

Research article

Haplometrosis and pleometrosis in the ant *Acromyrmex striatus* (Hymenoptera: Formicidae)

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Summary

Laboratory tests with mated females of the leaf-cutting ants *Acromyrmex striatus* (Myrmicinae, Attini) were conducted to determine if the colony foundation is a solitary or a mutualistic process. We have also tested the effect of foundresses density and number of available areas in this process. Three bioassays were performed: with single foundresses; with paired foundresses; and with groups of 8 to 18 foundresses. The results suggest that the foundation can be by haplometrosis or pleometrosis, possibly depending on physical distances between or densities of foundresses. Foraging activity was common in haplometrotic queens and in foundress pairs, but no foraging occurred in groups of foundresses.

Introduction

All ant species are eusocial and exhibit many different ways of starting their colonies. While apparently in many ant species method of colony foundation is fixed and haplometrotic, in many other species method of colony foundation is population-specific, e.g. haplometrotic and pleometrotic populations occur in *Formica* (Pamilo and Rosengren, 1984), *Acromyrmex versicolor* (Rissing et al., 1986, 1989; Rissing, pers. commun.) and *Messor pergandei* (Rissing and Pollock, 1991).

Most ant colonies are started by a single female (haplometrosis). This process can be claustral when the foundress raised her brood with stored energy reserves or can be semi-claustral, with the foundress foraging (Buschinger, 1990). A number of species, however, groups of females start colonies (pleometrosis). This process

appears to be mutualistic, females helping each other without respect to relatedness (Tschinkel and Howard, 1983; Rissing and Pollock, 1991; Nonacs, 1992).

From the Attini tribe, *Atta sexdens* was observed as haplometrotic and claustral (Mariconi, 1970). However, *Atta texana* colony foundation can be haplometrotic or pleometrotic (Mintzer, 1987), the same occurring in *Acromyrmex versicolor* (Rissing et al., 1986, 1989). Foundresses of *Acromyrmex lundii* (Weber, 1982) and *Acromyrmex striatus* (Diehl-Fleig and Lucchese, 1992) forage, which indicates semi-claustral foundation in these species.

Acromyrmex striatus is a leaf-cutting ant typical of open and sunny areas in the south of Brazil. Colonies are active outside the nest only at temperatures above 20 °C. Sexualls are produced from the end of October to mid-January (mid-Spring until mid-Summer). Small groups of males and females fly from each nest daily. After mating, females land and search a place to excavate a nest. Our objective was to investigate experimentally the process of colony foundation in *A. striatus*, whether by haplometrosis or by pleometrosis. We also analysed the effect of the number of foundresses as well as the number of available nest sites on colony foundation behavior.

Material and methods

Acromyrmex striatus females ($N = 164$) were collected after a mating flight on 10 December, 1991 in São Leopoldo (20° 45' S; 51° 08' W), State of Rio Grande do Sul. The females were used in three bioassays: **I** – 30 foundresses were distributed individually in pots (9 cm high × 8 cm diameter) with humid vermiculite. **II** – 15 foundress pairs were put in pots like the former. **III** – 8 (2 repetitions), 12 (2 repetitions) and 16 foundresses were put in the center of glass boxes (25 cm × 25 cm × 10 cm high) with humid vermiculite at the corners (25 cm² areas). In parallel, 12 and 18 (2 repetitions) foundresses were placed in the center of bigger boxes (40 cm × 25 cm × 10 cm high) with humid vermiculite in six areas (25 cm² each area).

All the pots and boxes were kept at room temperature (25–35 °C), 75–95% relative humidity and a 12 hours photoperiod. From the third day on leaves and petals of *Rosa*, *Hemerocales* and *Hibiscus* were offered daily. Observations of foundresses distribution, excavation, culture of the symbiotic fungus, foraging and interindividual relations were made during 90 consecutive days. The data were analysed by standard chi-square or the lambda statistics of Shields and Heeler (1979).

Results

By the first day, 77% of the isolated foundresses had excavated a chamber. This rose to 90% by the second day. As for the pairs of foundresses, 80% and 93% of them excavated a common chamber in the first and second day, respectively.

Fungus was cultivated by 96% of the isolated foundresses and by all pairs of foundresses (these frequencies were calculate from the number of foundresses that excavated). All the foundresses in Bioassay I foraged by the third day. In Bio-

assay II, 93% of the foundresses pairs foraged from the fourth day on, but less frequently than the single foundresses.

In Bioassay III, in all boxes regardless of the number of foundresses and available areas, the females were associated in only one chamber, in the left corner in front of the light source. Of the eight groups of foundresses, five closed their chamber. All groups cultivated fungus. In this bioassay, during ca. 15 minutes single foundress moved around in the box; as soon as this one joined the group another foundress went out. Interaction between foundresses were restricted to mutual antennation; no agonistic confrontation occurred. Autogrooming sessions were frequent, and allogrooming was never observed. In the eight groups with more than two foundresses no foraging occurred.

Across the three bioassays, the differences in frequencies of excavation and culture of the fungus were not significant ($\lambda = 0.308$ and 0.340 respectively; d.f. = 2 for both; $P > 0.50$). However, differences in foraging behavior were significant ($\chi^2 = 41.905$; d.f. = 2; $P < 0.001$).

Foundresses died from the end of the first week to the end of the fourth month. In pairs or groups of foundresses, the corpses were found far from those alive. Three foundresses were infected by *Beauveria bassiana*, but the remaining showed no infection or dilaceration signs.

Discussion

As haplometrosis followed by monogyny must result in high intranest relatedness, it can favour the maintenance and evolution of the social behavior through kin selection. However, mature colonies are highly territorial and can eliminate new conspecific foundresses (Hölldobler and Wilson, 1990). Thus in areas with high densities of nests it may be very hard for young foundresses to find suitable nest sites. In these restricted areas pleometrosis can be advantageous and helpful for rapid brood rearing (Tschinkel and Howard, 1983).

The frequencies of nest building and fungus culture in the three bioassays did not differ. All areas of the boxes were examined by the foundresses and independent of the areas and females density, one chamber only was excavated by the foundresses groups. Each association of foundresses cultivated a common fungus garden. These results are comparable to those obtained with *Acromyrmex versicolor* by Rissing et al. (1989). Our laboratory data are supported by field observations (data unpublished): in a small area (4 m^2) though each foundress excavates its own tunnel, only one chamber is found underground. A fungus garden is cultivated by several foundresses in this common chamber. In a bigger area (100 m^2) were the females landed far away, each one digs its own tunnel and chamber. The results suggest that colony foundation in *A. striatus* can be haplometrotic or pleometrotic, possibly relying on the distance and density of the foundresses.

The differences in foraging behavior observed in the three bioassays were very interesting. Individual queens foraged more than the pairs of foundresses, while the groups of foundresses never foraged. When more foundresses are associated the gathering of hyphae favors the development of the fungus garden. As there are more foundresses, there is an enhancement of body reserves and trophic-eggs,

foraging may thus be unnecessary. The advantages of pleometrosis are a shortening of nest building and no foundresses predation due to foraging. The *Atta texana* colonies started by pleometrosis produce more workers, the fungus gardens are more developed and the colonies have a higher survival rate than the haplometrotic ones (Mintzer, 1987).

In pleometrotic *Acromyrmex crassispinus* laboratory colonies, after worker appearance, all foundresses but one are executed (unpublished data). Laboratory colony foundation in *A. texana* is by pleometrosis and the colonies are polygynic, never occurring aggressions between the foundresses or between foundresses and workers (Mintzer, 1987). The same was reported for *A. versicolor* (Rissing et al., 1989).

Our laboratory results suggest that haplometrosis and pleometrosis are strategies of colony foundation in *A. striatus*. Under natural conditions, the adoption of one or other strategy can be related to the density of adult colonies and/or the physical proximity between the foundresses. As a result of the colony foundation process we can find monogynic and functional polygynic colonies of *A. striatus*, which was confirmed by electrophoresis (in prep.).

Foundresses corpses without indication of aggression and foundresses infected by *B. bassiana* were found far from the nest. We are not able to say if the ill foundresses moved away or were removed. In the first hypothesis we have an example of altruistic behavior; in the second, we have a grooming behavior. When a colony of *Acromyrmex* is inoculated with *B. bassiana*, removing of the corpses and ill workers are some of the first reactions observed (Kermarrec et al., 1986; Diehl-Fleig and Lucchese, 1991).

Finally, our laboratory results show that foundresses associations in *A. striatus* can be viewed mainly as a mutualistic process, not involving agonistic behavior or allogrooming. In natural conditions, it could as well decrease foundresses predation.

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