Distribution and Turnover Rate of a Population of Atta cephalotes in a Tropical Rain Forest in Costa Rica

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ABSTRACT

A population of *Atta cephalotes* was surveyed in 1989 and 1991 at the La Selva Biological Station in Costa Rica. Nests were mapped along trails that passed through old growth forest. Estimates of basic demographic parameters were examined in relationship to general soil categories, suggesting that colony mortality and natality is related to soil type. Results indicated that the population is increasing at a rate of 22 percent per annum. Based on initial nest size data and on demographic parameters, a complete forest soil turnover time of 200 to 300 yr was estimated. The significance of these results for plant community dynamics is discussed.

Key words:  
*Atta cephalotes*; colony mortality; colony natality; leaf-cutting ants; population ecology; rain forest dynamics.

LEAF-CUTTING ANTS are thought to be important in soil genesis and soil structure (Lyford 1963), nutrient cycling (Haines 1975, 1978) and plant community structure (Haines 1975) in tropical moist forests, yet few data are available on population-level temporal changes (i.e., populations of nests). Given the purported importance of this species and scant information on population density changes over time, demographic studies of the species would appear to be warranted.

At the La Selva field station in Costa Rica (owned and operated by the Organization for Tropical Studies), *Atta cephalotes* is abundant and presumably important to soil and plant processes. It also appears to exhibit substantial temporal variation. In 1969, colonies were found in seeming abundance, but by the mid-1970s, their abundance appeared to have declined dramatically, yet by the end of the 1980s they appeared to be quite abundant again (J. Vandermeer, pers. obs.). While such vague recollections can hardly be taken as actual data, they nevertheless suggest the hypothesis that the population density of *A. cephalotes* colonies may not be constant.

As an initial contribution to an understanding of temporal variation in this species we undertook a two-year study of its population on the La Selva field station, seeking preliminary estimates of basic demographic parameters and determining whether such parameters are related to general soil categories.

METHODS

The study was conducted during July 1989 and 1991 at the La Selva field station, near Puerto Viejo, in the Caribbean lowlands of Costa Rica, 83°59’W, 10°26’N. The forest is typical of the Caribbean lowlands, with an average precipitation of nearly 4000 mm per annum and little seasonality (Hart-shorn 1983). The soils are of two general categories, alluvial or residual, the latter deriving from lava flows emanating from the Barba volcano, at whose base sits the field station. Two major flows have been identified, forming three main ridges situated perpendicular to the Puerto Viejo river. Two alluvial terraces are easily recognizable, but since the only forest in the lower terrace is secondary forest and our study focused on old growth forests, we restricted the survey to the upper terrace and the residuals (henceforth alluvial refers to the upper terrace). The alluvial soils included in this study belong to the order inceptisols and fall into the categories andic dystropept and andic humitropept, while the residual soils are inceptisols in the category typic humitropept (the arboleda series), and ultisols of the category typic tropohumult (the jaguar and matabuey series) (Mata & Sancho 1987).

The La Selva field station’s system of trails makes it relatively easy to determine one’s exact position at any point in the forest, as long as one is on or near a trail. Using this trail system, we carried out a census of *A. cephalotes* colonies in 1989, recording position along the trail and estimating the size of

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1 Received 8 June 1992, revision accepted 18 January 1993.

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FIGURE 1. Map of the trail system at La Selva Field Station indicating the location of *Atta cephalotes* nests for the 1989 and 1991 censuses. Closed circles represent nests found living in 1989 and surviving through 1991, open squares represent nests found living in 1989 but having disappeared by 1991, and open triangles represent nests that were encountered in the 1991 census but not in the 1989 census. Thus closed circles indicate old surviving nests, open squares dead nests, and open triangles new nests. Shading indicates soil types based on Mata and Sancho (1987). Area within oval indicates a mosaic of abandoned pastures, abandoned cacao groves, and second-growth forest, all other sampled areas are in old-growth forest.

<table>
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<tbody>
<tr>
<td>Residuals</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Matabuey</td>
<td>4200</td>
<td>14</td>
<td>6</td>
<td>13</td>
<td>0.33</td>
<td>0.45</td>
</tr>
<tr>
<td>Jaguar</td>
<td>4100</td>
<td>30</td>
<td>14</td>
<td>30</td>
<td>0.73</td>
<td>1.02</td>
</tr>
<tr>
<td>Arboleda</td>
<td>1600</td>
<td>7</td>
<td>6</td>
<td>15</td>
<td>0.44</td>
<td>1.31</td>
</tr>
<tr>
<td>Aluvials</td>
<td>4900</td>
<td>23</td>
<td>15</td>
<td>8</td>
<td>0.47</td>
<td>0.47</td>
</tr>
<tr>
<td>Totals</td>
<td>14,800</td>
<td>74</td>
<td>41</td>
<td>66</td>
<td>0.50</td>
<td>0.71</td>
</tr>
</tbody>
</table>

all nests visible from the trail (size was estimated by imagining a rectangle imposed upon each nest and estimating the length and breadth). The census was done on trails traversing the various soil types and was restricted to old growth forest, although occasionally the trail would pass through or near abandoned pasture or abandoned cacao groves, as indicated in Figure 1. In both years the census included an area approximately 5 m on either side of the trail. The area passing through second growth habitats was too small to contribute significantly to the analysis, but was included in the analysis.

The same trails were walked in 1991, repeating the same methodology, but eliminating the nest size estimate. The exact position of each nest located in 1989 was found using the trail system, and its condition, alive or dead, noted. Furthermore, a search was made for any nests not included in the original census, presuming that they were new nests. Clearly it was not possible to distinguish between new nests that were a result of newly produced queens versus new nests that were the result of moving a nest from elsewhere. Nest size data would be irrelevant to this issue since small nests could equally be small remnants of former colonies moved from elsewhere or colonies from new queens. Thus, when we speak of mortality we are more accurately referring to nests that either died or moved, and when we speak of natality we are more accurately referring to nests that either appeared because of a new queen or were moved from somewhere else. Estimates of turnover rates and population growth rates are obviously not affected.

We are confident that any nest recorded in 1989 in fact was recorded accurately, and those recorded as dead colonies were in fact records of mortality, with the possible exception of those colonies that moved their nests. Another possible inaccuracy in our data, could be encountered within the “new nest” category in 1991. Many of the new nests were quite small and could conceivably have been overlooked in the 1989 census. On the other hand, while we must acknowledge the possibility of such error, the presence of a nest near the trail is usually so obvious that we are quite confident that the data reported herein are accurate.

Since, for the most part, the soil types are not presented in nice blocks, statistical testing is made quite difficult. To strengthen the analysis, we divided the various soil blocks into subunits which subend equal lengths of survey trails, and estimated all parameters (population density, colony mortality, natality) within each subunit of trail. Such a procedure is not strictly valid since it represents pseudoreplication, and we use it only when we wish to bolster arguments for the lack of statistical differences.

RESULTS

The basic data are presented numerically in Table 1 and in Figure 1 on a map of the field station, the latter showing all nests originally encountered, nests having died over the course of the two years between censuses, and all nests newly encountered in 1991. The basic soil types of concern to the study are also indicated on that map. Several interesting patterns are discernable on the map; namely, there appears to be a correlation between soil type and nest density, mortality (dead colonies), and natality (new nests encountered only in the 1991 census).

Comparing alluvial versus residual soils, we recorded a density of 0.47 nests per 100 m on alluvial soils versus 0.52 nests per 100 m on residual soils for the 1989 data, a trivial difference, but from an unchanged 0.47 nests per 100 m on alluvial soils to 0.85 nests per 100 m on residual soils (up from 0.52) for the 1991 data (Table 1). However, such large differences are largely illusory, since the variance along the trail is so large. Even if the largest value (for arboleda) is compared to the smallest
value (for matabuey), the difference is statistically insignificant with a simple Student’s t-test (using the pseudoreplicates described above, \( t = 0.56, \text{df} = 6, P = 0.6 \), for 1989; \( t = 0.324, \text{df} = 6, P = 0.8 \), for 1991). That there is no systematic relationship between soil type and population density might be surprising in light of what appears to be a strong pattern when first examining the data. But the excessively large concentration of nests along the central trail on the main jaguar flow must be viewed in conjunction with the relative sparseness of nests in 1989 on the lower part of the secondary lobe and the excessive sparseness along the back line of the property with the 1991 data (Fig. 1). The clump of high density would appear to be associated with something other than this classification of soils.

On the other hand, soil type appears to be important with respect to both colony mortality and natality (Table 2); although the small sample size precludes meaningful hypothesis testing (for natality, after arcsin transformation, \( t = 3.378, \text{df} = 2, P = 0.078 \), when comparing ultisols versus non-ultisols; for natality, \( t = 2.396, \text{df} = 2, P = 0.139 \), for a comparison of alluvial versus residual). Statistical significance aside, the ultisols have higher mortality rates, while the alluvials have lower natality rates (Table 2). The soil series “arboleda” is unusual because it has a very low mortality but a very high natality. The series arboleda is a typical humid trophohept which differs only slightly from a typical tropohumult, which is the taxon of both jaguar and matabuey. Yet, the andic humitropept which is the taxon of most of the alluvial soils is also very similar to the typic humitropept. Thus the series arboleda may represent a transition between the residual and alluvial soils. If the arboleda series is removed from the analysis, mortality rate on residual soils is estimated at 0.55 and the natality rate at 0.96, while on alluvial soils mortality is 0.35 and natality is 0.35. The crude rate of population increase is thus 0.41 for residuals (excluding arboleda series) and 0.00 for alluvials, suggesting that the population of *A. cephalotes* is increasing at a faster rate on residual than on alluvial soils. The turnover rate is dramatically different between the two soil types, with at least every other nest being replaced on the residuals while only slightly more than one of three is so replaced on the alluvials.

A final point to be noted about these data is that the population as a whole appears to be increasing. Even with considerable error in the estimations of either birth or death rates, the crude rate of population increase would still be positive. According to our data, the population is growing at a rate of 22 percent per annum (45% per two years—see Table 2).

Since the size of each nest was estimated during the 1989 census, it was possible to estimate the total area returned to forest during the intervening two years. Summing the surface area covered by each deceased nest, we arrive at a figure of 984 m², to be compared to an estimated total of 148,000 m² (Table 1), or 0.66 percent of the forest turning over every two years. If these were normal years, a period of 300 yr would be necessary for 100 percent of the forest soil to turn over (making the crude assumption that there will be no overlap in areas occupied by nests; if we were to relax this assumption the time estimates would be considerably longer). If we presume that the crude death rate remains the same and apply it to the 1991 data (in which more nests were encountered), we arrive at a figure of 0.99 percent turnover in two years, giving an estimate of 200 yr for 100 percent turnover. Roughly, then, we can say that our data indicate a time of complete forest soil turnover by *A. cephalotes* somewhere between 200 and 300 yr.

While there is little evidence that the population density is related to soil types, albeit a suggestion that some demographic parameters are thereby related, a glance at Figure 1 is sufficient to generate the hypothesis that various categories, especially mortality and natality, are clumped. The spatial distribution of “new nests” (nests having first appeared in the 1991 census) was determined to see if clumping could be detected either with respect to one another (new nest to new nest neighbors) or with respect to old nests that could potentially be

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<table>
<thead>
<tr>
<th>Soil type</th>
<th>Mortality</th>
<th>Natality</th>
<th>Crude population growth rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Residuals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Matabuey (Ultisol)</td>
<td>0.57</td>
<td>0.93</td>
<td>0.36</td>
</tr>
<tr>
<td>Jaguar (Ultisol)</td>
<td>0.53</td>
<td>1.00</td>
<td>0.47</td>
</tr>
<tr>
<td>Arboleda (Inceptisol)</td>
<td>0.14</td>
<td>2.14</td>
<td>2.00</td>
</tr>
<tr>
<td>Alluvials (Inceptisol)</td>
<td>0.35</td>
<td>0.35</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>0.44</td>
<td>0.89</td>
<td>0.45</td>
</tr>
</tbody>
</table>
queen sources (new nest to old nest neighbors). Additionally, the spatial distribution of dead nests with respect to one another was determined to see if any clumping in mortality occurred. These results are shown in Table 3. In all three cases, dead nests, new nests relative to old nests, and new nests, there is significant clumping.

**DISCUSSION**

It has been suggested that the well-known soil enrichment function of various Old World tropical termites is paralleled by leaf-cutting ants (tribe Attae) in the neotropics (Hölldobler & Wilson 1990). In some forests ants surpass earthworms in the amount of soil they move (Lyford 1963), and the large ground nests of some species in the genus *Atta* may have a particularly strong impact on local environments. In tropical rain forests were less than 0.1 percent of the nutrients normally filter deeper than 5 cm beneath the soil (Savage 1982), leaf-cutting ants carry large quantities of freshly cut vegetation into the nest chamber to more than 3 m below the surface, (Stahel & Geijskes 1939, 1941). Studies of the distribution of nutrients in the vicinity of *Atta* nests suggest that their contribution to nutrient cycling may be significant. For example, Haines (1983) reported that the flux of 11 elements through refuse dumps of *Atta cephalotes* averaged 224 times the background flux out of the forest in runoff and drainage.

In this study, we found a significant turnover of *A. cephalotes* nests during a two-year period (1989–1991). Preliminary estimates indicate that the turnover was faster on the residual ultisols than on alluvial-based soils. As to why soil type might be important we can only speculate. The ultisols with their very low pH and low nutrient content may suggest something of an r-selected environment encouraging a high birth rate in the face of an externally imposed high death rate, although it is doubtful that pH and nutrient content directly affect the ants (B. Haines, pers. comm.).

The data reported herein strongly suggest that *A. cephalotes* may be very important in soil turnover in this forest. Because ants transport vegetation material into their nest chambers mixing such materials with excavated earth, the nest area may be charged with high levels of carbon, nitrogen, and phosphorous. The soil surface may consequently be broken into a mosaic of nutrient concentrations, which in turn would create a patchy distribution of plant growth, especially during the early stages of succession (Beattie & Culver 1977, Petal 1978, Briese 1982), although Haines (pers. comm.) found only weak evidence for such a mosaic at this site. Others have reported just such an effect (Alvarado et al. 1981), and it is one of the components that caused Fowler et al. (1989) to suggest that leaf-cutters are keystone species. Based on the data from this study, we estimated that the soil in this forest can be expected to be fully turned over on the order of 200–300 yr. If this is an accurate estimation, that means that *A. cephalotes* could play an important role in structuring the understory plant community through the creation of a dynamic mosaic of soil microhabitats.

Leaf-cutting ants are dominant herbivores in the neotropics, consuming more vegetation than any other animal of comparable taxonomic diversity (including mammals and other herbivorous insects). The amount of vegetation cut from tropical forests by *Atta* alone has been estimated between 12 and 17 percent of leaf production (Cherritt 1986), and this herbivory is concentrated near nest locations. Much as falling trees create light gaps into which forest trees must regenerate, *Atta* nests create mini gaps of relatively vegetation-free zones, with respect to the forest understory. Haines (1975) reported a significant decrease in seedling survival in *Atta* nests and refuse dumps when compared to unaltered forest soil. Given the rapidity with which the nests appear to turn over, understory plants and tree seedlings may be as affected by the intrusion of an *Atta* colony as they are by falling trees. Indeed, it could be that for many understory plants and tree seedlings the presence of *Atta* is a more important force driving plant community dynamics than gap phase dynamics.

Although causes of colony mortality were not

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**TABLE 3. Student’s t-tests of observed versus random expectation of nearest neighbor distance for various categories.**

<table>
<thead>
<tr>
<th>Dead to dead</th>
<th>Random expectation</th>
<th>Observed</th>
<th>t</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead to dead</td>
<td>448.50</td>
<td>236.67</td>
<td>3.75</td>
<td>32</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>New to old</td>
<td>200.00</td>
<td>113.26</td>
<td>7.265</td>
<td>65</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>New to new</td>
<td>224.24</td>
<td>129.92</td>
<td>3.39</td>
<td>65</td>
<td>0.001</td>
</tr>
</tbody>
</table>

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examined in this study, it is well known that most mortality of leaf-cutting ants occurs during the colony establishment phase, especially during the first few months (Fowler et al. 1986). Dix and Dix (unpublished, cited in Fowler et al. 1986) found 90 percent mortality of incipient colonies of *A. cephalotes* over a three month period, with pathogens accounting for 74 percent of the failures. After the critical establishment period, mortality decreases considerably, but while the colony is still small it may be killed by attacks from conspecific colonies and armadillos (Fowler et al. 1986). With respect to colony survival, Weber (1966) reported the survival of *A. cephalotes* to be 10 yr (based on one queen maintained in a laboratory). Colony survival under field conditions is not well documented. Dix and Dix (unpublished; cited in Fowler, et al. 1986) estimated survivorship of *A. cephalotes* in the field at 14 to 15 yr. Based on the data collected in this study, colony survivorship (assuming number surviving is a negative exponential and taking one percent remaining of an original cohort as an estimate of “the survivorship”) is estimated at approximately 16 yr. However, it should be noted that this is an average which includes mortality at the colony establishment phase, and begins with a cohort that includes older nests. It should thus be taken as an extremely rough figure.

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**


