

ECOLOGY, BEHAVIOR AND BIONOMICS

Comparative Reproductive Biology of the Social Parasite *Acromyrmex ameliae* De Souza, Soares & Della Lucia and of its Host *Acromyrmex subterraneus subterraneus* Forel (Hymenoptera: Formicidae)

ILKA M F SOARES<sup>1,2</sup>, TEREZINHA M C DELLA LUCIA<sup>2</sup>, ALICE S PEREIRA<sup>2</sup>, JOSÉ E SERRÃO<sup>3</sup>,  
MYRIAM M R RIBEIRO<sup>2</sup>, DANIVAL J DE SOUZA<sup>2,4\*</sup>

<sup>1</sup>Univ do Estado da Bahia, Depto de Educação, Campus VIII, Av da Gangorra 503, Alves de Sousa, 48608-240 Paulo Afonso, BA, Brasil; [Ilka\\_soares@yahoo.com.br](mailto:Ilka_soares@yahoo.com.br)

<sup>2</sup>Univ Federal de Viçosa, Av P H Rolfs, Depto de Biologia Animal, 36570-000 Viçosa, MG, Brasil; [tdlucia@ufv.br](mailto:tdlucia@ufv.br); [alicinhapereira@yahoo.com.br](mailto:alicinhapereira@yahoo.com.br); [myriam.m.r.ribeiro@gmail.com](mailto:myriam.m.r.ribeiro@gmail.com); [danivalbr@yahoo.com.br](mailto:danivalbr@yahoo.com.br);

<sup>3</sup>Univ Federal de Viçosa, Av P H Rolfs, Depto de Biologia Geral, 36570-000 Viçosa, MG, Brasil; <sup>4</sup>actual address: Univ Federal do Tocantins, Campus de Gurupi, 77402-970, Gurupi, TO, Brasil; [jeserrao@ufv.br](mailto:jeserrao@ufv.br), author correspondent\*

Edited by Fernando L Cônsoli – ESALQ/USP

*Neotropical Entomology* 39(5):714-719 (2010)

**ABSTRACT** - Social parasites exhibit several characteristics that allow them to exploit their host species efficiently. The smaller size of parasite species is a trait commonly found in ants. In this work, we investigated several aspects of the reproductive biology of *Acromyrmex ameliae* De Souza, Soares & Della Lucia, a recently discovered parasite of *Acromyrmex subterraneus subterraneus* Forel. Sexuals of *A. ameliae* are substantially smaller than those from host species. Parasite queens laid significantly less worker eggs than host queens and inhibit sexual production of the host. The sex ratio of parasite species is highly female biased. Interestingly, we have observed parasite coupling on the laboratory, inside the nests and in the ground, opening the possibility to use controlled mating to study genetic approaches of parasitism in the ants.

**KEY WORDS:** Social parasitism, egg production, size reduction

One of the most remarkable traits of an insect society is the reproductive cooperation (Wilson 1971). However, social insects are vulnerable to reproductive parasitism, both interspecific and intraspecific. Host exploitation by parasitic species involves elaborated parasitic adaptations such as morphophysiological and behavioral alterations (Hölldobler & Wilson 1990). In the ants, sexuals of social parasite species are usually smaller than the queens of the host species. According to the miniaturisation hypothesis, size reduction might have evolved as a means of the species to take advantage in the system of host caste determination (Bourke & Franks 1991). Parasitic larvae may develop when the host does not produce sexuals; in addition, the parasite larvae develop into sexuals with lesser quantities of food than is required to produce workers (Bourke & Franks 1991, Nonacs & Tobin 1992). The smaller size reduces the capacity of host workers to distinguish between their immatures and those of the parasite as in *Plagiolepis pygmaea* (Latreille) (Aron *et al* 1999) and facilitates the subjection of the parasite to the host queen as in the extreme inquiline (those without the worker caste) such as *Teleutomymex* and *Pseudomymex* (Hölldobler & Wilson 1990).

Parasite queens and workers can also influence host reproduction. The workers of *Acromyrmex insinuator* Schultz,

Bekkevold & Boomsma, the inquiline of *Acromyrmex echinator* (Forel), are essential to the production of the parasite sexuals, indicating that this attribute is one of the main functions of the parasite workers (Sumner *et al* 2003). They are capable of inhibiting the reproduction of the host queen. This same behavior has been reported in *P. pygmaea*, the host of *Plagiolepis xene* Stärcke, in laboratory colonies (Passera *et al* 2001).

Internal differences of the reproductive tract are found between social parasites and their host species. In the ant *Ectatomma tuberculatum* (Olivier) the queens exhibit size dimorphism and differences in their oocyte numbers (Hora *et al* 2001, 2005). The microgynes – reproductive females of smaller sizes than macrogynes in the same nest – are specialized in microgyne and male production and seldom produce workers; macrogynes produce large number of workers but never microgynes (Hora *et al* 2003). Using a terminology developed to parasitoid wasps (Flanders 1950), ants are synovigenic, i. e., queens continue to mature eggs throughout their reproductive life, including the parasitic queens.

*Acromyrmex ameliae* has recently been described by De Souza *et al* (2007). It is a social parasite of the inquiline type that has a few minor workers similar to those of its hosts,

the leaf-cutting ants *Acromyrmex subterraneus subterraneus* Forel and *Acromyrmex subterraneus brunneus* (Forel), and appears to be closely related to these hosts.

This study investigated reproduction features of the social parasite *A. ameliae*, and compared some of these reproduction aspects with those of its host *A. subterraneus subterraneus*. Nuptial flight period in laboratory and size reduction in males and females were determined. Additionally, morphological and histological analyses of the female reproductive tract and comparative egg production by *A. ameliae* and its host *A. subterraneus subterraneus* were performed.

The following hypotheses were tested: 1) Females of *A. ameliae* have size reduction beyond the size observed in the major workers of the host; consequently 2) egg production in the parasite species is lower than in its host; 3) parasitic queens and/ or workers interfere in the egg production by the host queen.

## Material and Methods

Parasitized colonies of *A. subterraneus subterraneus* were collected in Paraopeba, Minas Gerais State (MG), Brazil (19° 17' S; 44° 29' W) in 2003 and 2004. Each of these colonies had one host queen and variable numbers of parasite queens (2-6).

**Nuptial flight in laboratory and sex proportion.** Ten *A. ameliae* colonies produced alates in the laboratory and two (with the highest numbers) were used to calculate sex ratio in the species. Numbers of parasite alates (males and females) were counted in each nest and sex ratio was obtained by dividing the total number of males by that of females.

**Size reduction of sexuals.** To verify if *A. ameliae* has alate individuals significantly smaller than the largest workers of the host *A. subterraneus subterraneus*, the total body length (from head to gaster) of 44 males, 30 females and 50 major workers of the host and 150 males and 151 females of the parasite species were measured under a stereoscopic microscope using a micrometric ocular (Leica MZ 7.5; Göttingen, Germany). Major host workers were measured for size comparison with those of the parasite queen.

**Description of the female reproductive tract.** Females of *A. ameliae* were removed from two colonies and dissected for ovariole and mature oocytes counting. Ovarioles of three females were transferred to Bouin solution for 24h, dehydrated in an increasing series of ethanol solutions, and imbedded in JB-4 resin (Souza *et al* 2006). The 5 µm-thick sections were dyed with hematoxylin and eosin (Antunes *et al* 2002). Description of the reproductive tract was based on microscopic observation (100x) of the thin sections.

**Comparison of *A. subterraneus subterraneus* and *A. ameliae* egg-laying and influence of parasite workers and queens on the oviposition of the host queen.** Three colonies of *A. subterraneus subterraneus* with fungus garden volumes of 5000, 3100 and 2000 ml were used in this experiment. Twenty dealate parasite gynes were recovered

from these colonies. The influence of the parasite species on the egg-laying of the host was tested by comparing the following treatments: 1) HQ – isolated host queen (n = 6); 2) HQ(HPW) – host queen with seven host and three parasite workers (n = 6); 3) PQ – isolated parasite queens (n = 20); 4) PQ(HPW) – parasite queens with eight hosts and two parasite workers (n = 16).

Oviposition of host and of parasite queens alone was evaluated and used for comparison of oviposition in the presence of workers of both host and parasite workers (n = 10). Test one consisted of evaluating oviposition of the host queen by itself and test 2 evaluated oviposition of the host queen in the presence of seven host workers and three parasite workers. This also had the purpose of verifying if the presence of the parasite queen interfered in egg production by the host queen. Due to the small numbers of parasite workers and the larger number of *A. ameliae* queens, a small number of parasite workers was used in test number 4. The previous estimation of the proportion of *A. ameliae* workers in the parasitized colony of *A. subterraneus subterraneus* was around 3% (authors unpublished data).

For each test, the individuals were isolated in closed containers for a period of 16h and fed a diet of water and honey solution (Marinho & Della Lucia 1998). The use of the queens was randomized throughout the experiments and they were giving one week intervals between the tests for recovery. The queens were always removed from the colonies at 8:00h and returned at 00:00h. The numbers of eggs laid were counted at 4h intervals (12:00, 16:00, 20:00, and 00:00h). The ovipositing queens were marked in the gaster with non-toxic ink at the end of test 3 and later used in test 4.

Test 5 aimed to verify the effect of the parasite queens on the host queen egg-laying capability. Since we observed that host and parasite queens generally are not together physically in the fungus garden, it was assumed that if there was an effect of the parasite queen on oviposition, it would be of a chemical nature. Therefore, the host queen was physically isolated from the parasite queens but glass tubes connected the glass containers to allow volatile substances from parasite queens to reach host queens.

To determine if all the parasite egg-laying queens had been fertilized, 30 of these queens were dissected and their spermathecae were examined.

## Results

**Nuptial flight in laboratory and sex ratio.** The 10 colonies of *A. subterraneus subterraneus* produced parasite alates in abundance from October to February resulting in drastic fungus reduction in all colonies and in subsequent death of two of these colonies. A smaller number of these alates occurred through May. Mating couples were observed. It is believed that some of these females were readopted by their colonies, since the observed number of female parasites in test 4, conducted a few weeks later, was higher, in some cases, than in test 3, conducted weeks before.

The sex ratio of alate males in relation to females was 1:5.3 (474 males and 2,514 females). In 2005 no mating

flights were observed under laboratory conditions as occurred in 2003 and 2004, however, some couples were observed mating inside the colony. In November 2006, a large production of males was verified in some colonies. During that period host workers transported live parasite males from the fungus garden and the foraging arena to the colony waste.

**Reduction in size of the sexuals.** *Acromyrmex ameliae* sexuals were significantly smaller in size than those of its host *A. subterraneus subterraneus*. Male size differed between *A. ameliae* (< 7.0 mm) and *A. subterraneus subterraneus* (about 8.0 mm in length) ( $F_{1,192} = 137.60$ ,  $P < 0.001$ ) (Fig 1a). Female parasites were also smaller about 8.0 mm in size, whereas females of the host were approximately 10 mm ( $F_{1,179} = 1071.2$ ,  $P < 0.001$ ) (Fig 1b). Body size of *A. ameliae* females is smaller than that of the major workers of *A. subterraneus subterraneus* (~ 10.0 mm) ( $F_{1,199} = 921.07$ ,  $P < 0.001$ ) (Fig 2).

**Description of the female reproductive tract.** The reproductive system of *A. ameliae* is composed by one pair of ovaries, formed by 13 to 15 ovarioles per ovary. The walls of the lateral and common oviducts are formed by a well developed musculature, layering a simple epithelium of flattened cells with nuclei having predominantly condensed

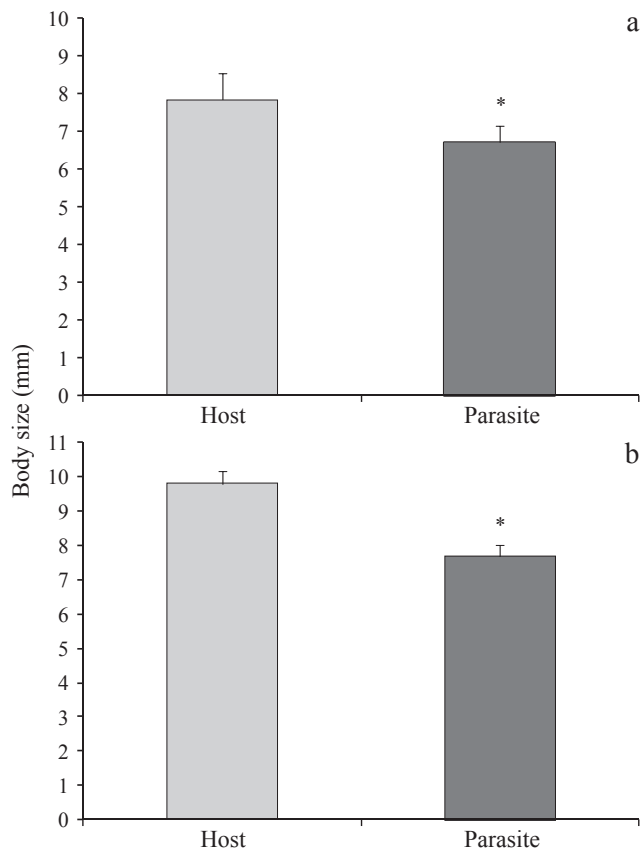


Fig 1 Comparison (mean + st. error) of the body size of the male (a) ( $F_{1,192} = 137.60$ ,  $P < 0.001$ ) and of the female (b) ( $F_{1,179} = 1071.2$ ,  $P < 0.001$ ) of *Acromyrmex subterraneus subterraneus* (host) and *Acromyrmex ameliae* (parasite).



Fig 2 Comparison of the body size of major workers of *Acromyrmex subterraneus subterraneus* (host) and of females of *Acromyrmex ameliae* (parasite) (mean + st. error) ( $F_{1,199} = 921.07$ ,  $P < 0.001$ ).

chromatin. Internally, the center of the oviduct is coated by a thick cuticle which has projections in the shape of spines toward the center (Fig 3a).

A few ovarioles had developed oocytes. A single mature oocyte was observed per ovariole (Fig 3d). Common oviduct, vagina and spermatheca were also observed. The large spermatheca is transparent when empty but has a pearly colour when the female is fertilized. As in all the Hymenopterans, the ovaries are meroistic – when there are nurse cells associated with the developing egg - and polytrophic – where each oocyte is closely associated with nurse cells in its follicle. At the apical portion of the germarium, the oogonies can be observed and they later divide giving rise to cysts, in addition to the oocyte, the nursing cells with a developed nucleus and little condensed chromatin (Fig 3b,c).

In the vitellarium zone it is possible to identify the follicles formed by the nursing and oocytic chambers, the first being delimited by follicular and flat cells while in the oocytic chamber, these cells are column-like.

**Comparison between egg-laying of *A. subterraneus subterraneus* and *A. ameliae* and effect of parasite workers on the oviposition of host and parasite queens.** Females of *A. subterraneus subterraneus* laid significantly more eggs than those of *A. ameliae* ( $F_{1,41} = 149.04$ ,  $P < 0.001$ ) (Fig 4). While queens of host subspecies alone laid approximately 230 eggs when isolated for 16h, those of parasite queens laid less than six eggs under the same conditions. The presence of queens and workers of the parasite did not reduce significantly the oviposition of the host queen, although a considerable reduction has been observed. Furthermore, the presence of workers of either parasite or host did not affect *A. ameliae* oviposition (Fig 4).

Of the 30 dealate females of the parasite which oviposited, 11 were fertilized, i.e., their spermathecae were full of spermatozoa; 10 females, although showing characteristic of oviposition in the ovaries, had empty spermathecae (Fig 5). It is possible that these females produced trophic eggs, or eggs which gave rise to males. The remaining females (n = 9) did not have developed ovaries.



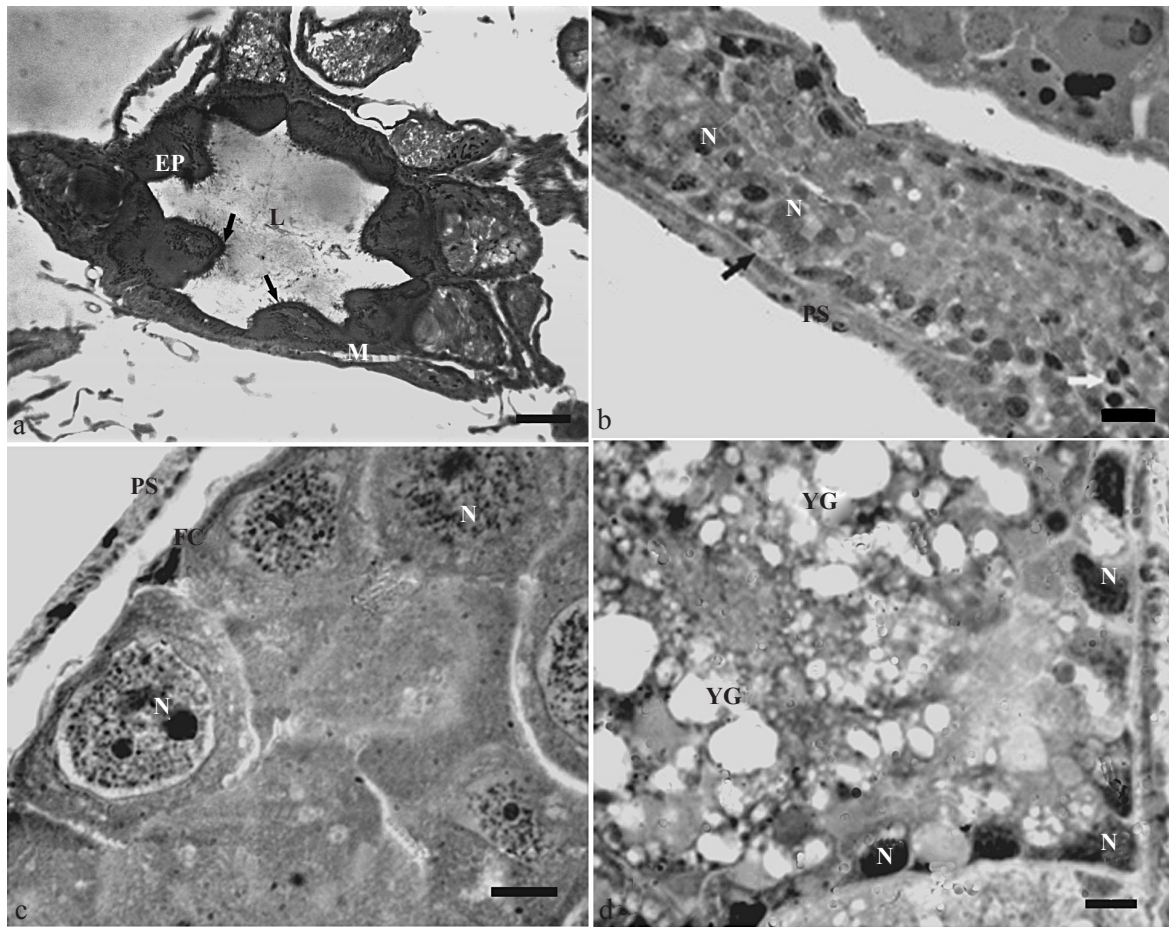


Fig 3 Female reproductive tract of *Acromyrmex ameliae*. a) common oviduct: L: lumen; M: muscle; arrows: cuticular projections in spine shape; EP: epithelium; b) germarium: PS: peritoneal sheath; black arrow: tunica propria; N: nucleus of the germinative cells; white arrow: nucleus of pre-follicular cells; c) nutrition cell: PS: peritoneal sheath; FC: follicular cells; N: nucleus of nutrition cells; d) oocyte: N: nucleus of follicular cells; YG: yolk cells. Scale: all figures are 10  $\mu$ m in size.

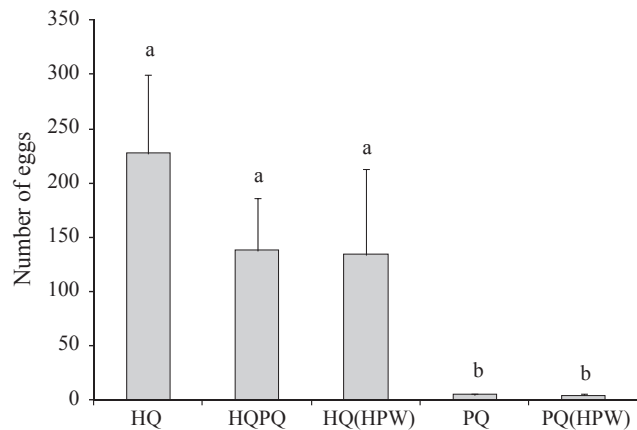


Fig 4 Mean number of eggs laid by *Acromyrmex subterraneus subterraneus* (host) and *Acromyrmex ameliae* (parasite) under different conditions (HQ = host queen; HQ(HPW) = host queen + host and parasite workers; PQ = parasite queen; PQ(HPW) = parasite queen + host and parasite workers; HQPQ = host queen + parasite queens. Bars represent the standard errors. Different letters indicate significant differences at 5%, Tukey test for different n values.

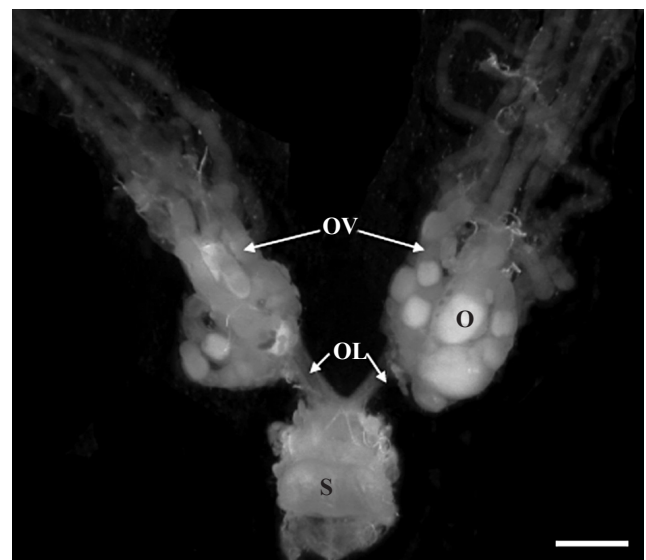


Fig 5 Partial structure of the female reproductive tract of *Acromyrmex ameliae*. S = spermatheca; OL = lateral oviduct; OV = ovary; O = ovariole. Scale: 0,5 mm in size.

## Discussion

The production of sexuals by *A. ameliae* during a few months of the year, especially from October to February, led to colony decline and, in some situations, to colony death, which is common in other Attini (Bekkevoold & Boomsma 2000, Bueno *et al* 2002). It is likely that the removal of males from the fungus chamber and from the foraging arena is a strategy of the host to decrease the destruction caused by the males due to their excessive feeding. A similar behavior was observed in *A. insinuator* when the food sources of host colonies were reduced (Bekkevoold & Boomsma 2000).

Mated females were readopted by their mother colonies; this explains the high number of parasite queens in some nests and the difference of this number in the experiments. Similar data were observed in the social parasite *A. insinuator* where dealate gynes remained in the mother-colony after stopping their production and food sources slowly declined (Bekkevoold & Boomsma 2000).

The behavioral change in mating (initially they had a mating flight and later mated inside the nest) could promote endogamy. Intra-nest mating is common in some species of social parasites of the genera *Epimyrma*, *Teleutomyrma* and *Anergates*; except for *Epimyrma*, the others are not endogamic. Such species have morphophysiological limitations such as: reduced wings and low dispersal ability (Dumpert 1981, Buschinger 1989), characteristics that together with nest aggregation are very common in social parasites. In *A. ameliae*, possible mating flight continues to occur in the field and there is less queen readoption since these nests occur very close to each other.

A female-biased population-wide sex ratio, that is, large production of alate females when compared to the number of males, as observed in *A. ameliae* is a common aspect of some species of social parasites, dulotic (species depending on workers of others species) or inquilines. In *Epimyrma krausseii* Emery and *Solenopsis daguerrei* (Santschi) the number of reproductive queens reaches three times that of males (Buschinger 1989, Calcaterra *et al* 1999); greater female production is also found in *P. xene* (Aron *et al* 1999). The larger number of females may lead to a competition between brothers (Bourke & Franks 1995) and may occur due to polyandry since, according to Calcaterra *et al* (1999), sexual ratio based on females is a characteristic originated from polyandry. This aspect was reported in *P. xene* (Aron *et al* 1999) and it seems to occur in *S. daguerrei* (Calcaterra *et al* 1999). However, the social parasite *A. insinuator* mates with only one non-brother male after leaving the nest for a short period of time (Sumner *et al* 2004). In *A. ameliae* the male has seminal vesicles about four times the size of the female spermatheca; from a biological stand point, this enables the male to fill the spermatheca and to mate with more than one female (Soares *et al* in preparation).

Sexual forms of *A. ameliae* are smaller than those of the host *A. subterraneus subterraneus*. It is likely that size reduction brings some benefit to the species, maybe allowing the immatures to develop more rapidly and with less food than the host immatures. In *P. xene*, whose male and female pupae are significantly smaller than the pupae of the host *P.*

*pygmaea*, size reduction is important especially in the males because host workers identify and destroy all male immatures of their own species (Aron *et al* 2004). In *A. ameliae*, the sexuals are significantly smaller than the largest workers of the host subspecies.

The large difference in egg production between *A. subterraneus subterraneus* and *A. ameliae* is directly related to the morphology of the reproductive tract of the species. Whereas females of *A. subterraneus subterraneus* have approximately 28 ovarioles in each ovary containing about 24 mature oocytes each (Antunes *et al* 2002), females of the parasite had smaller numbers of both ovarioles and oocytes. Differences between the number of ovarioles of host and parasite were also found by Hora *et al* (2001). They observed that the microgynes of *E. tuberculatum* have smaller number of ovarioles than the macrogynes; however, in this case, the number of oocytes was not different among females, suggesting that both micro and macrogynes have similar individual fecundity (Hora *et al* 2005).

It is likely that the small number of ovarioles and oocytes in *A. ameliae* is associated with its life style of parasitism in which it needs worker force from the host colony because its number of workers is very small (approximately 3%) and has only minors.

The negative impact of reproductive females and workers of the parasite species on the host queen is related solely with the production of sexuals; colonies parasitized by *A. ameliae* under laboratory conditions did not produce sexuals of the host species. The worker caste of *A. ameliae* is essential to production of its sexuals, as in *A. insinuator*, and it suppresses host queen reproduction. This means that parasite queens that do not produce workers or fail to reach a certain reproduction threshold will have zero fitness.

The minimum proportion of workers necessary to produce sexuals is smaller if there is more than one parasite queen present (Sumner *et al* 2003). Negative interference of the parasite species (*P. xene*) on egg and worker production by host queens was also observed by Passera *et al* (2001). The presence of only workers of the host *A. subterraneus subterraneus* did not affect oviposition as already reported by Marinho & Della Lucia (1998), and the presence of parasite workers also did not interfere on the number of eggs laid by *A. ameliae* (Fig 4).

It can be concluded that *A. ameliae* has sexuals significantly smaller than those of *A. subterraneus subterraneus* and produces a significantly smaller number of eggs than the host. The presence of queens and/or parasite workers did not negatively affect host queen egg laying but inhibited the production of sexuals by the host queen.

## Acknowledgments

We thank Dr Ricardo Della Lucia (Universidade Federal de Viçosa) and Dr Rosa Muchovej (University of Florida) for insightful comments on this manuscript, and Dr Leandro Souto (Universidade Federal de Sergipe) for his valuable help. We are also grateful to CNPq and Pronex/FAPESB (nº 158/03) for funding this project.

## References

- Antunes E C, Serrão J E, Della Lucia T M C (2002) Morphology of the reproductive tract of *Acromyrmex subterraneus subterraneus* queens (Hymenoptera: Formicidae). *Sociobiology* 39: 269-279.
- Aron S, Passera L, Keller L (1999) Evolution of social parasitism in ants: size of sexuals, sex ratio and mechanisms of caste determination. *Proc Biol Sci* 266: 173-177.
- Aron S, Passera L, Keller L (2004) Evolution of miniaturization in inquiline parasitic ants: timing of male elimination in *Plagiolepis pygmaea*, the host of *Plagiolepis xene*. *Insect Soc* 51: 395-399.
- Bekkevold D, Boomsma J J (2000) Evolutionary transition to a semelparous life history in the socially parasitic ant *Acromyrmex insinuator*. *J Evol Biol* 13: 616-623.
- Bourke A F G, Franks N R (1991) Alternative adaptations, sympatric speciation and the evolution of parasitic, inquiline ants. *Biol J Linn Soc Lond* 43: 157-178.
- Bourke A F G, Franks N R (1995) Social evolution in ants. Princeton, Princeton University Press, 529p.
- Bueno O C, Hebling M J A, Schneider M.O, Pagnocca F C, Bacci Jr M (2002) Occurrence of winged forms of *Atta sexdens rubropilosa* Forel (Hymenoptera: Formicidae) in laboratory colonies. *Neotrop Entomol* 31: 469-473.
- Buschinger A (1989) Evolution, speciation, and inbreeding in the parasitic ant genus *Epimyrma* (Hymenoptera, Formicidae). *J Evol Biol* 2: 265-283.
- Calcaterra L A, Briano J A, Williams D F (1999) Field studies of the parasitic ant *Solenopsis daguerrei* (Hymenoptera: Formicidae) on fire ants in Argentina. *Environ Entomol* 28: 88-95.
- Chapman R F (1998) The insects: structure and function. Cambridge, Cambridge University Press, 770p.
- De Souza D J, Soares I M F, Della Lucia T M C (2007) *Acromyrmex ameliae* sp.n. (Hymenoptera: Formicidae): a new social parasite of leaf-cutting ants Brazil. *Insect Sci* 14: 251-257.
- Dumpert K (1981) The social biology of ants. Boston, The Pitman Press, 298p.
- Flanders S E (1950) Regulation of ovulation and egg disposal in the parasitic Hymenoptera. *Can Entomol* 82:134-140.
- Hölldobler B, Wilson E O (1990) The ants. Cambridge, Harvard University Press, 732p.
- Hora R R, Delabie J H C, Poteaux C, Féron R, Doums C, Fresneau D (2003) Primeiro caso de parasitismo social na subfamília Ponerinae. In Encontro de Mirmecologia, Florianópolis, Anais... p.243-245.
- Hora R R, Doums C, Poteaux C, Féron R, Valenzuela J, Heinze J, Fresneau D (2005) Small queens in the ant *Ectatomma tuberculatum*: a new case of social parasitism. *Behav Ecol Sociobiol* 159: 285-292.
- Hora R R, Féron R, Valenzuela J, Favila M E, Fresneau D (2001) Queen-size dimorphism in the ant *Ectatomma tuberculatum* (Hymenoptera: Formicidae: Ponerinae). *Sociobiology* 38: 407-420.
- Marinho C G S, Della Lucia T M C (1998) Egg-laying in *Acromyrmex* spp. (Hymenoptera: Formicidae) under laboratory conditions. *Biociências* 6: 71-79.
- Nonacs P, Tobin J E (1992) Selfish larvae: development and the evolution of parasitic behavior in the Hymenoptera. *Evolution* 46: 1605-1620.
- Passera L, Gilber N, Aron S (2001) Social parasitism in ants: effects of the inquiline parasite *Plagiolepis xene* St. on queen distribution and worker production of its host *Plagiolepis pygmaea* Latr. *Insect Soc* 48: 74-79.
- Souza A L B, Soares I M F, Cyrino L T, Serrão J E (2006) The metapleural gland in two subspecies of *Acromyrmex subterraneus* (Hymenoptera: Formicidae). *Sociobiology* 47:19-25.
- Sumner S, Hughes W O, Pedersen J S, Boomsma J J (2004) Ant parasite queens revert to mating singly. *Nature* 428: 35-36.
- Sumner S, Nash D R, Boomsma J J (2003) The adaptative significance of inquiline parasite workers. *Proc Biol Sci* 270: 1315-1322.
- Wilson E O (1971) The insects societies. Cambridge, Harvard University Press, 548p.

Received 05/IV/09. Accepted 16/IX/09.