Effect of Mature Colony Density on Colonization and Initial Colony Survivorship in *Atta capiguara*, a Leaf-cutting Ant[1]

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ABSTRACT

Founding queens of the leaf-cutting ant *Atta capiguara* colonized fields at a rate directly proportional to the standing biomass of *Atta* colonies, which was estimated by the amount of soil excavated by ants. The percentage of queens that were successful in their initial colony foundation attempts (*i.e.*, that successfully excavated and sealed their embryo nest) was inversely proportional to the standing *Atta* colony biomass. Elimination of mature *Atta* colonies by poison baits led to a higher success rate during initial colony founding than found in control plots with mature *Atta* colonies.

RESUMEN

Las reinas aladas de la hormiga cortadora *Atta capiguara* colonizarón campos en relación proporcional a la biomasa existente de colonias maduras de *Atta*, estimada por la cantidad de tierra excavada por campo. El porcentaje de las reinas que tuvieron éxito al iniciar sus hormigueros tenía relación inversa con la biomasa existente de colonias maduras de *Atta*. La eliminación de colonias maduras de *Atta* por medio de cebos tóxicos resultó en un aumento en el procentaje de reinas nuevas que iniciarón sus hormigueros.

COLONIZATION BEHAVIOR BY ANTS has been little studied, particularly for tropical ground-nesting species. Wilson and Hunt (1966) demonstrated that queens of *Solenopsis molesta* (Say) and *Lasius neoniger* Emery were able to direct their nuptial flights and to actively select major habitat types. For leaf-cutting ants, Cherrett (1968) demonstrated that the founding queens of *Acromyrmex octospinosus* (Reich) and *Atta cephalotes* (L.) were found more frequently in pitfall traps located in their preferred habitat. Moreover, the initial successes of founding queens of most ant species tend to be quite low, due to the large number of vertebrate and invertebrate predators and their execution by conspecific workers as a manifestation of territorial behavior (Brian 1965, Wilson 1971).

During 1975 and 1976, we had the opportunity to study colonization and initial colony survivorship in the leaf-cutting ant, *Atta capiguara* Gonçalves. *A. capiguara* is a shade intolerant grass-cutting ant (Mariconi 1970) that is found in the grasslands of southern Brazil and eastern Paraguay. This species constructs diffuse nests, characterized by multiple tumuli of excavated soil dispersed over tens of square meters (Amante 1964). Colonies are initiated by a solitary queen (haplometrosis) (Mariconi 1970), and early colony growth has been studied by Mariconi (1974), and Pereira da Silva *et al.* (1982). Nuptial flights occur in the middle of the afternoon during spring (October–November), with males forming leks 200 m in diameter at heights of 150 m or more above ground level (Amante 1972).

METHODS

Studies were conducted near J. M. Frutos (ex-Pastoreo), Departamento de Caaguazú, Paraguay, approximately 200 km east of Asunción. The results reported here were obtained from a series of fields with varying degrees of human disturbance (Fowler and Haines 1983).

To examine the effects of intraspecific and interspecific aggression upon the success of founding queens, mature colonies of *A. capiguara* and *Atta laevigata* (Fr. Smith), which occurred sympatrically, were killed with toxic baits in a 2500 m^2 plot more than six months prior to the swarming of the reproductives. A contiguous 2500 m^2 plot was chosen at the same time to serve as a control. It should be emphasized that the toxic baits eliminated the ants, but did not affect the presence of the previously constructed nest tumuli, which remained in the plots, although these were subjected to weathering.

Following swarming (17 November 1975) each of the plots was diligently searched for new queen cells. New queen cells are highly characteristic. Each queen begins to excavate a small cavity in the soil, leaving a characteristic tumulus of soil, consisting of large rounded particles, above the ground. Colony foundation in *A. capiguara* is claus-

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TABLE 1. *The number of queens of* Atta capiguara *attempting to initiate new colonies and those successfully entering the claustral phase in plots (0.25 ha) with mature colonies present or excluded by toxic baiting. Open cells indicate that the foundress queen was killed before entering the claustral phase.*

Queen cell condition	*Atta* Excluded	Present	Total
Open	8	19	27
Closed	58	31	89
Total	66	50	116

tral, and it was relatively easy to record if a queen had reached the claustral phase by noting the presence or absence of a soil plug in the incipient colony gallery. Queens initiating colonies but not reaching the claustral phase could be easily detected due to the absence of the gallery sealing plug.

Following the nuptial flight, adjacent fields were censused by transects. Six 300 m^2 transects were run in each of five fields, and the number of attempts to initiate colonies and the number of claustral closings were recorded. Additionally, all colonies of *A. laevigata* and *A. capiguara* present in the transect belts were measured. The height and diameter of each nest or tumulus were recorded, and the volume (m^3) of excavated soil in each field was estimated by solving for the volume of a cone. All data were transformed to a per hectare scale. This method assumes that there is a proportional relationship between the number of workers in a colony and the volume of earth removed by the colony. Previous work (Bitancourt 1941) suggests that this is a valid extrapolation.

RESULTS

Data obtained from the paired plot experiment (Table 1) reveal that there was no significant difference in the number of colony initiation attempts in the mature colony exclusion plots when compared with the control ($\chi^2_{[1]}$ = 2.82, using Yate's correction factor). However, proportionally more queens were initially successful in initiating the claustral phase in the *Atta* excluded plot ($\chi^2 = 10.699$, $P < 0.01$), than in the control plot.

The transect census of the five fields (Fig. 1) strongly suggests that the number of colony initiation attempts was proportional to ant biomass, as indexed by the volumes of excavated soil (Fig. 1). Queen cell initiations were not equally distributed over all fields (Kolmogrov-Smirnov Test: $D = 0.5875$, $P < 0.001$; Siegel 1956), but rather were proportional to the standing biomass of *Atta* in the fields. However, the inverse was found for the proportion of queens that successfully entered the claustral phase (Fig. 1). The proportion of queens that entered the claustral phase declined as total *Atta* biomass increased, as estimated by the volumes of excavated soil.

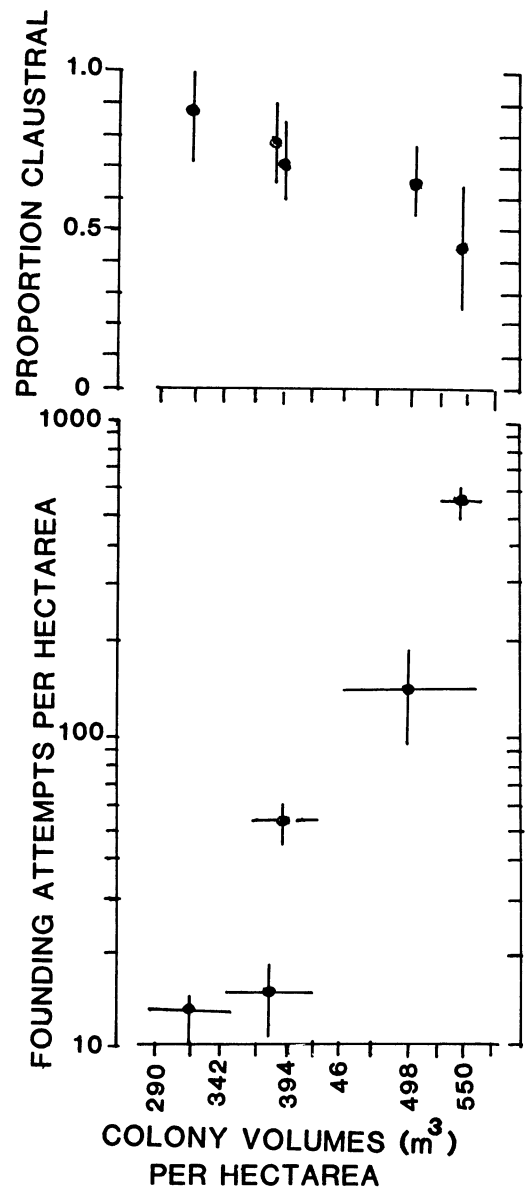

FIGURE 1. The relationship between queen cell initiations and the number of ants present, as indexed by soil volumes of colonies of *Atta laevigata* and *Atta capiguara*. The proportion of foundress queens which successfully sealed their incipient colonies to enter the claustral phase is given in the top graph. All values shown are means, with bars representing one standard deviation.

DISCUSSION

Two notable results are that the number of colonization attempts by founding queens is directly proportional to estimated standing biomass of *Atta* colonies, and that the percentage of these queens that successfully reach claustral phase is inversely proportional to the estimated standing biomass of *Atta* colonies. The reduced success of founding queens in high-density habitats may be directly linked with their execution. We observed founding queens on numerous occasions being dragged from their still open galleries by conspecific workers. Once discovered, these queens were dismembered by workers. Execution of founding queens by established colonies of leaf-cutting ants has been reported before (Bruch 1921, Mariconi 1970, Rockwood 1973, Fowler and Stiles 1980, Fowler 1982).

Our results, however, contradict the only other study of colonization and initial colony survivorship (Brian 1956). Brian (1956) found that founding queens of *Myrmica* were encountered in numbers inversely proportional to the number of mature colonies. Our results indicate that founding queens of *A. capiguara* are encountered in numbers directly proportional to the estimated total *Atta* biomass. The differences between our results and those of Brian (1956) may be due to sampling technique. Brian (1956) counted founding queens that were established, while we measured founding attempts. It is also possible that the long life span of colonies of *Atta,* 20 years or more (Mariconi 1970), and their demand for an abundant source of vegetation may make these ants more dependent upon habitat than the species studied by Brian.

Why should *A. capiguara* foundresses attempt to colonize habitats with large standing biomasses of *Atta* if their probability of being executed before entering the claustral phase is so high? In all cases, fewer than 2 percent of those queens that enter the claustral phase survive to reproductive maturity (Fowler 1983). Two separate mechanisms could give rise to the patterns of colonization reported here. In the first, virgin queens leave the colony, fly into leks, mate, and then directly drop to the ground to begin a search for a suitable nest site. Assuming that within a large area that there are many leks, a queen could alight in the regional neighborhood of her natal nest and attempt to found a colony. Theoretically, if the probability of survival after dispersal to more distant suitable habitats is not greater than remaining in the vicinity of the natal nest, queens should not disperse over a large area (Coumins *et al.* 1980). An alternative scenario would permit the queens to be able to discriminate the major features of the habitat while dispersing following mating in the leks. Under this model, if the standing biomass, or the area of excavated nest soil, is a reflection of the quality of the habitat, queens should actively choose those areas demonstrating a higher degree of ant activity, and proportionally higher density areas would attract more founding queens than low colony density areas. Unfortunately, we do not have data to allow us to ascertain which of these two mechanisms is employed by *A. capiguara.* Our exclusion plot was conducted in the highest colony density field, and we did not remove the nest tumuli. Queens on the wing would not be able to distinguish the area in which *Atta* workers were eliminated from the adjacent area in which they were still present. Moreover, similar paired plots were not established in each of the other fields to adequately test these mechanisms.

Regardless of the mechanisms which govern colonization by queens of *A. capiguara,* the results are the same: higher density areas tend to attract more colonization attempts. This result also implies a high degree of intraspecific regulation of populations, as more founding queens are executed in higher colony density plots than in lower colony density plots. Indeed, such a mechanism is undoubtedly present among all species of *Atta.*

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