

TERRITORIAL MECHANISMS IN POST-NUPTIAL FLIGHT GYNES OF THE LEAF-CUTTING ANT *Atta laevigata* (F. SMITH)

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ABSTRACT

Laboratory experiments were conducted to investigate territoriality in *Atta laevigata* (F. Smith) gynes. Before nest founding, gyne dispersal with respect to the first nearest neighbor was at random, with a trend towards regularity with respect to the second and third nearest neighbours. Gynes that digged a nest exhibited aggressive behavior towards intruding gynes, and always won during conflicts. Conflicts were often non-injurious. The territory of a foundress gynes existed up to, or in very close proximity to, the mouth of the new nest, and was not marked with a territorial pheromone. Tactile stimuli was an important aspect of gyne nest defense.

KEY WORDS: Insecta, Hymenoptera, Formicidae, Attini, ethology, insect behavior.

RESUMO

Territorialidade de Fêmeas Aladas de Formigas Cortadeiras *Atta laevigata* (F. Smith)
Após o Vôo Nupcial

Experimentos foram conduzidos em laboratório para investigar a territorialidade em fêmeas aladas de *Atta laevigata* (F. Smith), imediatamente após o vôo nupcial. Antes de iniciarem a fundação de seus ninhos, a dispersão dessas futuras rainhas em relação ao vizinho mais próximo foi ao acaso, com uma tendência a regularidade em relação ao segundo e terceiro vizinhos mais próximos. Fêmeas que começaram a escavar seus ninhos apresentaram comportamento agressivo em relação a fêmeas invasoras e sempre venceram nos combates. A grandeza do território de uma rainha fundadora se estendeu até ou nas suas proximidades da boca do próprio ninho. Os resultados sugerem que sua extensão não foi delimitada por feromônio territorial. O senso de tato foi um aspecto importante na defesa do ninho dessas rainhas.

PALAVRAS-CHAVE: Insecta, Hymenoptera, Formicidae, Attini, etologia, comportamento social.

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INTRODUCTION

Queens of the leaf-cutting ant genus *Atta* are able to survive up to 20 years (Weber 1972) and can give rise to huge colonies (Autuori 1942b, Moser 1963, Jonkman 1980) with millions of workers (Howse & Bradshaw 1977). By virtue of their size, abundance and distribution, leaf-cutting colonies can have great economic and ecological importance (Cherrett 1968, Lugo *et al.* 1973, Rockwood 1976, Jonkman 1978).

Intra and inter-specific aggression between workers of leaf-cutting ants has been documented both in the laboratory (Jutsum 1979, Jutsum *et al.* 1979) and in the field (Autuori 1941, Mariconi 1970, Rockwood 1973). Aggression is an important component of territoriality, affecting the territory size and the distribution of colonies (Rockwood 1973, Jutsum 1979, Jutsum *et al.* 1979). Jaffé *et al.* (1979) found a colony-specific and a species or genus-specific territorial marker pheromone in *Atta cephalotes* (L.) and speculated upon their importance in the defense of a spatially variable territory.

Fowler (1982) described how, in both *Atta* and *Acromyrmex*, gynes that landed within close proximity to their own colony were attacked by workers. Rockwood (1973) and Jutsum *et al.* (1979) reported that attacks were directed against gynes by workers of alien colonies, which may prevent the establishment of competitive colonies nearby (Jutsum *et al.* 1979).

By virtue of their role as founders and reproductive agents of the colony, gynes are an important caste. Behavioural accounts of leaf-cutting ant gynes during the period which follows the nuptial flight though are sparse and based primarily on observations (Autuori 1942a, Moser 1963, Weber 1972). This study is a laboratory investigation of the *Atta laevigata* (F. Smith) gynes after the nuptial flight period, to describe their pattern of dispersal; examine the role of territoriality in nest founding; and to test for the presence of a territorial marker pheromone.

MATERIAL AND METHODS

All experiments were performed in the laboratory at Altamira, Pará, Brazil. Gynes of the leaf-cutting ant *A. laevigata* were collected by hand immediately after they had landed from their nuptial flight. The collections were made between 15-15 hours and 17-45 hours on January 5th and 20th, 1984. Each gyne was immediately placed in a separate specimen tube and stored in the dark at $27 \pm 2^\circ\text{C}$ and 88% to 95% R.H. All tests were performed within 52 hours of capture.

Experiments involved gynes caught from the same nuptial flight, that is, gynes originating from the same nest. This was verified by locating the colony from which the nuptial flight had come. An inspection of other known colonies in the vicinity showed no evidence of nuptial flight activity on the same day, suggesting that no inter-colony mating was involved. Each gyne was used in one trial only.

Experiment A. The Distribution and Dispersion of Post-Nuptial Flight Gynes. The aim of this experiment was to measure the distribution and dispersion of gynes at high density, before they started digging a nest.

The trials were conducted in daylight between 9:00 hours and 15:00 hours, 18 to 24 hours after the gynes had been collected. The ambient temperature was $27 \pm 2^\circ\text{C}$ and the R.H. 90% to 95%. In each trial, 15 or 16 gynes were introduced into the arena through the central entrance flap (Fig. 1), over a 3 minute period. In the first four trials the gynes were left in the

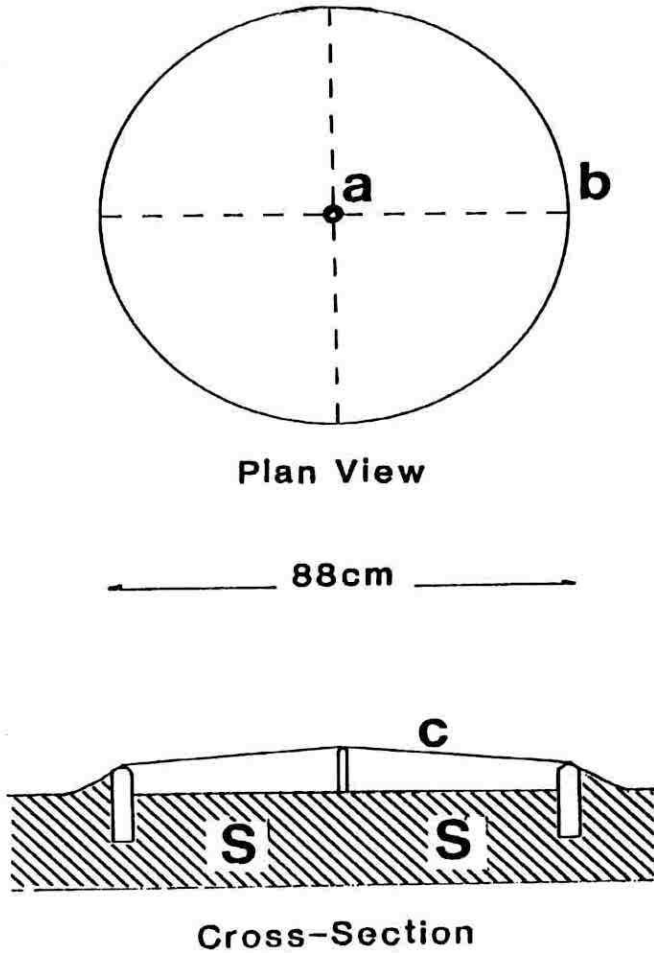


Figure 1. Arena used in Experiment A. S represents the 4cm deep sand substrate; a the entrance hole; c the mesh covering and b the metal rim perimeter.

arena for 3 hours, after which their positions were recorded. In the fifth trial the position of the gynes was plotted 4 min., 20 min., 80 min. and 180 min. after the trial had begun. Lines were drawn on the mesh covering the arena to divide it into four quarter segments to assist the accurate plotting of the ant's positions.

From the plotted data the distances between each gyne and its first, second and third nearest neighbor was measured. The gyne distribution with respect to the first, second and third nearest neighbor was determined by calculating a χ^2 value, using the n^{th} nearest neighbor statistic of Thompson (1956). Probability values obtained from the calculations of χ^2 indicated whether the gyne distribution was aggregated, random or regular.

Experiment B. Dual Chamber and Tunnel Trials to Test for Territoriality in Gynes Founding a Nest. The apparatus (Fig. 2) was set up under artificial lighting, at $26 \pm 2^\circ\text{C}$ and 88% to 94% R.H. All trials were conducted between 19:00 hours and 23:00 hours. Six hours before each trial began a "host" gyne was placed on the floor of Chamber A. A weighted cardboard lid was positioned over the top of the chamber and a cardboard strip inserted in front of the tunnel exit, to ensure that no ants escaped during the six hour establishment period.

Trials were performed only where the "host" gynes had excavated or started to excavate a nest in the sand substrate of the chamber. Each trial started when the chamber lid and the inserted card strip in front of the tunnel were removed, and a second gyne, the "intruder", introduced. Trials continued for 10 minutes, after the introduction of the "intruder". Only in trials where the "host" and the "intruder" contacted were the results used in the analysis.

"Host" victory, resulting from an aggressive conflict, was defined as a "host" maintaining its position in the nest and deterring the "intruder" from making persistent attempts at entering the nest. An "intruder" victory was defined as the displacement of the "host" from its nest. Trials in which conflicts escalated, that is they were not completed by the end of the allocated time, or involved both the "host" and the "intruder" receiving severe injuries (i.e. greatly impaired locomotion or fighting ability) were regarded as having no obvious victor. Gynes were deemed to have sustained an injury when they lost one or more limbs, and had their orientation and mobility impaired.

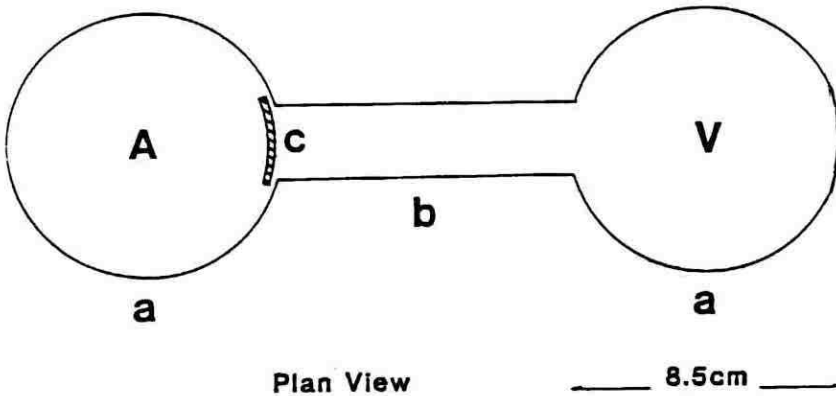
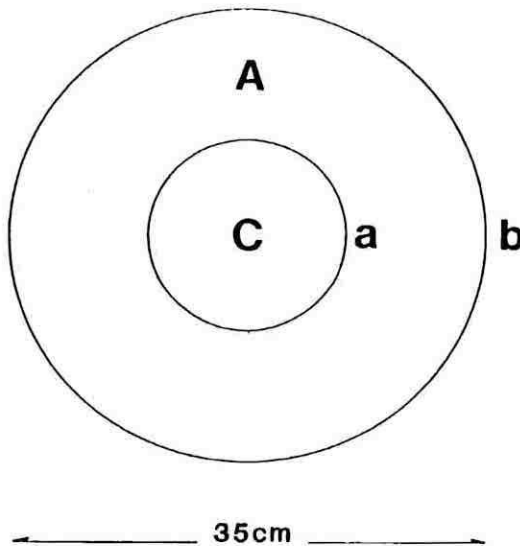


Figure 2. Dual arena and tunnel apparatus for Experiment B. A and V are the Chamber A and the vacant chamber respectively, with 3.5 cm deep sand substrates. a represents 9 cm tall transparent cylinders, and b the connecting tunnel. c is the cardboard strip used in the 6 hour establishment period to prevent the "host" gyne from leaving Chamber A.

Experiment C. Testing for the Presence of a Gyne Territorial Marker Pheromone. Trials were performed in daylight 18 to 36 hours after the capture of the gynes, between 9:00 and 18:00 hours. The laboratory temperature was $27 \pm 2^\circ\text{C}$ and the R.H. between 90% and 95%.

The first stage of the experiment involved placing a "host" gyne on the substrate, confirmed by a cylinder within the central zone of the arena (Fig. 3). The "host" gyne and the cylinder were removed after 30 minutes. Immediately afterwards, an "intruder" gyne was introduced to the arena, at a point midway between the perimeter and the central zone. The "intruders" behavior and the number of times she entered the central zone, previously occupied by the "host" gynes, was monitored during the subsequent 30 minutes period. In the control experiment a gyne was introduced to the arena after the central zone had been lightly marked out by the cylinder rim. No "host" gyne was involved.



Plan View

Figure 3. Arena to test for a territorial marker pheromone, Experiment C. Main arena A, with 3.5 cm deep sand substrate. The central zone, C, is delimited by a 9 cm tall cylinder. a is the plastic arena wall.

RESULTS

Experiment A. Calculations of the gyne distribution to the n^{th} nearest neighbor indicated that there is a trend from randomness to regularity between the first and third nearest-neighbor (Table 1). With respect to the first nearest-neighbor a random distribution (χ^2 , 30 or 32 d.f., $p > 0.05$, $p < 0.9$) resulted in four trials and an aggregated distribution (χ^2 , 30 or 32

Table 1. *Atta laevigata* gyne distribution with respect to the first, second and third nearest neighbors.

Trial Number	First Nearest Neighbor	Second Nearest Neighbor	Third Nearest Neighbor
1	Randon ($x^2=22.0, 32$ d.f.) ¹	Randon ($x^2=44.6, 32$ d.f.) ¹	Regular ($x^2=89.0, 32$ d.f.) ¹
2	Randon ($x^2=27.7, 32$ d.f.)	Regular ($x^2=55.2, 32$ d.f.)	Regular ($x^2=75.6, 32$ d.f.)
3	Aggregated ($x^2=14.6, 32$ d.f.)	Randon ($x^2=31.2, 32$ d.f.)	Regular ($x^2=54.4, 32$ d.f.)
4	Randon ($x^2=27.2, 30$ d.f.)	Regular ($x^2=64.3, 30$ d.f.)	Regular ($x^2=98.5, 30$ d.f.)
5	Randon ($x^2=31.1, 30$ d.f.)	Regular ($x^2=65.7, 30$ d.f.)	Regular ($x^2=92.7, 30$ d.f.)

¹d.f.= free degree

d.f., $p > 0.9$) in one trial. A regular distribution (x^2 , 30 or 32 d.f., $p < 0.05$) to the third nearest-neighbor occurred in all five trials. The second nearest-neighbor distribution is less clear, with three of the trials showing regularity and two indicating randomness.

The results of trial five, which measured the temporal variation in gynes distribution (Table 2) suggests that gynes disperse within less than 20 minutes. They established a consistent distribution of random, regular, regular to the first, second and third nearest neighbors respectively, after 20 minutes of the trial. Within the first 4 minutes of the beginning of the trial the first nearest neighbor gyne distribution was aggregated, but was regular to the second and third nearest neighbors.

Table 2. Change of *Atta laevigata* gyne distribution with time.

Nearest Neighbor	Time at which the distribution measured (mins.)			
	4	20	80	180
First	Aggregated (=11.9,30 d.f. ¹)	Randon (=23.6,30 d.f. ¹)	Randon (=29.6,30 d.f. ¹)	Randon (=31.1,30 d.f. ¹)
Second	Regular (=55.9,30 d.f.)	Regular (=68.4,30 d.f.)	Regular (=56.8,30 d.f.)	Regular (=65.7,30 d.f.)
Third	Regular (=125.4,30 d.f.)	Regular (=119.9,30 d.f.)	Regular (=116.0,30 d.f.)	Regular (=92.7,30 d.f.)

¹d.f.= free degree.

Collisions between gynes wondering in the arena were not infrequent. After collision, individuals invariably exhibited antennal-mandibular examination, which varied in intensity, ranging from brief antennal contact to intimate and prolonged bouts of antennal-mandibular probing, according to the individual.

After contact, gynes continued walking in the same or a different direction. No aggressive behaviour between colliding gynes was observed in any of the five trials, involving 78 gynes in total.

The results suggest that post nuptial flight gynes are predominantly randomly distributed with respect to their nearest neighbor. The degree of dispersal is greater between gynes and their second and third nearest neighbors, where the distribution tended towards regularity. Trial five indicated that gyne dispersal can occur within 20 minutes, to produce a distribution pattern which persists. Before founding a nest, sister gynes do not exhibit aggressive behavior towards each other.

Experiment B. Table 3 shows that as a result of aggressive conflicts there was a highly significant difference in the number of victories to the "host" gyne (two-tailed Binomial test $p < 0.008$, 15 d.f.). The four trials in which no obvious victor emerged were excluded from the test.

Table 3. Outcome of trial conflicts in *Atta laevigata* gynes founding a nest.

Outcome of Trial	Number of Trials ¹	Binomial Test
Host gyne victories	15	$p < 0.008$
Intruder gyne victories	0	15 d.f.
(No obvious victor 4)		

¹N = 19

The results suggest that the "host" initiated a significant number of the aggressive conflicts (two-tailed Binomial test $p < 0.002$, 14 d.f.) (Table 4). Although the "intruder" was not observed to initiate any of the conflicts there were five trials during which it was not possible to discern the aggression initiator.

Table 4. The initiator of aggressive encounters in *Atta laevigata* gynes founding a nest.

Aggression Initiator	Number of Trials ¹	Binomial Test
Host	14	$p < 0.002$
Intruder	0	14 d.f.
(Unable to discern 5)		

¹N = 19

The number of "host" and "intruder" injured is not significantly different (Fisher Exact test, $p=0.2378$). Table 5 shows that most trials did not involve gyne injury. This is a consequence of the "intruder" escaping from the conflict and the "host's" nest.

Table 5. Injury during an aggressive conflict among *Atta laevigata* gynes founding a nest.

	Host Gyne	Intruder Gyne	Fisher Exact Test
No injury	15	12	p=0.2378
Injury	4	7	

The data in Table 6 suggests that there is a significant difference in the positions of the gynes when the trials terminated (G-test, $p<0.001$, 2 d.f.). "Host" gynes were located predominantly in their nest, whilst "intruders" occupied the vacant chamber. At the end of four trials the "intruder" gyne was in the "host's" nest, still engaged in an aggressive conflict. Even after some of the aggressive conflicts, in or near the "host's" nest, the "intruder" was able to remain inside Chamber A, in close proximity to the "host's" nest.

Table 6. The final positions of the *Atta laevigata* gynes in the dual chamber when trials terminated (Experiment B).

	Host Gyne	Intruder Gyne	G-test
Host's nest	16	4	p<0.001 2. d.f.
Chamber A	2	4	
Vacant chamber	1	11	

Note: Numbers in each frequency class are low.

Trials began with the "host" inside or in close proximity to its nest. In exploring Chamber A, the "intruder" that located the "host's" nest always attempted to enter it, until deterred by aggressive behavior from the host. There was no indication that the gynes were aware of the presence of each other when the "host" was deep in the nest and the "intruder" at the nest entrance.

Not included in the results are four trials during which the "host" and the "intruder" did not make contact. At the end of all four of these trials the "host" was in its nest and the

"intruder" inside Chamber A. In one of these trials the "intruder" actually started excavating a nest on her own, within 7 to 8 cm of the "host's" nest entrance.

In the event of an "intruder" gyne attempting to enter a "host" gyne's nest the "host" retaliated by initiating an aggressive conflict. In defending its nest the "host" nearly always won, and never lost. The "intruder" never won and always lost. These encounters were frequently without injury to either ant, as the "intruder" normally attempted to escape from the "host's" nest once a conflict had commenced.

As a result of these aggressive encounters a high proportion of the "intruder" gynes occupied the vacant chamber. A few were able to remain inside Chamber A, as long as no further contact was made with the "host". This strongly suggests, as do the observations made, that the effective territory of the "host" gyne exists only within its nest or in very close proximity. The fact that the main defensive mechanisms appear to be tactile may be a significant factor contributing to the limited size of the "host's" territory.

As gynes did not attack each other in the distribution and dispersal trials of Experiment A, it would seem that the aggressive behaviour of "hosts" in this experiment was performed as an act of territorial defense, rather than an attack on another gyne per se.

Experiment C. There was no significant difference in the number of central zone entries by the "intruder" gyne during the experiment and the control ($t=2.275$, $p>0.02$, 35 d.f.).

In four out of the five experimental trials in which the "host" gyne had dug or began to dig a nest in the central zone, the "intruder" gyne subsequently used the vacant nest. "Intruders" continued to excavate the nest for all or part of the remainder of the trial. No nest excavation by the "intruder" gyne, in the central zone, was observed in the absence of a "host" gyne nest.

Location of the "host's" central zone nest by the "intruder" was accompanied by intense antennal and mandibular probing. The antennae passed around the inside circumference of the nest entrance and over the nest walls before the "intruder" entered.

These observations suggest that gynes that have undergone their nuptial flight do not use a territorial marker pheromone in defense against sister gynes. In the absence of the "host" gyne, sister gynes are not deterred from entering either an area previously occupied by the "host" or its newly excavated nest.

DISCUSSION

The experiment suggests that, at high density, after the nuptial flight, gynes show a tendency to disperse. In defense of its nest against an "intruder" gyne, the "host" gyne exhibited aggressive behaviour. As a result of aggressive conflicts the "host" always won and the "intruder" always lost, except when contests were escalated and incomplete. Tactile stimuli were observed to be essential components of gyne detection and nest defense. No evidence was found for the existence of a gyne nest-marking pheromone, to repel sister gynes.

In Experiment A, where gynes were without nests, aggressive conflicts were not observed. In Experiment B where a gyne had established a nest the "host" immediately exhibited aggressive behavior to the "intruder". The territorial aggression, and the fact that the "host" won and the "intruder" lost suggests that the outcome of aggressive territorial conflicts may be based on the asymmetry of resource values. The value of the new nest as a resource is exemplified by the fact that gynes occupied the vacant nests in Experiment C and have been observed to do so in the field (Echols 1966).

One of the factors thought to affect the distribution of mature leaf-cutting and colonies is the destruction of incipient colonies and founding gynes, by well-established colonies (Wilson 1971). Working with *Pogonomyrmex*, Holldobler (1977) regarded foundress gyne aggression as a principal mechanism in causing overdispersion. While in this study *A. laevigata* gynes exhibited aggression and a tendency to disperse it is unlikely that this will significantly affect the distribution of the mature colonies because of the magnitude of leaf-cutting ant gyne mortality at the founding stage (Autuori 1950, Ribeiro & Woessner 1982). This very high mortality factor is likely to distort significantly any pattern of distribution resulting from the behavioral interaction of founding gynes.

The allocation of resources to territorial defense would not appear to be very significant. The absence of a gyne territorial marker pheromone, the importance of tactite stimuli in detection and the restriction of the gyne's territory up to or very close to the mouth of the new nest all tends to support the conclusion of Jutsum & Fisher (1979) that gyne behavior is adapted to energy conservation. Jutsum & Fisher (1979) working with *Acromyrmex octospinosus* (Reich) gynes have demonstrated that gyne lipid and carbohydrate reserves enable them to survive for a period corresponding to the time taken for the first workers to emerge. In *Atta sexdens rubropilosa* Forel the gynes must survive at least 62 days before the first workers develop (Autuori 1942a). Since energy reserves as at a premium for survival during this colony founding period it is not envisaged that a gyne's inclusive fitness would be enhanced by utilizing energy reserves on elaborate territorial strategies. Moreover, as 99.5% (Autuori 1950) to 100% (Ribeiro & Woessner 1982) of *Atta* colonies fail to establish it is highly improbable that natural selection acts to increase the level of territoriality at the post-nuptial flight stage.

Gynes have been observed to commence digging a nest within minutes or hours of landing (J.T. Nicholas, unpublished). In so doing, they are able to both conserve energy reserves and utilize favourable environmental conditions. It is suggested that digging a nest quickly and laying eggs early, rather than engaging in an elaborate territorial strategy, would promote an early emergence of workers. Besides foraging, tending to the fungal garden and to the gyne herself, the workers would serve to establish and defend a territory around the incipient nest, before the emergence of workers from neighbouring incipient nest. Thus, competition between workers, which represents only an energy and labor debit, would be less deleterious than the loss of or injury to the gyne reproductive agent (Holldobler & Lumsden 1980).

Polygyny in *Atta texana* (Buckley) colonies is not uncommon (Walter *et al.* 1938, Echols 1966, Moser 1967, Moser & Lewis 1981) and is considered to have resulted from pleometrosis (Moser & Lewis 1981), where gynes excavated the same nest or incipient nests merged. Although documented, pleometrosis in *Atta sexdens* (L.) by Huber (1907) and *Atta cephalotes* (L.) by Weber (1937) is thought to be rare. Polygynous *Atta* nests are of interest as it is thought that they develop in to large colonies very rapidly (Moser & Lewis 1981). By virtue of the "host-intruder" aggression observed in these experiments it may be concluded that polygyny, as a result of pleometrosis, is unlikely to occur in *A. laevigata*.

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