

**Behavioral ecology of mating and colony founding in the grass-cutting ant,
Acromyrmex balzani (Hymenoptera: Formicidae)**

Harold G. Fowler*

Reproductive behavior of *Acromyrmex balzani*

ABSTRACT. *Behavioral ecology of mating and colony founding in the grass-cutting ant, Acromyrmex balzani (Hymenoptera: Formicidae).* - The grass-cutting ant *Acromyrmex balzani* conducts nuptial flights at dusk, often during light rain. The daily timing of flights is invariant, but annual occurrence is dependent upon meteorological conditions. Males form aggregations over shrubs or other prominent objects, into which females fly to be mated. These aggregation sites are used perennially. Sexual competition among males is intense, with an average of 4 males simultaneously competing for access to each female in a mating ball. Multiple matings of females are common. The male genital capsule is detached and retained in the female genitalia upon mating, and females remove these prior to flying to mate again. Females found colonies independently and are not claustral.

KEY WORDS: *Acromyrmex balzani*; behaviour; mating; sexual competition; haplometrosis; colony founding; sex-ratio

Introduction

Mating behaviour in ants is still poorly documented. Holldobler & Wilson (1990) recognize two mating strategies: the female-calling syndrome, and the male-aggregation syndrome. The first syndrome is found primarily in species with wingless females, while the second is found with alate females. In the later case, timing of nuptial flights is largely invariant (Holldobler & Wilson, 1990). The

formation of leks in the male-aggregation syndrome is also common (Holldobler & Wilson, 1990). Boomsma and Leusink (1981) demonstrated that, in spite of the diel rhythmicity of nuptial flights, climatic conditions, especially rain, are major determinants of which day they occur.

In the Neotropics, the leaf-cutting ants (*Atta* and *Acromyrmex* spp.) are considered major agricultural pests (Mariconi, 1970), but we still know very little about their basic biology. Some species, such as *Atta texana* (Buckley) swarm before dawn

* Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), 13506-900 Rio Claro, São Paulo, Brazil.

Harold G. Fowler

(Moser, 1967), others, such as *Atta sexdens* (L.) swarm during the day (Mariconi, 1970). However, species of *Atta* form mating leks at altitudes of at least 300 m which must be studied with helicopters (Amante, 1972). For species of *Acromyrmex*, we know relatively little about their mating behaviour (Kusnezov, 1959, 1962). Low leks have been reported for *A. striatus* (Roger) (Fowler, 1988) and *A. versicolor* (Pergande) (Rissing et al., 1986), both members of the subgenus *Moellerius* (Fowler, 1988). Additionally, attine ants tend to be polyandrous (Kerr, 1961; Fowler et al., 1986). In this paper, I present data on the reproductive behaviour of another member of this subgenus, *A. balzani* Emery. Specifically the formation of leks, diel and yearly timing, and the mating behaviour and colony foundation by newly mated females is discussed using data collected over a 5-year period.

Materials and methods

Studies were conducted from 1983 through 1988, in Rio Claro, state of São Paulo, Brazil, in 0.2 ha region of an abandoned pasture (campo sujo) in which the foraging behaviour of *A. balzani* was under intense study. During the period of nuptial flights (September through November), colonies were frequently observed during the day to detect pre-swarmer behaviours. When observed, these were then checked at 30 min intervals during the day to follow swarming.

Upon swarming, mating flights were followed intensely. Once leks were established, these were observed continuously and frequent collections made to determine the sex ratios of the population and the number of founding queens available per ha. These were determined by following either swarming in individual nests and counting the number of males per females, or by following swarms and counting the number of females entering each during the swarming interval. At least one sweep-net sample of each lek was taken to estimate the number of

males per lek. The lek sites for each year were mapped to verify their reuse in the following year.

Behavioral observations were performed on mating activity and colony foundation behaviours. These, as well as experimental manipulations, will be discussed in detail in the pertinent sections. Meteorological information was taken from a personal weather station mounted in the same area. The number of marked nests engaging in nuptial flights on a given date were also recorded.

Results

Males tended to form leks over small shrubs or other vegetation. Lek sizes, determined by sweep net samples were not large ($x=33.3$, 1 s.d. 12.92, $N=43$). Mating swarms occurred at dusk, often during a light rain (Table 1). In these shrubs, females were not present or hidden, but flew directly from grass blades near the nest entrance.

Table 1. The diel and seasonal timing of mating flights in *Acromyrmex balzani* in the interior of the state of São Paulo, Brazil. Also shown is the estimated sex-ratio, determined by sweep-sampling either nests or mating leks, the estimated number of females available per ha, as well as the number and frequency of reuse of lek sites used.

Year	Hour of swarm	Date of swarm ¹	Number of lek-sites	Reuse frequency ²	Sex Ratio ³	Estimated females/ha
1983	19:25	12 Oc	16	---	0.767n	630
1984	19:32	29 Sept	12	0.833	0.623s	800
1985	19:28	18 Oct	13	0.846	0.669s	429
1986	19:44	23 Oct	18	0.667	0.733s	593
1987	19:33	14 Oct	9	1.000	0.688n	683
1988	19:30	19 Oct	11	0.727	0.820n	543

¹ all mating flights occurred during light rain.

² frequency calculated by the number of same sites used in consecutive years/total number of sites used in the second year.

³ Investment in males = estimated number of males/estimated number of males and females; n are nest and s are lek estimates.

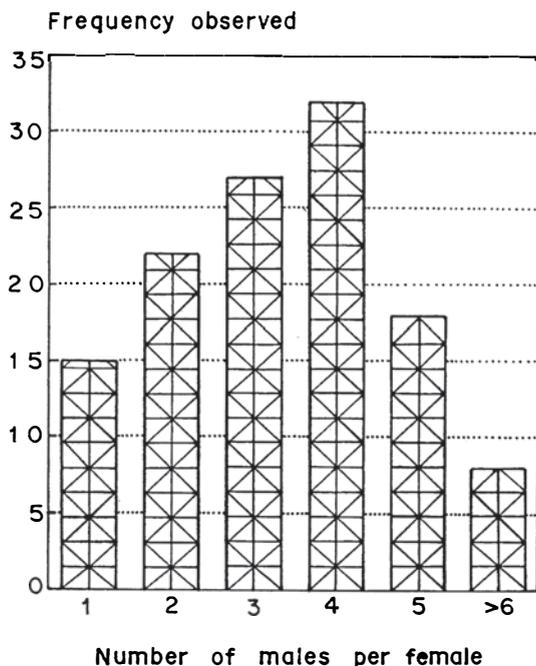


Fig. 1. The frequency of the number of males observed tempting copulations with female *A. balzani*. The observed distribution does not vary significantly from a zero-truncated Poisson distribution ($X^2_4 = 5.92, P > 0.05$).

Upon entering the lek, the female would then descend to the ground or vegetation over which the lek occurred with an engaged male. Often, at these times, a mating ball of near-by males would form (Fig. 1), with frequency distributions not differing from the Poisson. The couple would engage genitalia in spite of the mating ball, with each copulation lasting an average of 18 min (s.d., 4.6 min, $N=28$). Upon termination, the genital capsule of the male was detached, and the female removed the genital capsule with her mandibles before re-entering the lek. To remove the male's genital capsule, the female spent 9 min (s.d., 6.8 min, $N=11$), and then would have to climb the shrub over which the lek had formed to take flight again. Often male res-

ting in the shrub would ball the female before she could fly, and approximately 50% of the observed females were copulated again before flight (42 of 87). Males with their genital capsules removed, would fall to the ground and were rapidly preyed upon by other ants, in particular *Pheidole oxyops* (Forel) and *Solenopsis saevissima* (Fr. Smith).

After termination of the mating flight, isolated females disperse by walking over the ground. They rapidly break their wings (1 min.) and then either begin excavations, or find shelter under vegetation and begin excavations the next morning. Most (89%) of these mated females, however, produce a nest entrance and small chamber during the period immediately following mating. Excavated chambers were 30 cm or less in depth. No evidence of multiple queens (pleometrosis) was found in either observations following mating, or in nest excavations.

Incipient nest entrances were not plugged, and queens were seen foraging near the nest during short periods of the day.

Discussion

Ridley (1988) found a striking tendency for female fecundity of polyandrous insects to increase with mating success, unlike in monogamous insects. However, the detachment of male genitalia upon termination of mating and its retention in the female genitalia may serve to reduce the frequency of multiple-matings by females, as occurs in other Hymenoptera (Thornhill and Alcock 1983). Matings are limited to the temporal window available, and thus the efforts of females to rid themselves of the male genitalia limit time available for other matings. Therefore, we are still uncertain if Ridley's (1988) patterns for polyandrous insects are valid for *A. balzani*. Although we have no data on sperm numbers or the sperm storage capacity of the spermatheca of the female, it is likely that females do not mate with more than two to three males (Fowler et al., 1996). The strongly

male-biased sex ratio we found suggests that competition may be intense among males. As Arnold & Duvall (1994) suggest, males should experience a stronger sexual selection gradient, even in leks, used here in the broad form (Carraza, 1992), than females under polyandrous mating systems.

The strongly biased male sex ratio found in field colonies, as found in other species of *Acromyrmex* (Fowler et al., 1986) may indicate that local mate competition is weak (Thornhill & Alcock, 1983). The low density of potential lekking sites may serve to intensify mate competition, as females do not probably disperse at distances. The low availability of potential lekking sites also led to a high degree of year to year constancy of lek site usage.

Weather conditions and timing of the nuptial flights of *A. balzani* confirm other reported for temperate ants (Boomsma & Leusink, 1981). The seasonal timing of the recorded nuptial flights suggest that sexuals await the first days following spring rains for swarming, a pattern common in other leaf-cutting ants (Fowler et al., 1986).

Because of relatively small queen size, claustral colony foundation did not occur, as is common in species of *Atta* (Fowler et al., 1986). Queens were seen foraging near the nest on grass-blades, which were then planted into the incipient fungal garden. Initial colony survivorship for *A. balzani* is quite low (Fowler, 1992). This is in accordance with patterns reported for various other species (Autuori, 1950; Fowler et al., 1986). Given the apparent low vagility of females, and weak local mate competition, populations of *A. balzani* may show locally high concentrations, and may not be able to effectively colonize more distant suitable sites (Fowler et al., 1986). The mating behavior of *A. balzani* may thus induce locally high populations (Fowler et al., 1986), and may be more so or as important in the population dynamics of this species as are other ecological factors (Fowler, 1992).

Acknowledgments

Partial support for this research was provided by the Conselho Nacional de Pesquisas (CNPq) of Brazil, through grants 300171/88-9 and 500614/91-1, and the International Foundation for Science through a grant to Flavio Schlittler. I thank Hayden Fowler for his assistance during these studies, and Maria Thereza Fink and Marcelo N. Schlindwein for their constant support and encouragement.

Resumen

Ecología comportamental de vuelos nupciales y fundación de colonias en la hormiga arriera, Acromyrmex balzani (Hymenoptera: Formicidae). La hormiga arriera *Acromyrmex balzani* organiza los vuelos nupciales al atardecer, frecuentemente bajo lluvias ligeras. El horario de los vuelos nupciales es constante, pero su presencia anual depende de las condiciones meteorológicas. Los machos forman agregaciones sobre arbustos ou otros objetos prominentes. Las hembras entran esas agregaciones para copularse. Los sitios de agregación son usados de año a año. La competencia sexual entre machos es fuerte, con un promedio de 4 machos compitiendo simultáneamente para acceso a cada hembra en la bola de cópula. Las copulas multiples de hembras aon comunes. La cápsula genital del macho es perdida durante la cópula y se mantiene dentro de la genitalia de la hembra, las cuales la tiran antes de volar para buscar otro macho. Las hembras fundan colonias independientemente y no son claustrales.

References

- Amante, E., 1972. Preliminary observations on the swarming behavior of the leaf-cutting ant, *Atta capiguara* (Hymenoptera: Formicidae). *J. Ga. Entomol. Soc.*, 7: 82-83.

- Arnold, S.J. & Duvall, D., 1994. Animal mating systems: a synthesis based on selection theory. *Am. Nat.*, 143: 317-348.
- Autuori, M., 1950. Contribuição para o conhecimento da saúva (*Atta* sp., Hymenoptera, Formicidae). V. Número de formas aladas e redução dos saúveiros iniciais. *Arq. Inst. Biol.*, 19: 325-331.
- Boomsma, J.J. & Leusink, A., 1981. Weather conditions during nuptial flights of four European ant species. *Oecologia*, 50: 236-241.
- Carranza, J., 1992. Lekking in red deer? A comment on the concept of lek. *Etologia*, 2: 83-90.
- Holldobler, B. & Wilson, E.O., 1990. The ants. Cambridge: Belknap Press of Harvard University Press.
- Fowler, H.G., 1988. Taxa of the Neotropical grass-cutting ants, *Acromyrmex* (*Moellerius*) (Hymenoptera: Formicidae: Attini). *Científica*, 16: 281-295.
- Fowler, H.G., 1992. Patterns of colonization and incipient nest survival in *Acromyrmex niger* and *Acromyrmex balzani* (Hymenoptera: Formicidae). *Insectes Sociaux*, 389: 347-350.
- Fowler, H.G., Pereira-da-Silva, V., Forti, L.C., & Saes, N.B., 1986. Population dynamics of leaf-cutting ants: a brief review. pp. 123-145. In: *Fire ants and leaf-cutting ants: biology and management*: 123-145 (C.S. Lofgren & R.K. Vander Meer, Eds.). Boulder: Westview Press.
- Kerr, W., 1961. Acasalamento de rainhas com vários machos em duas espécies da tribu Attini (Hymenoptera; Formicidae). *Rev. Bras. Biol.*, 21: 45-48.
- Kusnezov, N., 1959. Un caso excepcional del vuelo nupcial de *Acromyrmex lundii* Guérin. *Neotropica*, 5: 70.
- Kusnezov, N., 1962. El vuelo nupcial de las hormigas. *Acta Zool. Lilloana*, 18: 385-442.
- Mariconi, F.A.M., 1970. *As saúvas*. São Paulo: Editora Ceres.
- Moser, J.C., 1967. Mating activities of *Atta texana* (Buckley, 1860)(Hymenoptera: Formicidae). *Ins. Soc.*, 14: 295-312.
- Ridley, M., 1988. Mating frequency and fecundity in insects. *Biol. Rev.*, 63: 509-549.
- Rissing, S.W., Johnson, R.A. & Pollock, G.B., 1986. Natal nest distribution and pleometrosis in the desert leaf-cutter ant *Acromyrmex versicolor* (Pergande) (Hymenoptera: Formicidae). *Psyche*, 93: 177-186.
- Thornhill, R. & Alcock, J., 1983. *The evolution of insect mating systems*. Cambridge: Harvard University Press.