeared. The young nests were active at night until early in the morning. Nest four died at the beginning of the year and was regularly explored by workers of neighboring nest three which emerged from the dead heap with pellets of sand which they carried to their nest. Conflicts were observed between two neighboring mounds of nests one and two which formed a battle front since a foraging mounds of nest two started to emerge in the foraging territory of nest one.

APRIL 1988: Nest three showed a decrease of its foraging activity and nest two benefited using some of its neighbor's trails (Figure 1). Conflicts between
FIGURE 1. Topographic layout of the four Atta laevigata nests. Dark mounds represent young nests less than one year old. Trails are drawn to show nest activities at two different dates. Black pine trees are never attacked during the study period.
FIGURE 2. (1) the intensity of reproductive activity (represented by the number of young nests less than one year old in the site); (2) temporal fluctuations of the number of foraging nests; (3) number of pine trees connected with trails; and (4) length of active trails.
nests one and two continued underground. Fighting workers and cadavers emerged from foraging mounds of nest one suggesting that the galleries of both societies probably crossed. This conflict was observed for one month, taking place on the site with the highest foraging mound density. This fact was probably related to the low activity of nest one after the mating flights of June 87.

SEPTEMBER 1988: Fifty nine young nests resulted from the 1988 flights; only one nest survived from those founded in 1987. Mounds of nest four were collapsed. Nests two and three showed foraging activity, nest three had 75\% of the 41 m of active trails leading to 25\% of trees joined through trails to the nest.

In addition to these observations, it is interesting to note that each nest maintained a constant proportion of foraging mounds during the entire observation period, despite changes in their absolute number (Table II).

Forty-eight trees of the 70 trees at the experimental site were regularly foraged and represented 78\% of the trees in the inter-nest-heap area. Ants foraged only 25\% of pine trees situated on the nest heaps, a percentage significantly less than expected from random attacks ($p < 0.05$, $X^2$ test $= 3.98$). The trees on which foraging activity was observed more than three separate times had a diameter (1.5 m above the ground) smaller by 15\% than trees which were never attacked (means of the diameters were: 19 cm, and 22.5 cm, $N= 18$; $p < 0.05$, Student’s t-test).

The highest reproductive activity was observed at the beginning of the rainy season (June in our study site). Foraging activity decreased at this time but increased between November and March.

Laboratory and field observations showed that 24 hours after the nuptial flight, each queen closed her nest entrance and initiated egg-laying three to four days later. *Atta laevigata* queens stayed in their chamber, eating trophic eggs and part of the fungus. The first workers appeared seven to eight weeks later; they stayed with their mother about one week before they opened the nest and started to forage. At this stage, the workers closed their nest following a short period of foraging activity.

**DISCUSSION**

This study demonstrates the existence of *Atta laevigata* colony-specific territories in the field; i.e., defended areas used exclusively by a colony. The colony territory consists of the trail system and the ant nest, similar to territory described for *Pogonomyrmex* (Hölldobler and Lumsden 1980), but in *Atta* spatio-temporal patterns of different colonies allow trail-sharing.

Territories seemed stable, with few observed conflicts between colonies. However, one inter-colony conflict was observed. A. auropalli (1947) first reported spontaneous wars between *Atta* societies. Our study confirmed his observations and found that such battles may take place on the boundaries of two foraging territories, above and below ground, and may last for over four weeks, affecting the foraging activity of the colonies involved.

The four societies studied followed the same seasonal rhythm and the expansion of territory resulted in the reduction of that of its neighbors. This relative stability in foraging areas and number of mounds between neighboring nests suggests an established dominance of leader nests which
TABLE 2. Number of foraging mounds and annual distribution of mounds per nest (in % of the total mounds on the study site). Nest four died at the end of 1987 and was not included.

<table>
<thead>
<tr>
<th></th>
<th>MAR 87</th>
<th>JUN 87</th>
<th>NOV 87</th>
<th>MAR 88</th>
<th>SEP 88</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOTAL MOUNDS</td>
<td>70</td>
<td>51</td>
<td>117</td>
<td>147</td>
<td>78</td>
</tr>
<tr>
<td>(absolute value)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NEST Nr 1 (%)</td>
<td>16</td>
<td>22</td>
<td>19</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>NEST Nr 2 (%)</td>
<td>50</td>
<td>45</td>
<td>47</td>
<td>53</td>
<td>57</td>
</tr>
<tr>
<td>NEST Nr 3 (%)</td>
<td>34</td>
<td>33</td>
<td>34</td>
<td>35</td>
<td>31</td>
</tr>
</tbody>
</table>

occupy the more spacious territories and control the expansion of neighboring nests, possibly younger or less combative. This limitation forces neighboring societies to adopt a spatio-temporal foraging strategy that allows them to share in time trails of a common territory. This system is advantageous because it avoids fatal conflicts between conspecific nests; it also allows societies to make better use of available space.

Trees on the nest heap were usually not attacked, a phenomenon also observed in *Atta laevigata* and *Atta cephalotes* (see Salzmann and Jaffé; and Cherrrett this volume). The unforaged trees on the inter-nest area suggest the existence of a boundary between nest territories, a neutral "no ants land," which prevents massive and inopportune encounters between workers of neighboring colonies. By contrast, two to four mounds of the same nest may forage on the same tree. This shows the possible benefits to workers of a single pheromone being used for both orientation and mound specification (Hölldobler and Wilson 1986). As suggested elsewhere (Salzmann and Jaffé, in preparation), this pheromone seems to be identical to the territorial pheromone; i.e. the same secretion has two complementary functions.

The killing of inseminated queens before their newly-excavated nests are closed has been reported for *Atta cephalotes* (Cherrrett in Rockwood 1973), *A. colombica* (Rockwood 1973), *A. capiguara* (Fowler et al. 1984), *A. laevigata* (Jaffe 1986) and *A. bisphaerica* (Fowler 1987). The search for newly-mated queens and incipient colonies were preferential in the direction of the last foraging area used by each adult nest. Thus, this area can be considered as a territory in agreement with the definition of Noble (1939, in Krebs and Davies 1978), i.e., an actively defended area for the colony’s exclusive use. The elimination of competitors controls population density, as had also been reported for *A. bisphaerica* (Fowler 1987). Young queens dig their nests in areas without vegetation, often next to old trails or mounds of adult nests. Fowler (1987) also observed high colonization rates of the young *A. bisphaerica* queens in sites already occupied by mature nests of the same species. These behaviors, together with the low dispersal ability of *Atta* queens, may explain why an *Atta* nest occupies the same site for several decades. A nest that recently died will soon be occupied again.
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REFERENCES


