Reproductive Strategy of the Ponerine ant *Gnamptogenys striatula* Mayr (Hymenoptera: Formicidae)

by

R. Blatrix¹ & P. Jaisson¹

**ABSTRACT**

The knowledge of the social structures of Ponerinae species helps to understand the evolution of sociality in ants in general because this subfamily is often considered as ancestral. *Gnamptogenys* is among the most derived ponerine genera. We studied the reproductive strategy of *Gnamptogenys striatula* by laboratory and field observations. The dimorphism between workers and queens was pronounced and the worker caste presented a monophasic allometry between head width and thorax width. Queenright and queenless colonies were both present in the field. The latter contained several gamergates whereas queenright colonies had several functional queens and no mated worker. Thus, both types of colonies were polygynous, and queens seemed to impede the presence of gamergate. Reproductive workers from queenless colonies seemed to be selected among the individuals with the largest size and number of ovarioles. Although we did not observe any behavioral dominance between queens, they did not lay eggs equally. This suggests a more subtle kind of hierarchy. At the laboratory, isolated gamergates were able to found a colony individually, like in many queenright ant species.

Key words: Polygyny, gamergate, *Gnamptogenys*, Ponerinae

**INTRODUCTION**

Ponerine ants show a high diversity of social structures. They are often believed to be close to the first ants morphologically and behaviorally. Thus, the study of Ponerinae might provide information on the evolution of social behavior. In most ponerine ant species, queens fecundity and queen–worker dimorphism are low (Peeters 1997). Moreover, in a hundred of species, workers keep a spermatheca (Peeters 1991, 1997; Camargo-Mathias et al. 1997), which allows them to mate and reproduce (Peeters 1991). Such mated workers were named “gamergates” (Peeters & Crewe 1984). Co-occurrence of gamergates and morphologically differentiated queens is known in less than twenty species (Whelden 1960; Haskins & Whelden 1965; Ward 1980; Villett

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1990, 1993; Sommer & Hölldobler 1992; Ito & Ohkawara 1994; Peeters & Hölldobler 1995; Gobin et al. 1998a). The study of this particular strategy might provide information on the evolution of reproductive polymorphism. Polygyny (simultaneous reproduction of several females) with morphologically differentiated queens is uncommon in the subfamily Ponerinae. The simultaneous presence of several queens in a colony raises the question of their interaction. In some species, a hierarchy takes place and results in a functional monogyny (Buschinger 1968; Francoeur & Loiselle 1985), which is interpretable in terms of kin selection if queens are related. In other species, different queens coexist without conflict (Yamauchi et al. 1981; Higashi 1983; Herbers 1986; Bourke 1991; Satoh 1991; Lipski et al. 1992; Evans 1996; Ito et al. 1996).

The genus Gnamptogenys belongs to the tribe Ectatommini. Only few studies dealt with behavior and life history in this genus (Pratt 1994; Gobin et al. 1998a, b, c; Giraud et al. 1999; Blatrix & Jaisson 2000; Blatrix et al. 2000). We present here new field and laboratory observations which provide information on the biology and reproductive strategy of Gnamptogenys striatula. This species is distributed over most of tropical and subtropical South–America (Kempf 1972). It is present in areas with sparse vegetation: urban zones, sea shores (restitico), semiarid areas (caatinga), savanna (cerrado) and secondary growth (capoeiras) (Delable, personal communication). Lattke (1990) also found the species in Neotropical rain forests. In this paper, the term “queen” was used for morphologically differentiated individuals with wings’ vestiges (i.e. excluding gamergates).

MATERIAL AND METHODS

Since 1995, 51 colonies of Gnamptogenys striatula were collected in North–East Brazil (Bahia) between Ilheus and Ilbarai along a 50km transect (Fig. 1). All individuals were counted immediately after collecting. Field observation of foraging activity was carried out in 1999.

As many dealate queens could be found in a same colony, we investigated if several of them from the same colony were able to produce worker brood. Two, seven, three, four, and six queens were chosen at random from five colonies respectively. Each queen was isolated in a chamber separated by a grid from the rest of the nest. They were returned to their mother colony after the emergence of their first adult offspring. In addition, 135 queens from ten other polygynous colonies and 83 winged females from eight colonies (two colonies were common) were dissected under a stereomicroscope. We noted whether they were mated or not and their egg-laying activity (number of mature oocytes
and presence of yellow bodies).

Experiments were carried out on three laboratory colonies to observe the behavior of queens. These colonies (96IT1a, 96IT1d, 96IT1c) contained respectively 9 (three queens died before observation), 9 (two winged females had cut their wings) and 19 queens. All queens were individually marked with numbered labels stuck on the first tergite of the gaster. Each colony was then observed through transparent red Plexiglas for a total of 30 hours distributed over a five day period. During observation we recorded the four following behavioral acts of queens: grooming received from workers, feeding, oviposition, and cannibalism towards eggs. Correlations were calculated between these items. All interactions between queens (except simple antennations) were also noted. On the day following the last observation, each colony was randomly split into two equal parts in order to test for hierarchical relationships between queens. Each half colony was then observed continuously for 10 hours. If a hierarchy existed, colony fission should result in conflicts and the formation of a new stable hierarchy in the group which had not received the putative dominant queen.

The occurrence of gamergates in queenless condition at the laboratory has been reported in this species (Blatrix & Jaisson 2000). In the present study, two queenless natural colonies were entirely dissected in order to confirm the presence or absence of gamergate. In addition, two queenright colonies were dissected to control the absence of gamergate together with queen(s), as suggested by previous laboratory experiments (Blatrix & Jaisson 2000). These colonies were frozen for dissection once transported in France. Males had been removed.
immediately after collection in order to avoid mating.

Head and thorax width of individuals (excluding queens) from the four latter field colonies were measured under a stereomicroscope equipped with a micrometer. The pooled data from the two queenless colonies allowed to calculate size differences between workers and gamergates. Moreover, we computed regression lines between the Log-transformed measurements in order to compare the allometric growth of the two populations of individuals (workers and gamergates). The aim of this comparison was to confirm that individuals we termed “gamergates” were (mated and fertile) workers and not ergatoid queens. Measurements from the four colonies pooled together with measures of 60 queens from two additional colonies were used to determine the number of morphological groups, and thus the type of polymorphism, if any. Comparison between regression lines was computed following Zar (1996).

Since 1996 a total of 3616 females were dissected. These data were pooled to calculate the mean number of ovarioles per ovary (MNO). MNO was compared with a Fisher’s test between the three following casts: queens, gamergates, workers.

As workers kept the ability to reproduce (Blatrix & Jaisson 2000) we investigated if an isolated worker could also rear its haploid or diploid

Table 1. Composition of 51 colonies of Gnamptogenys striatula collected since 1995 in Brazil (Bahia). Continued on the next page.

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| Mean   | 14     | 372     | 3              | 16    | 108    | 115     | 140   |
| sd     | 18     | 299     | 8              | 34    | 99     | 103     | 135   |

a. when counted b. seven cocoons of winged females

brood alone and initiate a new colony in the latter case. For this, 21 workers from laboratory queenless colonies and eight workers from queenright colonies were isolated in individual tubes and were given food ad libitum until death.

RESULTS

Field data

The results of field collection are summarized in Table 1. Two queenless colonies were found in Ibiçará. They represented 4% of the colonies collected. Queenright colonies were found between Ilhabela.
and Ilheus. They contained between one and 63 queens and 30 to 1207 workers. The number of workers was positively and significantly correlated to the queen number \( (r = 0.34, p < 0.02, N = 47) \). Nests were found in the soil in open areas near houses, at less than 20cm depth and they never showed any construction. We recorded the foraging activity during the observation sessions, i.e. 14:00-16:00; 19:00-20:00; 21:30-22:00; 23:30-00:00; 01:30; 03:30-04:00; 06:00; 06:30; 08:00-08:30; 09:30-12:00.

The reproductive status of queens

All the isolated queens oviposited within hours after isolation and produced worker offspring, demonstrating that they were all mated. Dissection of queens and winged females are summarized in Table 2. Most queens were mated (97.8%), the few non–mated queens were likely unmated queens who lost their wings accidentally. In seven out of ten colonies all queens laid eggs. Over all the colonies dissected, 58.5% of the queens laid eggs. Fifty three percent of the winged females were mated and 26.5% laid eggs.

Table 2. Reproductive status of queens from ten ploygnous colonies and winged females from eight colonies of *Gnamptogenys striatula*.

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*with yellow bodies and several mature oocytes*
The behavior of queens

Among the four behavioral acts recorded during the observation of queens, a positive correlation was found between feeding and oviposition in all experimental colonies (colony 96IT1c: \( r = 0.68, p < 0.01, N = 19 \); colony 96IT1a: \( r = 0.69, p < 0.05, N = 9 \); colony 96IT1d: \( r = 0.70, p < 0.05, N = 9 \)). Queens ate a large proportion of eggs (colony 96IT1c: 60 eggs laid, 18 eggs eaten; 96IT1a: 20:15; 96IT1d: 12:16). Nevertheless, although queens did not guard their eggs, we never observed oophagy by other queens during the 20 minutes following oviposition. There were four types of interaction between queens: simple antennation, rapid antennation, grooming, and stealing eggs during oophagy by another queen. Stealing eggs during oophagy failed in approximately 60% of the cases (\( N = 23 \)) because the queen which started to feed on an egg escaped when another queen attempted egg stealing. Rapid antennation (one queen antennated another at high frequency) was brief (less than a second). It was applied to any body part of the recipient but did not modify her behavior. There was no correlation between egg-laying and rapid antennation or grooming. Although they laid different numbers of eggs (0 to 6 eggs in colonies 96IT1a and 96IT1d, and 0 to 9 eggs in colony 96IT1c, and 25% of queens produced 50% of all eggs) queens appeared, thus, to cohabit without conflict. They did not display any aggression or a new type of interaction during the 10 hours following colony fission.

Dissections

Results of dissections of the four entire colonies (two queenless and two queenright) are given in Table 3. The two queenless colonies (99IB1a and 99IB1b) contained several gamergates (i.e. mated fertile workers) which represented 4.4% and 11.7% of the individuals, respectively. No mated worker was found in the queenright colonies dissected (colonies 99BV1c and 99IT2h). The numbers of individuals given in Table 3 are

Table 3. Composition of four natural colonies of *Gnamptogenys striatula* entirely dissected.

<table>
<thead>
<tr>
<th>colony</th>
<th>queens(^1)</th>
<th>gamergates</th>
<th>non laying mated workers</th>
<th>laying unmated workers</th>
<th>non laying unmated workers</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>99IB1a</td>
<td>–</td>
<td>25</td>
<td>2</td>
<td>1</td>
<td>537</td>
<td>565</td>
</tr>
<tr>
<td>99IB1b</td>
<td>–</td>
<td>31</td>
<td>3</td>
<td>3</td>
<td>229</td>
<td>266</td>
</tr>
<tr>
<td>99BV1c</td>
<td>61</td>
<td>–</td>
<td>–</td>
<td>4</td>
<td>1169</td>
<td>1234</td>
</tr>
<tr>
<td>99IT2h</td>
<td>3</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>133</td>
<td>136</td>
</tr>
</tbody>
</table>

1. Details on the dissections of queens are given in Table 2.
different from those given in Table 1 because colonies were not dissected immediately after collection.

The distribution of the mean number of ovarioles per ovary (Table 4) was obtained from the 3616 dissections performed since 1996. MNO for workers, gamergates and queens were respectively (mean ± SD) 1.72 ± 0.54 (N = 3121), 2.16 ± 0.47 (N = 243), 4.41 ± 0.68 (N = 252). MNO was significantly higher for queens than for gamergates (Fisher's test, FI = 547, p < 10^-9) and for gamergates than for unmated workers (FI = 174, p < 10^-5). However, gamergates had an ovary pattern similar to those of non mated workers who had two ovarioles per ovary. 40.1% of workers but only 6.6% of gamergates had less than two ovarioles per ovary.

Morphometry

Measurements of individuals from both field queenless colonies showed that head width (HW) and thorax width (TW) were significantly greater for gamergates (HW: mean ± sd = 0.887 ± 0.034mm; TW: mean ± sd = 0.726 ± 0.035mm; N = 56) than for non mated workers (HW: mean ± sd = 0.847 ± 0.039mm; TW: mean ± sd = 0.687 ± 0.038mm; N = 697); HW: t = 7.53, p < 10^-3; TW: t = 7.27, p < 10^-5. The distribution of HW and TW values was unimodal (Fig. 2). Parameters of the regression line (y = ax^b) between HW (= x) and TW (= y) were calculated for gamergates (y = -0.079x^{1.159}) and workers (y = -0.080x^{1.159}). The growth coefficients (b) and the elevations (a) were not significantly different between workers and gamergates (t-test; b: t = 0.006, NS; a: t = 0.367, NS).

Plotting of HW versus TW for all individuals measured (N = 2075) showed that they were separated into two distinct groups (Fig. 3), one corresponding to workers (HW: mean ± sd = 0.844 ± 0.039mm; TW:

<table>
<thead>
<tr>
<th>MNO</th>
<th>workers</th>
<th>gamergates</th>
<th>queens</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>867</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>1.5</td>
<td>386</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>1613</td>
<td>168</td>
<td>0</td>
</tr>
<tr>
<td>2.5</td>
<td>148</td>
<td>31</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>85</td>
<td>18</td>
<td>6</td>
</tr>
<tr>
<td>3.5</td>
<td>17</td>
<td>7</td>
<td>24</td>
</tr>
<tr>
<td>4</td>
<td>5</td>
<td>3</td>
<td>72</td>
</tr>
<tr>
<td>4.5</td>
<td>0</td>
<td>0</td>
<td>69</td>
</tr>
<tr>
<td>5</td>
<td>0</td>
<td>0</td>
<td>47</td>
</tr>
<tr>
<td>5.5</td>
<td>0</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
</tbody>
</table>
mean ± sd = 0.683 ± 0.039mm; N = 2015) and the other one to queens
(HW: mean ± sd = 1.035 ± 0.024mm; TW: mean ± sd = 1.073 ± 0.035mm;
N = 60). The distribution of HW and TW values was bimodal (Fig. 3).
Parameters of the regression line (y = ax^n) between HW (= x) and TW (= y)
were calculated for queens (y = 0.013x^{1.201}) and workers (y = 0.080x^{1.189}). Growth coefficients (b) were not significantly different
between workers and queens (t-test; t = 0.377, NS) whereas elevations
(a) were different (t-test; t = 65.768, p < 10^{-9}). The growth coefficient for
workers was significantly different from 1 (t-test; t = 16.307, p < 10^{-9}),
which reveals a monophasic allometry.

**Experimental foundation by individual workers**

Two of the 21 workers isolated from queenless colonies founded a new
colony. They produced more than 100 workers each in less than nine
months. After three months of isolation another mated worker pro-
duced two daughters which died a few days after emergence. The 18
remaining workers were unsuccessful in rearing brood. One of the eight
workers isolated from the queenright colonies produced two males. The
others could not rear brood until emergence. The survivorship of
isolated workers (except the two which initiated a new colony) varied
between six days and nine months (mean ± SD = 74 ± 81 days).

**DISCUSSION**

Data on the collection of colonies indicated that the number of
workers raised up to 1200. It is surprisingly high compared to the
maximum number of 200 found by Lattke (1990) in Venezuela. This
discrepancy may be due to a difference of habitats: Lattke collected
specimens in rain forest whereas we collected close to human areas. As
*Gnamptogenys striatula* appeared to be highly reproductive at the
laboratory and as seemed to be opportunistic in the field (unstructured
Fig. 3. Double logarithmic plotting of head width versus thorax width of individuals taken from four colonies of *Nemipterogea striatula* and histograms of size frequency distribution. All Pearson correlation coefficients are significant at \( p < 10^{-6} \).

nests, frequent migrations, high degree of polygyny, two reproductive strategies) we might expect that it overcame other species in disturbed habitats like in human environment.

Isolation and dissection of queens demonstrated that several queens reproduced simultaneously in natural colonies. *G. striatula* is then polygynous. Polygyny with morphologically differentiated queens is a common strategy in ants (Hölldobler & Wilson 1990) but it seems scarce in the subfamily Ponerinae. Four ponerine genera were known to have polygynous queenright species (*Amblyopone*: Traniello 1982; *Ectatomma*: Paiva & Brandão 1989; *Odontomachus*: Medeiros et al. 1992; *Brachyponera*: Dejean & Lachaud 1994) but none showed more than 10 queens per colony. Up to 13 queens have been found in colonies of *Centromyrmex bequaerti* but they generally stayed in separate nest chambers (oligogyny) (Dejean & Fénér 1996). So far, *G. striatula* is the only ponerine ant with so many queens per nest (up to 60). Moreover, in some colonies not all queens laid eggs, suggesting a possible hierarchy or other regulation process. Experimental colony fission did
not induce agonistic behavior between queens. Egg production by G. striatula queens was not regulated by any behavioral dominance, unless the considerable oophagy by queens (53% of the eggs were eaten) was directed towards eggs laid by others. Rapid antennation between queens did not seem to be aggressive and was not related to reproductive fitness. It differed from antennal boxing in its short duration and in not being specifically oriented towards head parts. This behavior has already been described between workers in laboratory queenless colonies (Blatrix & Jaisson, 2000). Dissection of winged females of natural colonies revealed that they could be mated, and even have egg-laying activity. This might support the hypothesis that groups of newly inseminated winged females could be accepted in the colony. Thus, in this species, the status of “winged female” does not imply virginity. The analysis of queen behavior revealed a positive correlation between feeding and oviposition, as previously documented in *Leptothorax acervorum* (Bourke 1991).

Blatrix and Jaisson (2000) described the occurrence of gamergates in artificial queenless colonies. Here, we reported the existence of natural queenless colonies containing several gamergates showing that polygyny occurs both in queenright and queenless colonies. Ward (1983) described two similar strategies in species of the *Rhytidoponera impressa* group, but in these cases queenright colonies were monogyrous. In many *Rhytidoponera* species (Haskins & Whelden 1965) and in *Gnamptogenys menadensis* queens seem to be less frequent than in *G. striatula* (Gobin et al. 1998a). We found that head width (HW) and thorax width (TW) measured on individuals from the two natural queenless colonies were significantly greater for gamergates than for workers. However, the distribution of HW and TW was unimodal and the parameters of the regression lines (corresponding to the allometric growth between HW and TW) were not significantly different between unmated and mated workers. Consequently, they belonged to the same morphological cast and mated individuals were true mated fertile workers (or gamergates). Only two colonies (both collected at Ilheus) were queenless. If queenless colonies were randomly distributed in the population, we should have found some of them among the 49 colonies collected between Itabuna and Ilheus. Consequently, occurrence of queenless colonies probably depends on geographical or environmental conditions. As Ilheus is farther from the sea, the whether is dryer and the gamergate strategy might be an adaptation to dry habitats, as it was proposed for the related genus *Rhytidoponera* (Ward 1983). Queen production is costly and might become difficult when resources are scarce. Moreover, queen dispersal could be risky because of rapid
desiccation. A wingless queen strategy might be advantageous in such condition (Buschinger & Heinze 1992). Collection of more colonies in semiarid habitat is needed to support a correlation between dryness and queenlessness.

Experiments carried out by Blatrix & Jaisson (2000) suggested that queens of G. striatula inhibit the presence of gamergates. We did not find any mated worker in two dissected queenright colonies whereas gamergates occurred in queenless colonies. This result strongly supports that queens inhibited worker mating. Most of the workers had empty ovaries or with few trophic oocytes and only four (unmated) workers seemed to lay chorioned eggs. Queenless groups of unmated workers produced a large male–destined brood. Thus, mating did not trigger egg-laying. This observation is in accordance with data on other queenless species (Villet 1992).

Blatrix and Jaisson (2000) found that the mean number of ovarioles per ovary was significantly higher for queens than for gamergates and for gamergates than for unmated workers. Moreover, they found that gamergates with less than two ovarioles per ovary were infrequent, compared to workers (this work relied on 222 individuals). The present study confirm these results from a sample of 3616 individuals. Distributions of HW and TW from 2075 individuals were bimodal, separating workers and queens (especially for TW). Pronounced dimorphism between workers and queens is scarce in ponerine ants (Peeters 1997). The high (and significant) correlation coefficient between the two measurements for workers, and the unimodality of their distribution excluded strict polymorphism or polyphasic allometry within workers. The growth coefficient of the regression line between HW and TW of workers was different from 1, demonstrating that the worker caste presented a monophasic allometry which is the elementary form of worker polymorphism (Wilson 1953; Oster & Wilson 1978).

Isolation of mated workers showed that they were able to found their own colony. Only gamergates of Rhytidoponera chalybaea and Harpegnathos saltator were shown to present a similar capacity (Ward 1981; Liebig et al. 1998). Haskins & Whelden (1965) obtained males from isolated workers of Rhytidoponera metallica, suggesting that gamergates might be able to found alone, too. Besides, G. striatula workers could survive over nine months of isolation. Even if rearing conditions were artificial and a gamergate alone may not survive in natural conditions, this experiment showed a potential capacity. At this stage, we cannot determine whether it has been recently selected under selective pressure or it results from phylogenetic constraints.

To our knowledge, polygyny without aggression and the occurrence
of queenright and queenless (with gamergates) colonies constitute a unique reproductive strategy in social insects. Many species belonging to the subfamily Ponerinae display strange social structures. An extensive study of this subfamily will allow comparative analyses and provide information on the different paths followed by evolution after sociality emerged among insects.

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REFERENCES


