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Carton nest allometry and spatial patterning of the arboreal ant *Azteca chartifex spiriti* (Hymenoptera, Formicidae)

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ABSTRACT. Strong isometric relationships were found between maximal carton nest length and width for the ant *Azteca chartifex spiriti*. These variables, as well as estimated colony volume, were highly related to supporting tree trunk diameter. This suggests that physical support may limit principal nest sizes, and may be responsible for the formation of secondary and satellite carton nests. Principal nest spatial patterning was significantly dispersed, indicating variation in colony population sizes. However, the number of satellite nests at the colony territorial arboreal borders was significantly larger than in the center of the territory. This suggests that satellite nests may serve as an advanced garrison to inhibit territorial encroachment by nearby colonies.

KEYWORDS. ALLOMETRY; ANT; *AZTECA CHARTIFEX*; NEST; DISPERSION; TERRITORY.

INTRODUCTION

In the cocoa plantations of southern Bahia, species of the dolichoderine *Azteca* are among the canopy dominant ants (LESTON, 1978; WINDER, 1978; MAJER *et al.*, 1994; MEDEIROS *et al.*, 1994a). However, the largest colonies are formed by *A. chartifex spiriti* (Forel) (BONDAR, 1939; SILVA, 1955). *A. chartifex* is one of the few dominants of the ant mosaic. This ant mosaic is characterized by aggressive territorial species, which actively exclude other canopy dominant ants from their territory. Territories, composed of cocoa trees and dominant emergent trees, are large, and *A. chartifex* is one of the few species to expand territorial coverage over time (MEDEIROS *et al.*, 1994a).

The large aerial carton nests of *A. chartifex* may attain 2 m in diameter. Since the 1900's, some cocoa growers have actively protected and managed colonies of *A. chartifex* in their plantations because of their belief that its presence reduced pest incidence (ZEHNTNER 1917; TORREND, 1917, 1919). Trees with *A. chartifex* produce higher fruit yields than trees without (VELLO & MAGALHÃES, 1971). MAJER & DELABIE (1994), based upon pyrethrium knock-down studies, and MEDEIROS *et al.* (1994b), using visual counts, noted reduced numbers of thrips and hemipterans in trees with *A. chartifex* than in trees dominated by other species.

A. chartifex was considered a pest because its large nest mass occassionally caused branch breakage and its carton constructions interfered with flower emission (BONDAR, 1939; SILVA, 1955), and was selectively eliminated from cocoa plantations with insecticides. Additionally, *A. chartifex* protects homopterans, especially *Planococcus citri* Risso, by constructing carton protection over colonies.

DELABIE *et al.* (1991) commented on the polydomous nature of *A. chartifex*. Colonies are comprised of a large principal carton nest, secondary carton nests, and a number of smaller carton homopteran protectors. These smaller nests, here collectively called satellites, are spread throughout the colony territory. However, does this descentralization of nesting strategy improve foraging through reducing foraging time (brood are also found in satellite nests), or are satellite nests used principally for territorial defense? Polydomous nesting has been implicated as being responsible for both (HOLLDOBLER & WILSON, 1990), and indeed, both of these possibilities are probably not mutually exclusive.

Here, we examine spatial patterns of nest distribution and their importance for territorial maintenance in the ant mosaic of Bahian cocoa plantations. In addition, we also examine nest allometry and its relation to tree size.

MATERIAL AND METHODS

The distribution of principal and satellite nests in individual trees was mapped in a Bahian cocoa plantation. We used these maps for spatial analysis. We performed a nearest neighbor analysis (EBDON, 1985) to examine dispersion patterns of principal nests. We also compared the number of satellite nests within the colonial territory and at the inferred colonial territorial borders using a t-test for unequal sample sizes (EBDON, 1985).

For 10 principal carton nests, we measured the major length and width of the nest (see Fig. 1), and the diameter of the tree trunk at chest height. These variables were then analyzed through linear regression to determine their relationships.

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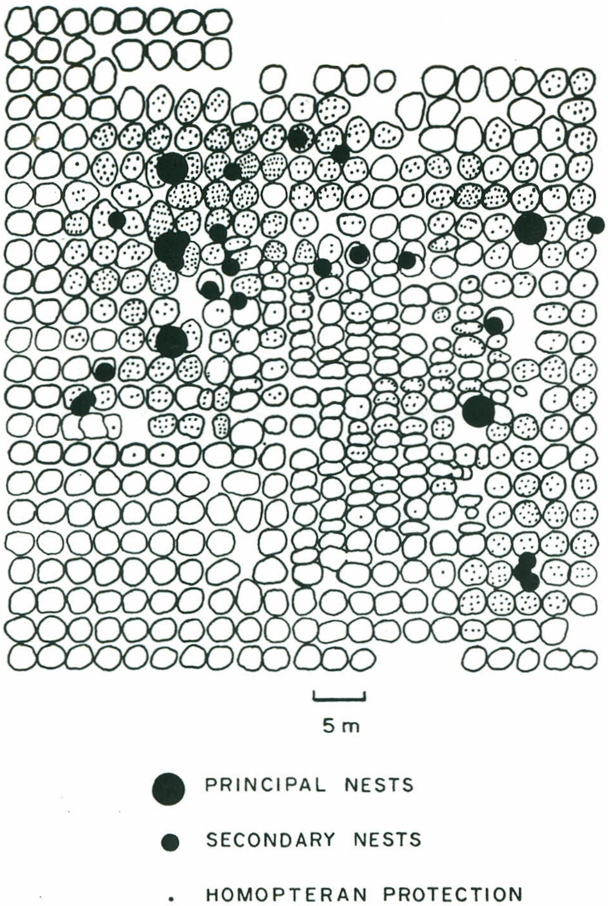

Fig. 1. Schematic diagram of principal and satellite carton nests of the arboreal ant, *Azteca chartifex spiriti*.

RESULTS

The spatial distribution of principal and satellite carton nests (Figs. 1-2) revealed a strong patterning of territorial occupation. Nearest neighbor analysis produced a significant dispersed pattern ($R = 1.679$, $P < 0.005$). The number of satellite carton nests per cocoa tree, although highly variable (Fig. 2), was more concentrated at inferred borders of neighboring colonies (Fig. 3).

A strong isometric pattern of nest architecture was evidenced. Nest length was significantly related to nest diameter (Fig. 4), and with tree trunk diameter (Fig. 5). Moreover, we found a significant relationship between estimated nest volume and tree trunk diameter (estimated volume: log cm^3 = 6.141 + 0.037 (tree trunk diameter) ($r^2 = 0.770$, $F = 11.664$, $P = 0.009$).

DISCUSSION

The significantly dispersed pattern of principal nests registered in the cocoa plantation suggests that this pattern is due to population differences of the colonies, rather than other environmental parameters. The lack of a regular pattern of principal nest positioning, expected under the hypothesis of competition assuming that colonies are the same size, we suggest, cannot be used to properly evaluate inter-colony competition (Fowler *et al.*, 1991). The most salient feature of these data suggest that competition and territorial defense are indeed important if the distribution of satellite nests are examined. Significantly more satellite nests are present at inferred colonial territorial borders than in the center of the colony territory. This suggests that satellite nests may serve as advanced garrisons to protect territorial integrity from encroachment of nests of conspecific or other dominant canopy ant mosaic ants (Holldobler & Lumsden, 1980; Delabie *et al.*, 1991).

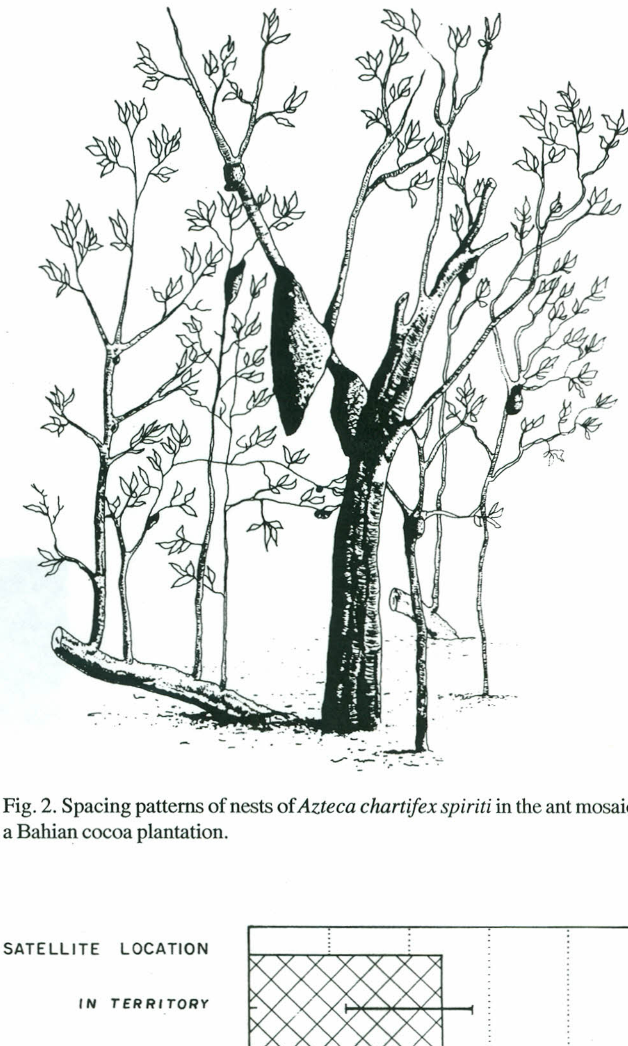

Fig. 2. Spacing patterns of nests of *Azteca chartifex spiriti* in the ant mosaic of a Bahian cocoa plantation.

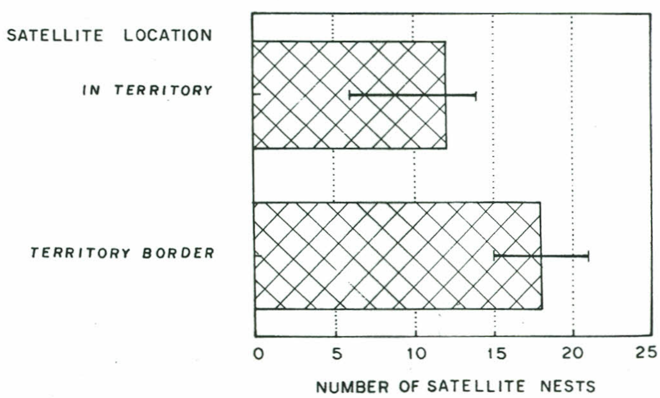

Fig. 3. The relation between the mean number of satellite carton nests per cocoa tree within the canopy territory and in trees at territorial borders of *Azteca chartifex spiriti* in a Bahian plantation.

Strong isometric relationships were found in measurements of nest dimensions. Additionally, these were highly related to tree diameter, suggesting that tree trunk size may limit the final size of the principal nest, as well, we assume, smaller secondary nests found on smaller plants. Therefore, polydomy may also be the result of physical infrastructural limitations, in addition to territorial defense and possible increased foraging efficiency.

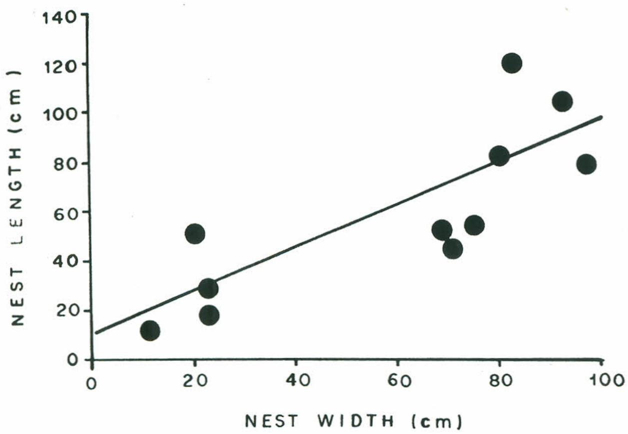

Fig. 4. The relationship between the major nest length and width. Major nest length = 12.723 + 0.831 (nest width) [$r^2 = 0.824$, $F = 16.885$, $P = 0.003$].

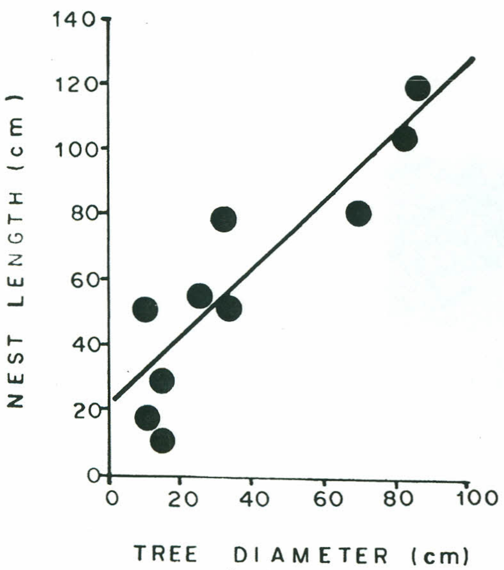

Fig. 5. The relationship between the major nest length and tree trunk diameter. Major nest length = 16.612 + 1.076(tree diameter) [$r^2 = 0.898$, $F = 33.446$, $P < 0.001$).

Although these data provide baseline information on the biology of *A. chartifex*, much is still to be learned to incorporate this ant into integrated management schemes of phytophagous cocoa pests. Althouth *A. chartifex* is associated with decreased incidence and intensities of thrip and mirid damages (Delabie, 1990; Medeiros *et al.*, 1994b; Majer & Delabie, 1994), it is also associated with black pod rot (Delabie, 1990; Medeiros *et al.*, 1994c). Our data do not provide estimates of breakage losses due to nesting behavior, as reported for other ants (Fowler & Roberts, 1982). We believe that *A. chartifex* is still more beneficial than detrimental in cocoa plantations. Data on nest size with respect to tree diameter, for example, could be used to manipulate colonial growth by removing colony portions. Breakage, we feel, is an unexpected effect of nest size, and colonies construct satellite nests when potential risks of nest colapse are percieved, as our data suggest.

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