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Original Article

Reproduction of leaf-cutting ant workers: breaking the queen monopoly

Reprodução de operárias de formigas cortadeiras: quebrando o monopólio da rainha

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Abstract

The complex colony organization with labor division, age polyethism and polymorphism, specialized tasks among younger and older workers, subdivision into subcastes, and the cultivation of symbiotic fungus as the primary food source, distinguishes leaf-cutting ants of the genera *Atta*, *Acromyrmex*, and *Amoimyrmex*. The queen of these ants usually monopolizes reproduction, but polyandry, polygyny, and orphaning can favor egg-laying by unfertilized workers, resulting in the production of males. Behavioral and chemical mechanisms, including egg protection and recognition through cuticular signals, regulate complex interactions between individuals and the colony. Understanding the evolution of social behavior and the mechanisms sustaining highly organized societies depends on studies of social structure, labor division, and reproductive strategies of leaf-cutting ants. This knowledge may facilitate the management of biological fascinating species yet agricultural and forestry pests.

Keywords: *Acromyrmex*, leaf-cutting ants, polygyny, worker reproduction.

Resumo

A complexa organização da colônia, com divisão de trabalho, polietismo etário e polimorfismo, tarefas especializadas entre operárias mais jovens e mais velhas, subdivisão em subcastas e o cultivo de fungo simbionte como principal fonte de alimento, distingue as formigas cortadeiras dos gêneros *Atta*, *Acromyrmex* e *Amoimyrmex*. A rainha dessas formigas geralmente monopoliza a reprodução, mas poliandria, poliginia e a orfandade da colônia podem favorecer a postura de ovos por operárias não fecundadas, resultando na produção de machos. Mecanismos comportamentais e químicos, incluindo proteção dos ovos e reconhecimento por meio de sinais cuticulares, regulam interações complexas entre os indivíduos e a colônia. A compreensão da evolução do comportamento social e dos mecanismos que sustentam sociedades altamente organizadas depende de estudos sobre estrutura social, divisão de trabalho e estratégias reprodutivas das formigas cortadeiras. Esse conhecimento pode facilitar o manejo de espécies biologicamente fascinantes, mas que também são pragas agrícolas e florestais.

Palavras-chave: *Acromyrmex*, formigas cortadeiras, poliginia, reprodução de operárias.

1. Leaf-cutting Ants

The tribe Attini, with 49 genera and 2,726 described species (Bolton, 2025), includes the leaf-cutting ants of the genera *Atta, Acromyrmex,* and *Amoimyrmex*, which are pests in forest plantations, agriculture, and livestock (Britto et al., 2016; Camargo et al., 2025; Soares et al., 2025), but play important roles in nutrient cycling and seed dispersal (Schaefer et al., 2021; Oliveira et al., 2023) across the Americas. These ants comprise 53 species and 26 subspecies, those species and subspecies of *Atta* and *Acromyrmex*, besides *Amoimyrmex bruchi*, *Amoimyrmex silvestrii*, and *Amoimyrmex striatus* (Cristiano et al., 2020).

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2. Sex Determination and Reproduction of Leaf-cutting ant Workers

Ants are social insects, often living in populous colonies with the queen laying fertilized and unfertilized eggs, with a haplodiploid sex determination system in which females are diploid and males haploid, the latter produced by arrhenotokous parthenogenesis (Hamilton, 1964a, b). Leaf-cutting ants are divided into two castes: the queen, responsible for reproduction, and the workers, performing most other colony functions, although with colony structure, behavioral diversity, and inter- and intraspecific conflicts (Wilson, 1971). The behavior of leaf-cutting ant workers is altruistic due to kin selection, even in the presence of reproductive conflicts among nest females over male parentage (Hamilton, 1972; Heinze et al., 1997). The rearing of their own offspring by workers, instead of those of the queen, generates potential reproductive conflict in monogynous (single-queen) and monandrous (single-mated) colonies. The kin selection hypothesis is based in the concept of inclusive fitness, in which individuals increase their evolutionary success by producing direct offspring and favoring close relatives who sharing part of their genes (Hamilton, 1964a, b). The coefficient of relatedness (r) expresses the probability of two individuals sharing an identical allele by common descent, with r= 0.375 between half-sister workers, and the queen being genetically closer to her worker offspring (r= 0.5) than workers are to each other (r= 0.25). Workers may invest to producing their own offspring to increase their fitness, while the queen favors her direct descendants, resulting in reproductive conflict within the colony (Ratnieks, 1988). Polyandrous queens mate with two or more males (Ratnieks, 1988), which increases the relatedness of the workers produced to the offspring of their half-sisters (r= 0.125), thereby reducing reproductive conflict in male production. Polyandry enhances control over the reproductive hierarchy within the colony but exposes the queens to greater risks as they seek additional mates during the nuptial flight. Hypotheses proposed to explain the evolution of polyandry in social insects (Page Junior, 1986) include an increase in population longevity and, consequently, in colony size (Wilson, 1962); enhanced genetic variability among the brood and the colony, which improves caste determination and/or increases genotypic diversity among workers (Wilson, 1962; Walker, 1980); energetic efficiency, since queens mate during one period in their lifetime (Parker, 1970; Alcock et al. 1978); and the maintenance of populous colonies, as queens store large numbers of spermatozoa to use throughout their lives (Parker, 1970; Trivers and Hare, 1976; Cole, 1983). Polyandry varies among leaf-cutting ant species, with queens of *Acromyrmex octospinosus*, *Acromyrmex versicolor*, *Atta colombica*, *Atta laevigata*, *Atta sexdens*, and *Atta texana* mating on average with four to six (Boomsma et al., 1999); three (Reichardt and Wheeler, 1996); one to five (Fjerdingstad and Boomsma, 1998); more than three (Corso and Serzedello, 1981); three to eight (Kerr, 1961); and one (Moser 1967) males, respectively, thereby increasing genetic variability within highly complex societies comprising thousands of individuals. Haplometrosis and pleometrosis are additional reproductive strategies that maintain and enhance genotypic variability, leading respectively to monogynous colonies founded by one, and polygynous colonies by two or more newly fertilized females (Hölldobler and Wilson, 1990). Polygyny increases genetic variability in social insects, especially in monandrous queens, such as those of lower attine ants with smaller colonies and using different substrates for fungal cultivation compared to higher Attini, such as *Atta* and *Acromyrmex* (Urrea-Valencia et al., 2023). The effective number of matings in *Apterostigma collare* (Villesen et al., 1999), *Apterostigma mayri* (Murakami et al., 2000), *Cyphomyrmex costatus* (Murakami et al., 2000), *Cyphomyrmex longiscapus* and *Myrmicocrypta ednaella* (Villesen et al., 1999), and *C. rimosus* (Murakami et al., 2000) was 1.09, 1.04, 1.0, and 1.14, respectively, indicating monandry. Polygyny has been reported in colonies with polyandrous queens of the leaf-cutting ants *Acromyrmex subterraneus brunneus* (Delabie, 1989), *Acromyrmex subterraneus molestans* (Souza et al., 2005), *Acromyrmex subterraneus subterraneus* (Della Lucia and Vilela, 1986), *A. versicolor* (Rissing et al., 1986), and *A. texana* (Moser and Lewis, 1981; Mintzer and Vinson, 1985; Mintzer, 1987). Two to three queens were found during the excavation of *A. octospinosus* nests in the reproductive period when males and queens were produced (Boomsma et al., 1999), and virgin females of *Acromyrmex rugosus* foraged for plant substrates alongside workers (Camargo R.S., personal observation). Workers detected the relatedness of male brood through policing behavior and removed eggs laid by others (Cole, 1983; Ratnieks, 1988), thereby reducing asymmetry in male relatedness and, consequently, the conflict between queen and workers (Sundström and Boomsma, 2001). Moreover, conflict among multiple workers favoring their own offspring can replace that between individuals of this caste and the queen, but the queen's mating frequency influences the degree of conflict over male relatedness. Queen death renders the colony orphaned, as leaf-cutting ants do not replace their queen, but workers can lay eggs producing males (Dijkstra and Boomsma, 2006) (Figure 1). Workers reproduced in orphaned colonies of *Acromyrmex echinatior* and *A. octospinosus* (Dijkstra et al., 2005; Febvay and Ogier, 1984), *A. lobicornis*, *A. subterraneus brunneus*, and *A. rugosus rugosus* (Fowler, 1978; Weber, 1972; Camargo et al., 2006a), with greater phenotypic variation among males produced by workers than by queens (Fowler, 1978; Camargo et al., 2006b; Dijkstra and Boomsma, 2007). The production of males in orphaned colonies of *Atta cephalotes*, *A. colombica*, and *A. sexdens* suggests an active participation of workers in this additional reproductive role (Dijkstra and Boomsma, 2006).

3. Trophic Eggs or Reproductive Eggs?

The queen of leaf-cutting ants, during colony foundation, produces trophic eggs, which are large and soft, and reproductive ones, smaller and firmer (Autuori, 1940; Bazire-Benazet, 1957). The queen or larvae consume the former, and the unconsumed ones are left on the fungus garden and probably colonized by it (Bazire-Benazet, 1957). Medium and young workers of *A. laevigata* (body length 4 to 8 mm)

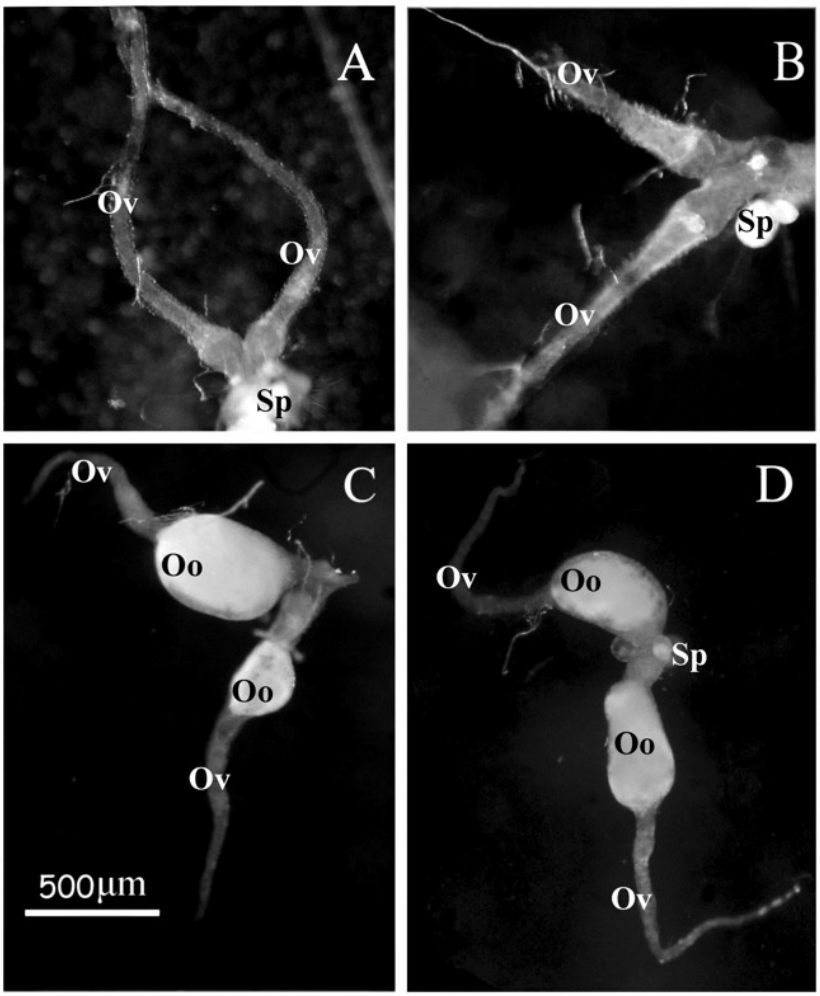

Figure 1. Ovaries of medium and large workers of *Acromyrmex subterraneus brunneus* (Hymenoptera: Formicidae) with ovarioles (Ov) without (A and B) and with (C and D) oocytes (Oo). Sp – Spermathecae.

produced trophic eggs while attending the queen, which were consumed by her or by her brood. However, *Acromyrmex* workers can produce unfertilized, haploid eggs (Weber, 1972), as reported for *A. lobicornis* after two months isolated from the queen (Bazire-Benazet, 1970). Males of different sizes were observed in orphaned colonies of *A. subterraneus brunneus* and *A. rugosus*, apparently capable of mating (Fowler, 1978; Camargo et al., 2006a), but those from orphaned colonies of *A. colombica* were unable to mate due to reduced body and genital size and rudimentary wings (Dijkstra and Boomsma 2006). Tiny sexual forms were found in queenright colonies, such as the microgynes of *A. cephalotes* and males of *Atta sexdens rubropilosa* (Bueno et al., 2002), but workers in orphaned *Acromyrmex* colonies, maintained in the laboratory with extremely reduced fungus gardens, did not reproduce and discarded late-instar larvae onto refuse piles outside the nest, probably due to their poor nutrition (Dijkstra and Boomsma, 2006). *Acromyrmex* larvae fed on trophic and reproductive eggs in queenless colonies (Camargo et al., 2006b), and queens during the claustral period (nest founding) (Autuori, 1940, 1942), as well as larvae in adult colonies of *Atta sexdens rubropilosa*, fed on the former (Schneider, 2003). Most *Atta* worker ovaries are rudimentary, producing large, soft, and yolkless trophic eggs, unlike those of the queen; however, *Acromyrmex* worker eggs resemble those of the queen but with less yolk, appearing as food for larvae, especially in *A. echinatior* (Dijkstra et al., 2005). The consumption of protein-rich trophic eggs improves larval growth and enhances reproduction in *Acromyrmex*. Queen eggs from subspecies of *A. subterraneus* are not all viable, and not all larvae developed in small fungus chambers; the smallest ones were isolated from the original colony to serve as food for other larvae (Figure 2). *A. subterraneus* queens laid viable and nonviable eggs, the latter probably as food for their larvae and workers, but the lack of trophic eggs compromises larva development in this ant (Andrade, 2002). The number of trophic eggs produced by larger *Acromyrmex* workers is often higher than that of smaller ones, indicating that these workers are the main source of these eggs, although the contribution of small workers (head width 0.7–1.1 mm) should also be investigated (Dijkstra et al.,

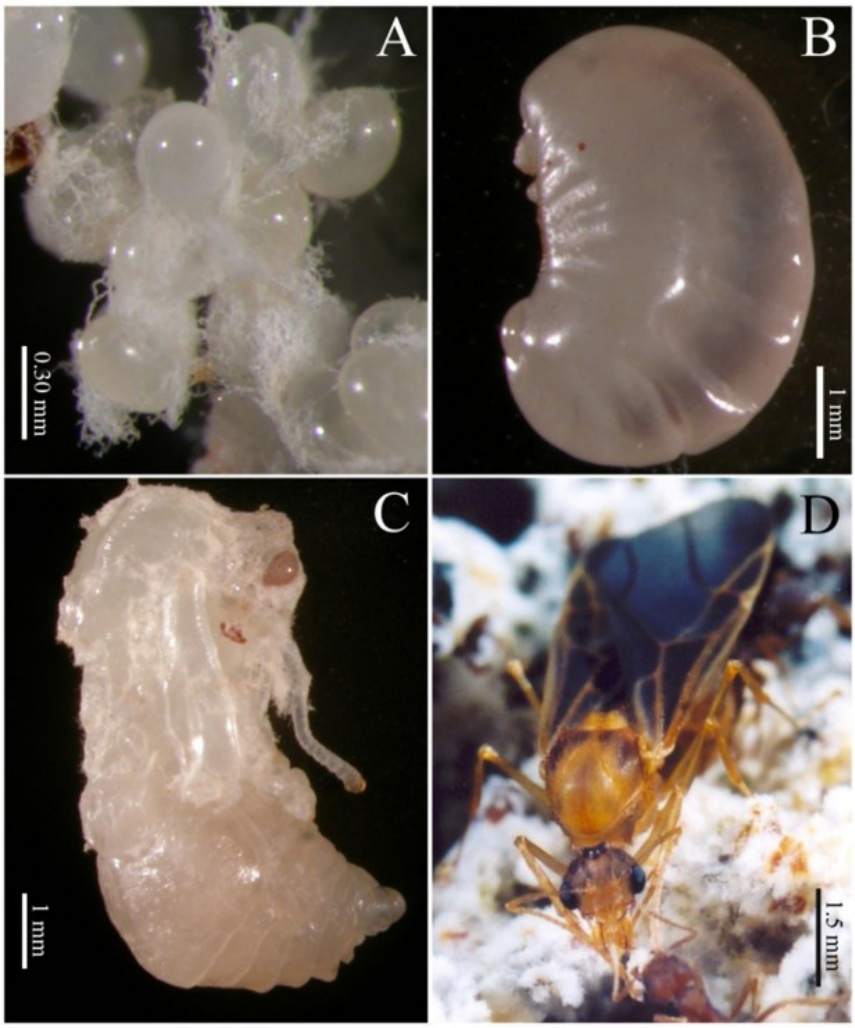

Figure 2. Developmental stages of males of *Acromyrmex subterraneus brunneus* (Hymenoptera: Formicidae) in queenless subcolonies with eggs covered by mycelia (A), larva (B), pupa (C), and newly emerged adult (D).

2005). Larger workers of *A. subterraneus brunneus* care for the brood during the first weeks of life (up to 13 weeks) and may leave the nest from the 14 weeks. Age polyethism, with tasks changing according to age, was described in *A. subterraneus brunneus* and *A. versicolor*, with young larger workers caring for the brood (Julian and Fewell, 2004). Morphological and age-based subcastes within the nest increase interaction among groups and energy transfer to larvae through feeding on the symbiotic fungus (via staphylae) and trophic eggs. The provision of essential nutrients to the brood reduces sibling cannibalism, especially in extreme environments with a high risk of starvation risks (Perry and Roitberg, 2006), and consequently larval mortality.

4. Brood Care in Queenless Colonies

Brood care by leaf-cutting ants is complex, as reported for 13 behavioral acts for *Atta sexdens rubropilosa*, including cleaning, assistance during emergence, transport of eggs, larvae, and pupae, and feeding larvae with staphylae, manipulated fungus, intact hyphae, and trophic eggs (Schneider, 2003). Many of these behaviors are poorly known (Fowler, 1983; Wilson, 1983), but likely its functions are similar to those described for *A. subterraneus brunneus* (Table 1). Licking the brood is associated with cleaning and sanitation; transport is related to microclimate management or response to nest disturbances (Bollazzi and Roces, 2002); and larval feeding involves nutrition and the transfer of substances via ingestion of fecal fluid (Figures 3, 4, 5) (Schneider, 2003; Lopes et al., 2005). The behavioral repertoire of winged adults in leaf-cutting ants is generally more limited, including self-grooming, mutual grooming among workers, food reception, and in some cases, independent feeding (Hölldobler and Wilson, 1990). Males of lower Attini, such as *Mycetarotes parallelus*, receive minimal care, limited to cleaning (Diniz and Bueno, 2010), unlike those of *A. cephalotes*, requiring greater effort to obtain food in quantities similar to females

(Bass and Cherrett, 1995) due to the need of carbohydrate for the nuptial flight and locating females, and dying after copulation (Jutsum and Quinlan, 1978). The behavioral repertoire in orphaned colonies reflects adaptations and social organization in leaf-cutting ants, especially in the absence of the fertile caste (Camargo et al., 2006b)

5. Communication between Queen and Workers

The division of labor in social colonies is clear, with the queen responsible for reproduction, and the sterile workers maintaining the colony (Robinson, 1992). Chemical and physical signals are more important for

Table 1. Behavioral acts (BA) including licking the larvae body (La), transporting larvae (Tr), feeding larvae with hyphae (Al), scraping the larval mouthparts (Ra), ingesting fecal fluid excreted by larvae (In), and depositing hyphae on larvae (De), and their likely functions performed by workers of *Acromyrmex subterraneus brunneus* (Hymenoptera: Formicidae) in brood care and references (Ref.).

BA	Description	Probable function	Ref
La	Licking the larval body, especially the oral and proctodeal regions	Cleaning and sanitation of the larva	1
Tr	Removal and transport of larvae to other parts of the fungus garden	Handling of larvae according to microclimatic conditions and response to nest disturbance	
Al	Feeding the larva with manipulated hyphae and staphylae (macerated by mandibular movements of the workers)	Larval nutrition	3,1
Ra	Cleanin the larva oral region with their mandibles	Cleaning and sanitation of the larva	1
In	Ingestion of fecal fluid droplets excreted by the larvae	Substance exchange via trophallaxis between larvae and workers	5, 1
De	Deposition of hyphal tufts on the external tegument of the larvae	Protects larvae against parasites or camouflaging them from predators	1,4, 5, 6

1-Lopes et al. (2005), 2-Bollazzi and Roces (2002), 3-Schneider (2003); 4-Weber (1972); 5-Swartz (1998); 6-LaPolla et al. (2002).

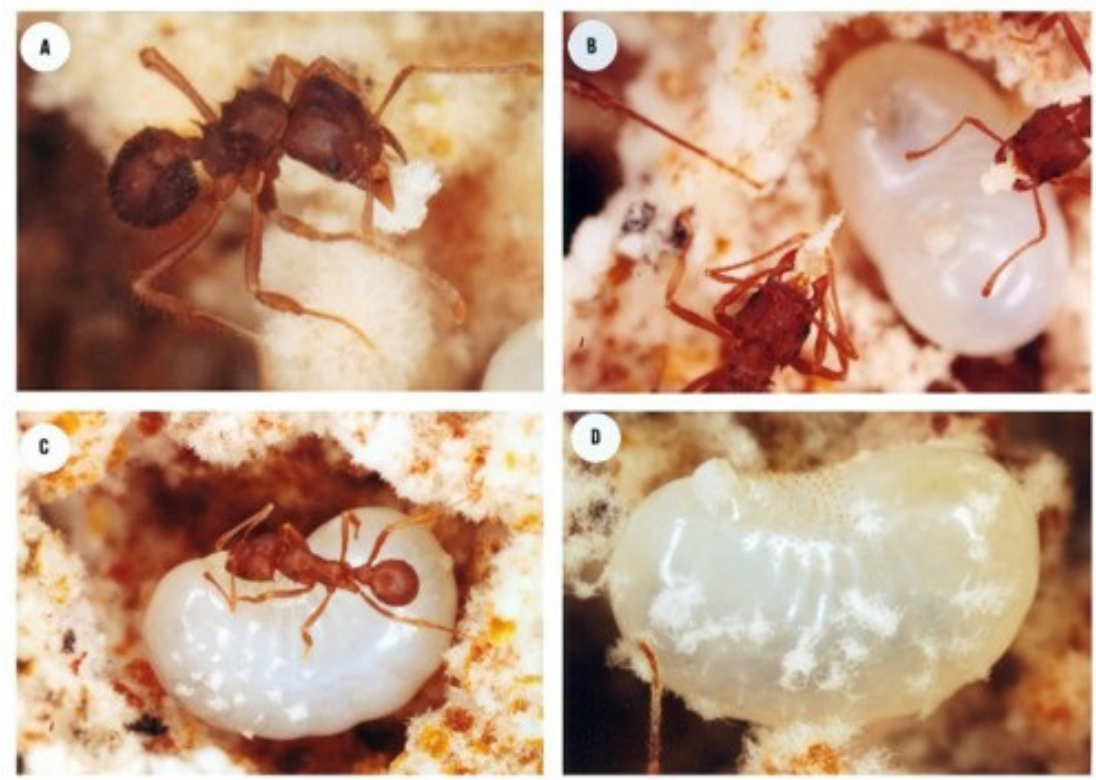

Figure 3. Behavioral acts performed by workers of *Acromyrmex subterraneus brunneus* (Hymenoptera: Formicidae): Transport of hyphae or staphylae (A); chewing/manipulating hyphal or staphylae tufts (B); feeding larvae with hyphae (Ali) (C); placing hyphae on the larvae (D). The photos are a courtesy of Camargo et al. (2006a).

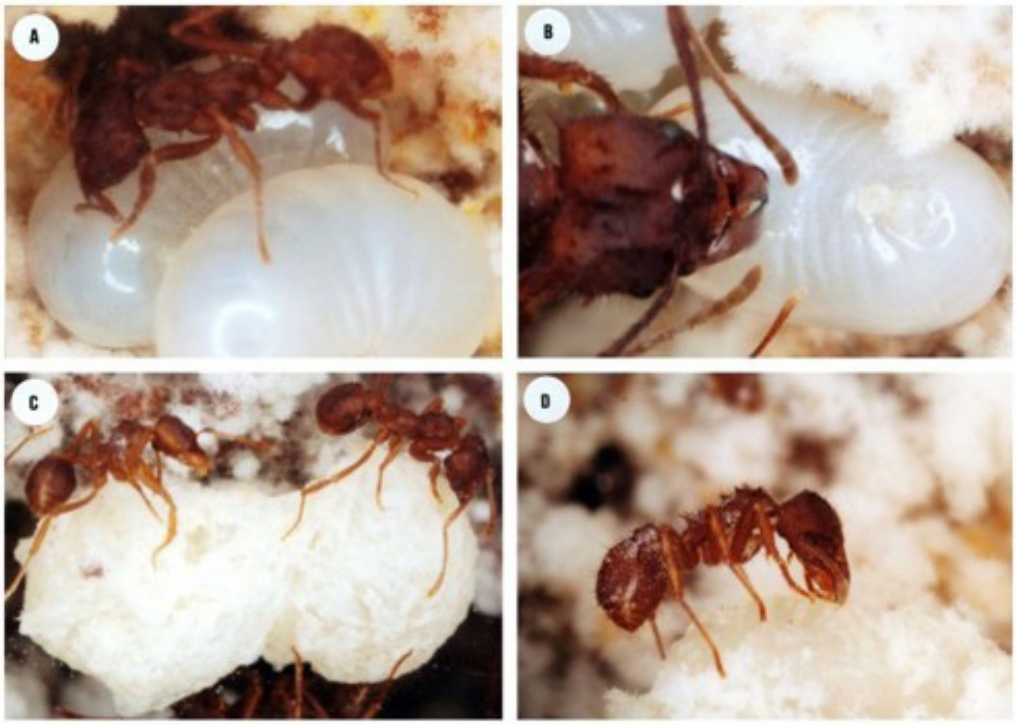

Figure 4. Behavioral acts performed by workers of *Acromyrmex subterraneus brunneus* (Hymenoptera: Formicidae): licking the larval body (La) (A); ingesting fecal fluid excreted by the larva (In) (B); licking the pupal body (C); detail of licking the pupal body (D). The photos are a courtesy of Camargo et al. (2006a).

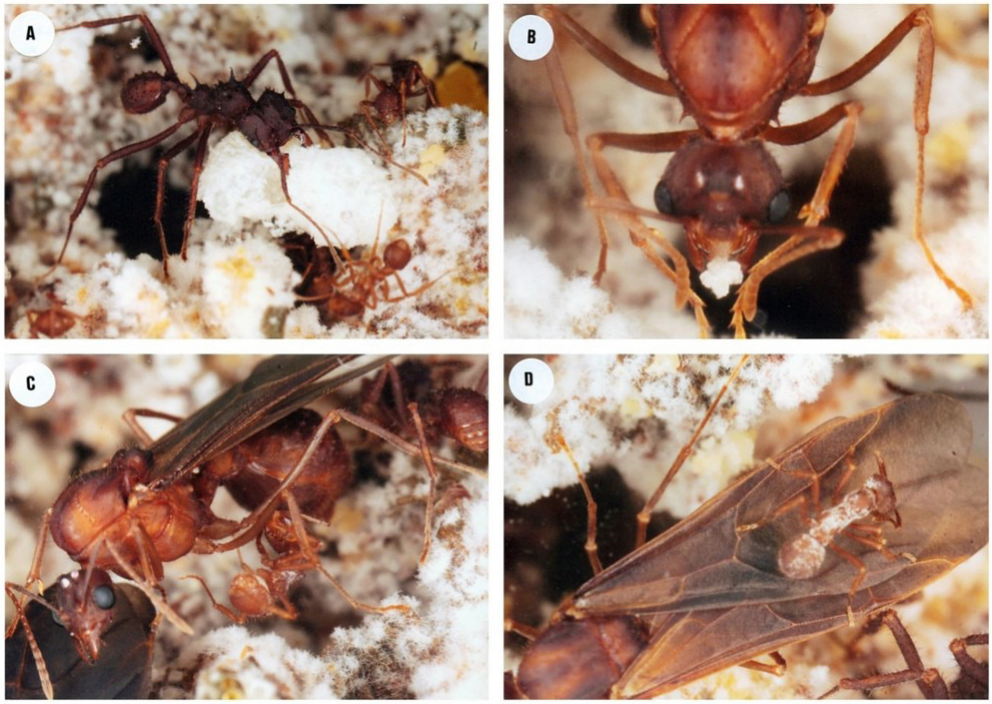

Figure 5. Behavioral acts performed by workers and males of *Acromyrmex subterraneus brunneus* (Hymenoptera: Formicidae): transport of pupae (A); collecting staphylae and self-feeding (B); mutual grooming between worker and male (C and D); and worker on the male wing covered by the specialized symbiotic bacterium (Pseudonocardiaceae) associated with *Acromyrmex* (D) (Currie et al., 2003). The photos are a courtesy of Camargo et al. (2006a).

individual and collective behaviors in larger societies with more pronounced dimorphism, predominantly via pheromones, with the queen not only reproducing and maintaining social cohesion in the colony through chemical control of worker reproduction in larger colonies (Wilson, 1971; Keller and Nonacs, 1993; Moreira et al., 2004). On the other hand, her power relatively lower than in smaller societies (Keller and Nonacs 1993; Bourke and Ratnieks 1999), with dimorphism between worker and reproductive castes and direct physical suppression, including aggression and egg cannibalism, occurring more frequently (Wilson, 1971; Keller and Nonacs, 1993; Bourke, 1999). Cuticular hydrocarbons, through mutual grooming and self-grooming, maintain colony odor homeostasis for communication between the queen and workers (Wilson, 1971; Naumann, 1991; Jaccoud et al., 1999). Hydrocarbons produced by the queen of *Camponotus floridanus* and conveyed on the eggs regulated worker reproduction (Endler et al., 2004), which may also occur in leaf-cutting ants. Oral trophallaxis, a common mechanism in ants to transferring food and substances, may also disperse chemical signals, although its frequency and importance in leaf-cutting ants are controversial. Fluid absorption species of *Acromyrmex* is low, suggesting that this process is not the main pathway to transferring substances between these ants (Wilson, 1971; Littledyke and Cherrett, 1976; Paul and Roces, 2003; Erthal Junior et al., 2004). Selective pressures adjust behavioral acts for colony continuity and caste hierarchical rigidity, including reproduction among leaf-cutting ant workers, breaking the queen's reproductive monopoly. Understanding the mechanisms that regulating reproduction by workers is essential to elucidate the evolutionary processes that shaped the complex social organization of leaf-cutting ants.

6. Conclusion

Reproduction among leaf-cutting ant workers may breake the queen reproductive monopoly under certain social and ecological conditions. This reproductive flexibility indicates that caste hierarchical rigidity is the result of dynamic selective pressures, allowing behavioral adjustments ensuring colony continuity. Thus, understanding the mechanisms regulating reproduction among workers is essential to elucidate the evolutionary processes that shaped the complex social organization of leaf cutting ants.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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