Insectes Sociaux, Paris
1987, Volume 34, n° 2, pp. 108-117

PRIMARY POLYGYNY IN THE ANT *ATTA TEXANA* : NUMBER AND WEIGHT OF FEMALES AND COLONY FOUNDATION SUCCESS IN THE LABORATORY

A. C. MINTZER

Department of Entomology, Texas A & M University
College Station, Texas 77843, U.S.A.

Reçu le 27 octobre 1986 Accepté le 27 avril 1987

SUMMARY

Inseminated females of the leafcutting ant *Atta texana* (Buckley) may cooperate during colony foundation. Cooperative efforts in the laboratory lead directly to large stable polygynous colonies, which is an uncommon pattern in ants.

Although single females successfully reared worker offspring and started fungus cultures, grouped ants produced more workers and larger fungus cultures. Larger females and grouped ants had a higher survival rate before workers emerged in the laboratory.

Grouped and single females both lost about 30 % of their initial weight before the first workers appeared. The females lost an additional 25-35 % over the next five months, suggesting that continuing investment by foundress females may be critical to colony survival after workers emerge.

Females of *A. texana* are among the smallest known in the genus, and I suggest that primary polygyny is adaptively associated with small female size in this species.

RESUME

La polygyrie primaire chez la fourmi Atta texana : nombre et poids des femelles et succès dans la fondation de la colonie au laboratoire

Des femelles inséminées de la fourmi champignonniste *Atta texana* (Buckley) peuvent coopérer au cours de la fondation de la colonie. Au laboratoire, des efforts coopératifs aboutissent directement au maintien de grandes colonies polygynes, ce qui est un patron peu répandu chez les fourmis.

Bien que des femelles isolées élevèrent avec succès une progéniture d'ouvrières et initièrent la culture du champignon, les femelles groupées produisirent davantage d'ouvrières et de jardin à champignon. Les plus grandes femelles isolées et les femelles groupées ont eu un taux de survie plus élevé avant l'éclosion des ouvrières, au laboratoire.

Les femelles groupées, comme les femelles isolées, perdent environ 30 % de leur poids initial avant l'apparition des premières ouvrières. Les femelles en perdent encore 25 à 30 % dans les cinq mois suivants, ce qui suggère que l'investissement continuel des fondatrices peut être critique pour la survie de la colonie après l'éclosion des ouvrières.

Les femelles d'*A. texana* sont parmi les plus petites dans le genre, et je suggère que la polygynie primaire est adaptativement associée à la petite taille des femelles dans cette espèce.

INTRODUCTION

Colony foundation by fungus-growing ants requires more elaborate behaviours and more intensive investment than in other ant groups. In addition to rearing worker offspring, the foundress female must also nurture the initial fungus culture. Females in the genus *Atta* do not forage for fungal substrate during the colony foundation period. *Atta* females are among the largest ants known, and most of the weight in young females is concentrated in flight muscles and fat bodies in the massive thorax and gaster (WEBER, 1972). The flight muscles and fat bodies are broken down to provide nutrients needed during colony foundation. *Atta* females supply droplets of fecal fluid to the fungal culture during colony foundation (HUBER, 1905). The larvae are fed eggs directly by the female; the growing fungus is not consumed until after the first workers emerge.

Although most species of *Atta* are believed to have monogynous colonies (WILSON, 1985), polygynous colonies of *A. texana* (Buckley) have been found in the field on several occasions, and foundress females are known to excavate burrows together in the field (MOSER, 1967; MOSER and LEWIS, 1981). In an attempt to identify possible advantage of female cooperation over independence during colony foundation, I examined the behaviour and success of single and grouped foundress emales of *A. texana* in the laboratory.

MATERIALS AND METHODS

Dealate females of *A. texana* were collected as they excavated burrows after mating flights in 1984-86 at Washington-on-the-Brazos State Park, Washington Co., TX. This site has three mature *A. texana* colonies within 300 m of each other. The flights occur just before dawn on days after rainfall in April, May and June. There are no artificial lights in the immediate vicinity, which can attract alates (MOSER, 1967). On May 18, 1984, 30 females were collected between 1000 and 1200 h. In 1985, 11 females were collected on May 9-10 and 17 more were collected on June 19. 69 females were collected on April 30 and May 2, 1986.

Females were weighed after collection, before installation in clear plastic culture containers. 48 females were grouped for study of colony foundation, creating 18 pairs and four groups of three females. A group of five females found excavating a common burrow in the field was also kept together in the lab. Grouped females were placed in 10 cm diameter, 7 cm high culture dishes. 56 females were cultured separately in 8 × 8.5 cm high dishes. The culture dishes were lined along the bottom with perlite granules premoistened with distilled water, and were kept in an incubator at approx 27C and 65 % RH with a 16 h day/8 h night photoperiod.

The closed dishes were not re-opened until worker eclosure was imminent. However, dying females were promptly removed for dissection and spermathecal examination. When worker eclosure was expected within 24 h, the dishes were opened and the females were removed and weighed. The brood was counted and the fungal mat was photographed against a grid to permit measurement of surface area (peripheral silhouette minus any interior gaps). The females were then returned and the dish was covered with a lid fitted with a vertical plastic tube, initially plugged with a cork. When worker foraging began, the dish and tube were placed in a larger arena and young colonies were maintained on a diet of oatmeal and cornmeal.

RESULTS

Weights of 110 dealate *A. texana* females after collection ranged from 301 to 455 mg (mean 376.7 mg ± 30.6 SD). Spermathecal examination or rearing results showed that most females were inseminated. Two to six females were observed cooperating in burrow excavation on five of six collection dates. Cooperating groups in the field can include several inseminated females, as well as uninseminated ants. In 1986, females collected in groups in the field ($n = 16$) did not differ in mean weight from females collected alone ($n = 53$). At Washington-on-the-Brazos Park, dealate females were usually concentrated in one small area (approx 6 × 10 m) of low grass and barren soil, although some scattered individuals were found elsewhere in low grass and barren soil. No ants were found under tree crowns ; in all cases, females were in the open or under gaps in the canopy. Discarded wings were often found within 50 cm of the incipient burrow.

Females grouped into pairs or triplets had a higher survival rate than single females (see *table I*). Larger females had a higher survival rate before worker emergence than smaller females (63 % vs 33 %, $z = 2.009$, $p = 0.022$). All successful females required a similar length of time to rear workers. In 1984, each of five pairs of females required 36 days. In 1985, eight single females required 35-38 days, and a group of three females reared workers in 37 days after installation in the culture dish. Grouped females required 32-37 days to rear workers in 1986, while single females reared workers in 32-42 days.

All females lost weight during colony foundation (mean 123.6 ± 26.3 mg ; $n = 47$), and larger ants tended to lose more weight than smaller ants (see *fig. 1*). Grouped females lost less weight than single females (unpaired $t = 2.015$, $p < 0.05$). Mean weight loss for successful single females was

Table I. — Survival of females in laboratory until worker emergence. Percentages for for each category are shown in parentheses.

Tableau I. — Survie des femelles au laboratoire jusqu'à l'éclosion des ouvrières. Les pourcentages pour chaque catégorie sont figurés entre parenthèses.

Initial weight (mg)	Total Set up	Number Surviving	Single set up	Females Surviving	Grouped set up	Females Surviving
301-350	21	7 (33 %)	15	6 (40 %)	6	1 (17 %)
351-400	58	31 (53 %)	27	11 (41 %)	31	20 (65 %)
401-450	24	15 (63 %)	13	7 (54 %)	11	8 (73 %)
Total	103	53 (51 %)	55	24 (44 %)	48	29 (60 %)

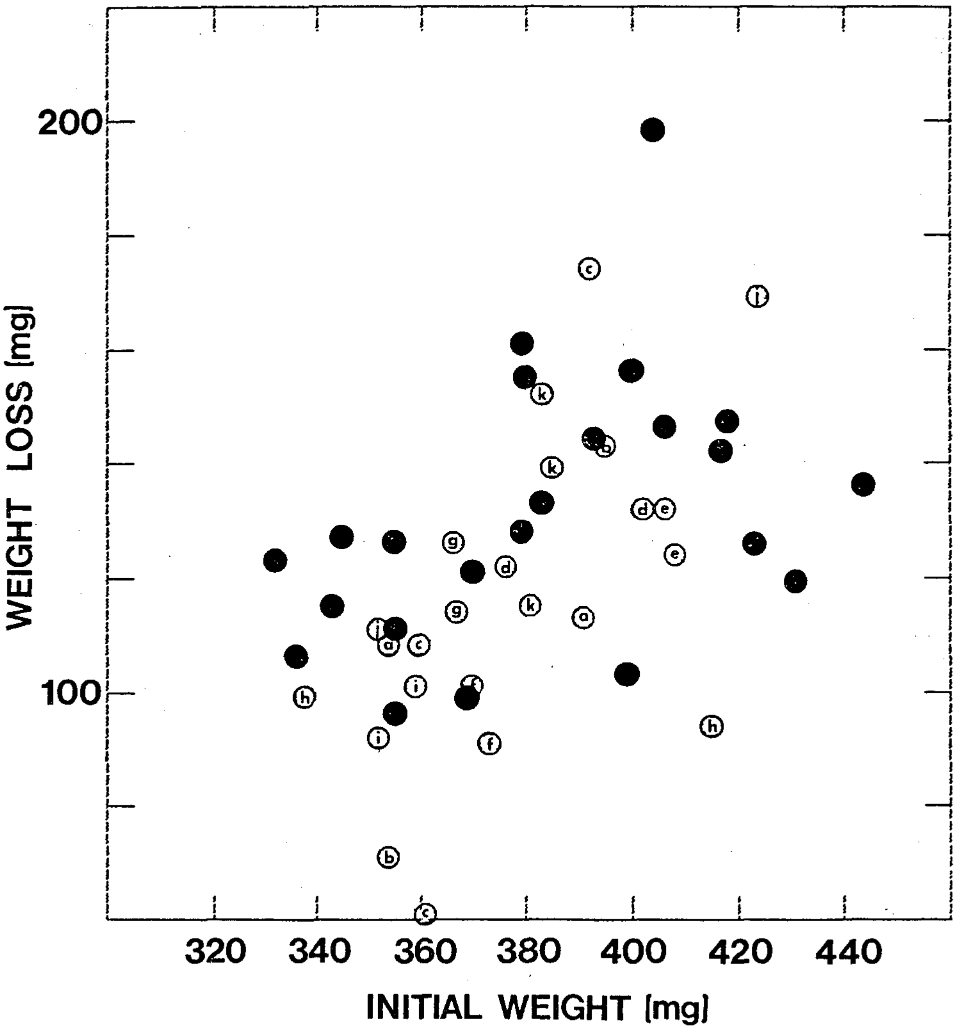

Fig. 1. — Relationship of initial female weight to weight loss before worker emergence, for single ants (solid circles) and grouped ants (circles enclosing letter identifying group).

Fig. 1. — Relation entre le poids initial de la femelle et le poids perdu avant l'éclosion des ouvrières, pour des femelles seules (cercles pleins ; r = .413, p = .05) et des femelles groupées (cercles entourant une lettre d'identification de groupe ; r = .594, p = .002).

131 ± 23 mg (n = 23), or an average of 34.4 % of initial weight. For surviving grouped females, mean weight loss was 116 ± 27 mg (n = 24), or about 30.7 % of initial weight.

Nearly all females collected in 1984, 1986 and in June 1985 had infrabuccal fungus pellets, which they regurgitated within 48 h after installation in culture dishes. Females collected on May 9-10 1985 did not have infrabuccal pellets, but these ants accepted and cultured fungal pieces taken from established lab colonies. Two single females collected in 1986 carried non-viable pellets which did not grow, but these females successfully cultured fungus when the pellet was replaced. Whether started from an infrabuccal fungus pellet or an adopted piece, the fungal culture grew at similar rates, until the mycelial mat was at least 20 mm across after four weeks. When the first workers eclosed, the fungal mat surface area ranged from 3.0—5.5 cm^2 for single females (mean 4.0 ± 0.7 cm^2; n = 23), and from 3.9—7.8 cm^2 for grouped females (mean 6.4 ± 1.1 cm^2; n = 11 groups). Fungus surface area was not correlated with initial weight for single ants, but a significant positive association between individual weight loss and fungus area was observed (see *fig.* 2).

Grouped females produced more workers in the first brood than single females (Mann-Whitney U = 249, $p < 0.0001$) (see *fig.* 3). Single and paired females produced a similar distribution of worker sizes in the first brood (body length 2-4 mm). The number of first brood workers produced by single females was not correlated with initial weight, but a significant positive association between individual weight loss and worker production was noted (see *fig.* 3). No significant associations between individual weight loss and worker production or fungus area were noted for paired ants.

In 1984 and 1986, surviving females were reweighed five to six months after collection. 19 surviving grouped ants with healthy colonies had lost an additional 80-194 mg (mean 117.0 ± 23.7 mg) after the first workers emerged; the corresponding range for 12 single ants was 82-176 mg (mean 117.6 ± 29.8 mg). The cumulative individual losses correspond to 49 - 78 % of initial weight (mean 63.7 ± 5.5 %). At this point in 1986, fungal volumes for polygynous colonies were 60 - 150 ml (n = 6 surviving) and 20 - 100 ml for monogynous colonies (n = 12). None of the foundress females have been attacked or eliminated by worker offspring in a two year period following cooperative colony foundation in 1984. During this time, the worker force has increased to at least 10000 ants and each polygynous colony has produced major workers.

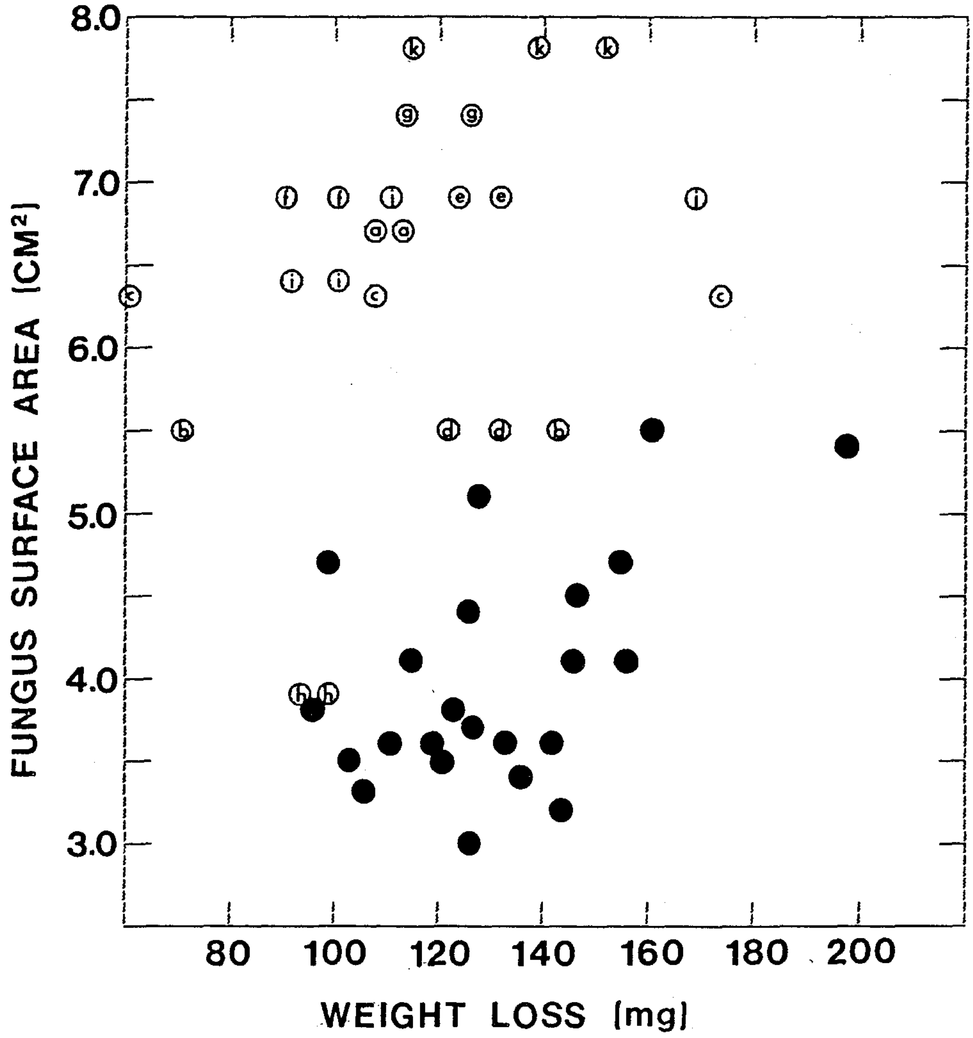

Fig. 2. — Relationship of individual weight loss before worker emergence to fungus mat surface area, for single females (solid circles ; r = .512, p = .012) and grouped females (circles enclosing letter identifying group).

Fig. 2. — Relation entre le poids perdu par les individus avant l'éclosion des ouvrières et la surface externe du champignon, pour les femelles seules (cercles pleins ; r = .512, p = .012) et pour les femelles groupées (cercles entourant une lettre d'identification de groupe).

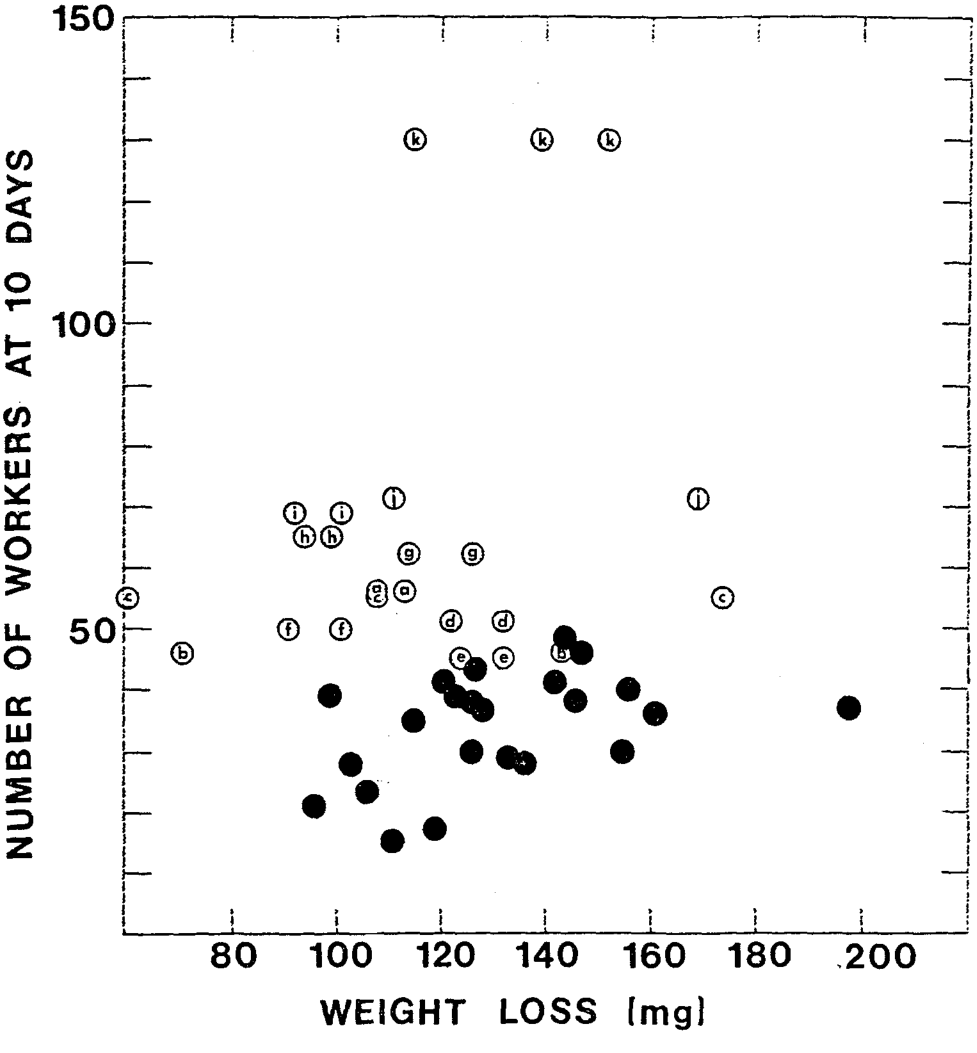

Fig. 3. — Relationship of individual weight loss before worker emergence to number of workers counted 10 days after the first one emerged, for single females (solid circles ; r = .424, p = .044) and grouped females (circles enclosing letter identifying group).

Fig. 3. — Relation entre le poids perdu par les individus avant l'éclosion des ouvrières et le nombre d'ouvrières comptées 10 jours après la première éclosion, pour des femelles isolées (cercles pleins ; r = .424, p = .044) ou des femelles groupées (cercles entourant une lettre d'identification de groupe ; r = .256, p = n.s.).

DISCUSSION

The selective forces maintaining cooperative colony foundation and primary polygyny in *A. texana* and opposing it elsewhere in the genus need clarification. Primary polygyny is rare in ants (Hölldobler and Wilson, 1977). Most polygynous colonies apparently originate through the secondary adoption of additional mated females by established colonies, rather than from cooperative attempts at colony foundation.

Females which lack infrabuccal fungus pellets will obviously benefit by joining groups with viable fungus. However, I have collected field groups where nearly all members had pellets. Also, females of other *Atta* species have been collected without pellets, but they do not cooperate in colony foundation (Weber, 1972). The incidence of non-viable pellets seems to be too low to account for the observed cooperative behavior. During colony foundation, *A. texana* females do not groom each other, so there are no obvious hygienic benefits for cooperating ants, as Waloff (1957) suggested for other species.

Cooperation during digging may allow groups of females to seal and complete the natal burrow more quickly, escaping some predation. *Atta* females are consumed in the air and on the ground by a variety of birds, amphibians, insects and mammals including humans (Weber, 1972). Ants in the genera *Iridomyrmex, Forelius, Solenopsis* and *Pheidole* may be major predators on foundress females on the ground. *Solenopsis invicta* Buren frequently attacks *A. texana* females, and I have observed *S. xyloni* McCook, *Forelius* sp. and *Pheidole* spp. attacking *A. mexicana* (F. Smith) females. However, *A. mexicana* females do not cooperate in colony foundation (pers. observation), and no evidence suggests that *A. texana* faces more numerous surface predators than neotropical congenerics.

High genetic relatedness between females is not a prerequisite for cooperative colony foundation. Females collected 20 km apart have been placed together without difficulty and dominance or aggressive behaviour between females is rarely observed and never escalates to fighting. Nevertheless, females may be encountering and cooperating with related ants frequently in the field, because local *A. texana* populations consist of a few mature widely spaced colonies and only a small number of colonies may contribute alates to each mating swarm.

The relationship between female weight and survival and successful colony foundation is not simple, but polygyny may be adaptively associated with small female size in *A. texana.* Females of *A. texana* are among the smallest in the genus (H.G. Fowler, pers. comm.). Quantitative data on initial weights of other species are scanty, but dealate females of *A. capiguara* Goncalves may weigh 800 mg or more at the start of colony foundation, and lose 70 % of this weight over a 3-4 month period (Pereira da-Silva, 1979).

Dealate females of *A. mexicana* ranged from 319-502 mg (mean 445 ± 41 mg, n = 30; MINTZER, unpub. data) while those of *A. sexdens rubropilosa* ranged from 334-504 mg (mean 451 ± 49 mg, n = 35; VILELA, pers. comm.). Single *A. texana* females of all sizes were capable of rearing similar sized worker broods to maturity in the lab, and initial female weight was also a poor indicator of fungus mat production during colony foundation. However, survivorship data show an advantage for larger females, and suboptimal field conditions might amplify this advantage. Continuing investment by females after workers emerge and begin foraging may be critical to long term colony survival, and small females may be disadvantaged in this regard. Grouped ants produced more workers, larger fungal mats (MANN-WHITNEY $U = 241$, $p < 0.0001$), and survived better than single ants ($z = 1.62$, $p = 0.05$) during colony foundation. For this small *Atta* species, the increased initial worker force resulting from cooperative colony foundation might have a more positive effect on incipient colony survivorship than that which would result from cooperation among larger females of other species. Young polygynous colonies producing more workers will gain an advantage in nest defense or intraspecific interference competition for foraging territory and food resources, but this advantage will also apply for neotropical *Atta* which nest in higher local densities, where territorial behaviour is best documented (FOWLER *et al.*, 1984; JAFFE *et al.*, 1979; ROCKWOOD, 1973). However, adding a second female to the foundress group in the larger species may result in a smaller proportionate increase in the initial worker force, and the increase may have a less significant positive effect on survivorship of incipient colonies. If other automatic, unavoidable disadvantages accompany female cooperation, their optimal strategy may be shifted towards female independence. A detailed comparative field study of colony foundation and incipient colony survivorship in *A. texana* and other species is needed.

ACKNOWLEDGEMENTS. — This study was supported by the Texas Agricultural Experiment Station. Additional assistance was provided by S.B. VINSON, M. AGUIRRE, C. MINTZER and K. HAACK. I thank D. WALLER and H.G. FOWLER for comments and suggestions on the manuscript.

References

FOWLER H.G., ROBINSON S.W., DIEHL J., 1984. — Effect of mature colony density on colonization and initial colony survivorship in *Atta capiguara*, a leaf-cutting ant. *Biotropica, 16,* 51-54.

HÖLLDOBLER B., WILSON E.O., 1977. — The number of queens: an important trait in ant evolution. *Naturwissenschaften, 64,* 8-15.

HUBER J., 1905. — Uber die Koloniegrundung bei *Atta sexdens. Biologisches Centralblatt, 25,* 606-635.

JAFFE K., BAZIRE-BENAZET M., HOWSE P.E., 1979. — An integumentary pheromone secreting gland in *Atta* sp., Territorial marking with a colonyspecific pheromone in *Atta cephalotes. J. Ins. Physiol., 25,* 833-839.

MOSER J., 1967. — Mating activities of *Atta texana. Ins. Soc., 14,* 295-312.

MOSER J., LEWIS J., 1981. — Multiple nest queens of *Atta texana. Turrialba,* 31, 256-257.

PEREIRA-DA-SILVA V., 1979. — *Dinamica populacional, biomassa e estructura dos ninhos inicias de Atta capiguara Goncalves na regiao de Botucatu,* SP. Lh.D. Thesis, UNESP Botucatu, Sao Paulo, Brazil.

ROCKWOOD L., 1973. — Distribution, density and dispersion of two species of *Atta* in Guanacaste Province, Costa Rica. *J. Anim. Ecol., 42,* 803-817.

WALOFF N., 1957. — The effect of the number of queens of the ant *Lasius flavus* on their survival and on the rate of development of the first brood. *Ins. Soc., 4,* 391-408.

WEBER N.A., 1972. — *Gardening Ants, the Attines.* Memoir American Philosophical Society, Philadelphia, Vol. 92.

WILSON E.O., 1985. — The sociogenesis of insect colonies. *Science, 228,* 1489.