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Population structure and mating biology of the polygynous ponerine ant *Gnamptogenys striatula* in Brazil

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Abstract

***Gnamptogenys striatula* is a polygynous ponerine ant, whose colonies contain either several differentiated queens or several gamergates. Population structure, queen mating frequency and deviation from random mating were investigated in a north-eastern Brazilian population. Eight workers from each of 33 queenright colonies and 17 queens and their progeny (20–40 offspring) were genotyped using eight variable microsatellite markers. Population differentiation tests indicated limited gene flow at the scale of several kilometres, and tests of isolation by distance revealed population viscosity at the scale of a few metres. This population structure, together with the frequent colony migrations and fissions observed in the field, suggest that new nests are founded by budding in *G. striatula*. Genetic data showed that 13 of our 17 queens were single-mated and four were double-mated. The estimation of the range of maximal frequency of double-mated queens in the population was 0.232–0.259, demonstrating that mating frequency is low in *G. striatula*. The low estimated mean relatedness between the 17 queens and their mates (–0.04 ± 0.49) indicated no evidence of inbreeding in *G. striatula*.**

Keywords: ants, budding, mating frequency, outbreeding, polygyny, population viscosity

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Introduction

Among the social Hymenoptera, most females are sterile or sub-fertile, and rear the young of others instead of their own. Hamilton (1964a,b) showed that this reproductive sacrifice could be favoured by kin selection if, by rearing the progeny of relatives, sterile workers transmitted more copies of their genes to subsequent generations than they would have done by producing offspring themselves. In social Hymenoptera, colonies are indeed often composed of closely related individuals. However, in several species, multiple reproductive queens are found in a single colony (Keller 1995), with a reduction in relatedness between brood and workers; this makes the maintenance of a non-reproductive worker caste more difficult to explain by Hamilton's concept of inclusive fitness. This question is particularly striking in species where workers are still able to reproduce (Hamilton 1964b; Trivers & Hare 1976; Bourke & Franks 1995, pp. 12–38). It is therefore essential to study the mating biology (mating frequency and degree of inbreeding) in these species, as this is one of the factors determining the kin structure of colonies. Investigating the mating pattern of the polygynous ponerines is especially interesting because of the existence of gamergates (mated, fertile workers producing diploid offspring) in several species of this group (Peeters 1991), and also because ponerines are regarded as 'primitive' and have a greater diversity of mating systems than any other sub-family of ants (Peeters 1991).

Studies of the genetic structure of polygynous species are also particularly interesting because this syndrome is often associated with a limited dispersal of females (Hölldobler & Wilson 1977). Queens of monogynous species typically take part in mating flights and found colonies independently, whereas in secondary polygynous species females often mate within or close to the mother colony and colonies are founded by division of existing ones (Hölldobler & Wilson 1977; Rosengren & Pamilo 1983; Keller 1991). In the species which produce new colonies

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by budding, the limited dispersal has been shown to lead to population subdivision or population viscosity (e.g. Pamilo 1983; Crozier *et al*. 1984; Pamilo & Rosengren 1984; Seppä & Pamilo 1995; Tay *et al*. 1997). Population viscosity has also been found in those polygynous species described as polydomous or unicolonial, in which the new nests produced by budding remain connected to the mother colony, with individuals moving freely between them (e.g. Chapuisat *et al*. 1997).

Gnamptogenys striatula (Hymenoptera: Ponerinae) occurs throughout Central and South America. In this species, all workers are potentially able to mate, and some colonies contain gamergates (mated and fertile workers, *sensus* Peeters & Crewe 1984) instead of queens. Differentiated queens are bigger than workers (Blatrix & Jaisson 2000) and possess wings. Both queenright (with morphologically differentiated queens) and queenless (with gamergates) colonies are polygynous. Under natural conditions, several functionally differentiated queens or several gamergates live together in the same nest without conflict (up to 60 nestmate queens). Removal of the queens leads to worker mating (near the nest) and reproducing in laboratory colonies (Blatrix & Jaisson 2000). Males and queens are winged but no nuptial flight has been reported in this species. Polygyny and the existence of gamergates make this species a particularly interesting subject for studies on social evolution. Our first aim was to investigate the structure of a Brazilian population of *G. striatula* at different levels to detect possible population subdivision and/or population viscosity. Field observations were also carried out to obtain data on the ecology of this species, which has never been studied. We then examined queen mating frequency and deviations from random mating in *G. striatula.* Both these factors affect the genetic diversity among offspring, and the relatedness among colony members and knowledge of them is essential for understanding the social structure of *G. striatula.* Furthermore, such data are useful for comparative studies testing evolutionary hypotheses on mating frequencies in social insects.

Materials and methods

Field observations and sample collection

Field observations and collection were carried out in January and February 1999 in north-east Brazil near Itabuna (Bahia). A total of 23 nests of *Gnamptogenys striatula* were located for observations to detect colony migrations, with 318 ants from 20 nests marked with paint (6–26 workers per nest). Only ants on the nest surface were marked to avoid disturbing the colonies. We returned to the 23 nests 2–13 days later, and two of them were observed for several hours.

Thirty-three colonies along a 50 km transect were collected (Fig. 1). The names of the colonies reflect their locations: the first letter indicates the location of collecting, the number indicates the colonies collected within a

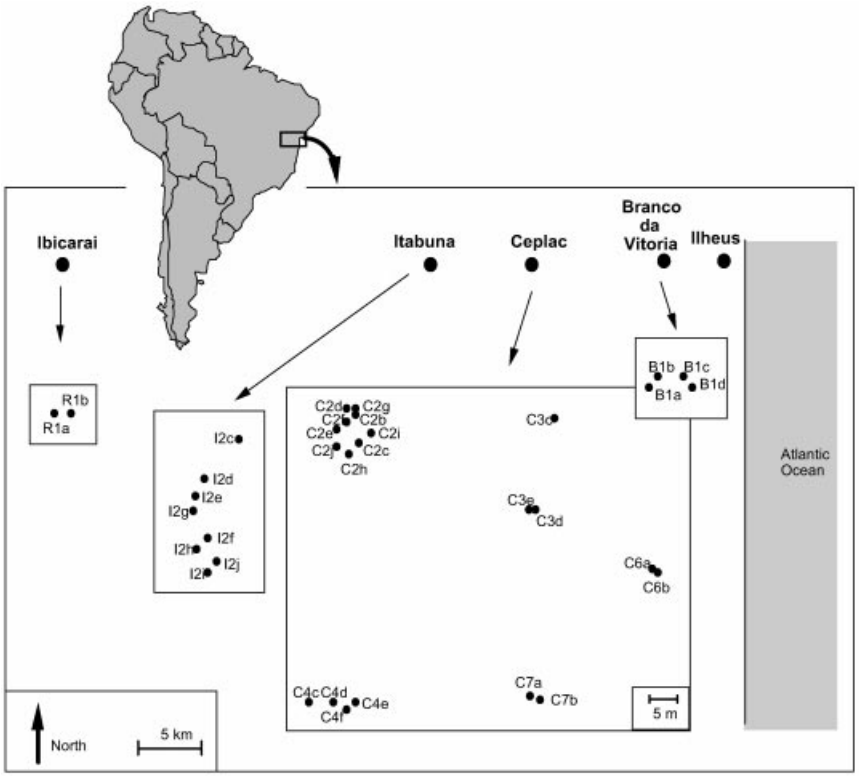

Fig. 1 Map of locations in Brazil where colonies of *Gnamptogenys striatula* were collected in January and February 1999. The squares represent focus of the four locations of collection. The scale is the same within the squares, but different from outside.

circle of 100 m diameter, and the last letter indicates the colonies collected within a circle of 15 m diameter.

Eight workers from each nest were genotyped, and 17 differentiated queens were isolated to analyse their progeny. After two months of queen isolation, we genotyped 20 eggs and 16 adult workers from one queen of colony C2c, 20 adult workers from one queen of colony C6b, 20 eggs from one queen of colony I2d, 20 eggs and 20 adult workers from each of two queens of colony I2h, 20 eggs from each of two queens of colony B1b, 20 larvae from one queen of colony B1d, 20 larvae from each of two queens of colony C3c, and 20 larvae from each of seven queens of colony C2b. Mothers were also genotyped. The genotypes of mothers and daughters allowed us to infer the haplotype of the father(s).

DNA extraction and microsatellite amplifications

Genomic DNA from adult individuals, larvae or eggs was isolated using the QIAamp DNA Mini Kit (Qiagen). The DNA from the eggs was concentrated (4 ×) by evaporation for 3 h at 80 °C. Only the heads and alitruncks (thorax and front part of the abdomen) of queens were used for DNA extraction.

Primer sequences and amplification conditions for the eight microsatellite loci (L2, L4, L6, L8, L12, L16, L19 and L20) can be found in Giraud *et al*. (1999). DNA extracted from eggs was amplified with 60 cycles, instead of 35, as this gave better results for all loci. PCR products were separated in 6% polyacrylamide gels and visualized by autoradiography. Alleles were scored by length in base pairs.

Data analysis

Population differentiation between the four localities (Ibicarai, Itabuna, Ceplac and Branco da Vitoria) was investigated using the exact *G* test advocated by Goudet *et al*. (1996), and by calculating the F_{ST} values (Weir & Cockerham 1984). The number of migrants per generation was estimated according to Slatkin (1985). Population viscosity was investigated by plotting $F_{ST}/(1 - F_{ST})$ coefficients between pairs of nests against the logarithm of geographical distances (Slatkin 1993; Rousset 1997). The significance of the Pearson correlation coefficient between genetic differentiation and geographical distances was assessed with Mantel tests (Mantel 1967). These calculations were performed using the GENEPOP 3.1d software (Raymond 1995).

Relatedness between mates was calculated using the computer program RELATEDNESS 5.0 (obtained from the website http://www-bioc.rice.edu/~kfg/GSoft.html), which estimates regression relatedness values (*R*) from gene frequency data based on formulae given in Queller & Goodnight (1989). The *R* values are negative when gene sharing is lower than expected by chance. Standard errors of *R* were obtained by jack-knifing over loci. As there was a significant population structure at the level of the locality, the relatedness estimates were calculated using the allelic frequencies (all nests being weighted equally) of the locality from which each focal queen had been collected.

The number of haploid fathers per colony was obtained by comparing the mother–offspring genotypes. Two sources of error are possible in estimating queen mating frequency from genotypic pedigree data, and both lead to underestimation of the number of fathers (Boomsma & Ratnieks 1996). The first is non-detection due either to males with identical genotypes or to heterozygous queens masking the different genotypes of the two mates in heterozygous offspring. The second source of error is non-sampling of paternal genotypes when the number of offspring analysed is too small. We used the procedure of Pedersen & Boomsma (1999a) to estimate the probability of non-identification of males (due to both non-detection and non-sampling) and the mean number of queen matings in the population, corrected for both sources of error.

Results

Field data

Nests were located in the soil, at a depth of less than 20 cm, without any solid construction made by the ants. Only seven of the 23 nests first located (30%) could be found again at the same place a few days later. Other colonies were collected in places that were devoid of nests at the beginning of field observations. Of the 318 marked ants from 20 nests, only 37 ants from seven nests were found again. Sixteen ants from three colonies were collected at the site where they had been marked. Eighteen ants from three colonies were found in nest sites different from the one where they were originally marked, but less than 1.5 m distant. The original nest sites were empty, indicating that these three colonies had moved. In one nest site, we found marked ants from this nest together with three marked ants from another nest.

These observations show that colonies of *Gnamptogenys striatula* move often. Indeed, we observed two colonies in the process of migrating but we could not identify a cause. In the first colony, workers were transporting workers, males, eggs, larvae and cocoons from their nest to an empty site, 1 m away, from 03:30 until at least 08:00 h. No transport was recorded after 22:00 h. Excavation 6 days later showed that the original nest was empty, whereas the new one was occupied. In the second migrating colony, a split was observed. There was a single nest within a circle of 1.5 m diameter on 27 January 1999. We found workers transporting queens, workers, males, eggs, larvae and cocoons to two new nests from 08:30 to 10:00 h on 30 January. The three sites were approximately equidistant (less than 1 m

Table 1 The number of offspring genotyped, relatedness (*R*) with their mate, and probabilities that a second mate could not be detected, sampled or identified for each *Gnamptogenys striatula* queen analysed

Queen	Mate	Number of offspring	*R* (± SE)	Non-detection error*	Non-sampling error*	Non-identification error*
I2h (queen no. 1)		40	−0.45 ± 0.32	0.0010–0.0011	0.0004–0.1216	0.0010–0.1226
I2h (queen no. 2)		40	−0.47 ± 0.38	0.0013–0.0018	0.0000–0.0148	0.0014–0.0166
B1c (queen no. 1)		20	+0.00 ± 0.28	0.0001–0.0002	0.0004–0.1216	0.0003–0.1217
B1c (queen no. 2)		20	−0.02 ± 0.34	0.0011–0.0038	0.0004–0.1216	0.0012–0.1249
I2d		20	+0.58 ± 0.12	0.0069–0.0272	0.0004–0.1216	0.0069–0.1455
C2c		36	−0.55 ± 0.29	0.0166–0.0321	0.0000–0.0225	0.0657–0.0539
C6b		20	+0.77 ± 0.25	0.0016–0.0016	0.0004–0.1216	0.0170–0.1361
B1d	Male no. 1	20	+0.60 ± 0.40	—	—	—
	Male no. 2		+0.56 ± 0.20	—	—	—
C3c (queen no. 1)		20	−0.04 ± 0.20	<0.0001	0.0004–0.1216	0.0001–0.1216
C3c (queen no. 2)	Male no. 1	20	+0.68 ± 0.44	—	—	—
	Male no. 2		−0.09 ± 0.40	—	—	—
C2b (queen no. 1)		20	−0.52 ± 0.40	0.0033–0.0060	0.0004–0.1216	0.0030–0.1267
C2b (queen no. 2)	Male no. 1	20	−0.65 ± 0.33	—	—	—
	Male no. 2		−0.63 ± 0.34	—	—	—
C2b (queen no. 3)		20	+0.10 ± 0.10	0.0000–0.0001	0.0004–0.1216	0.0001–0.1215
C2b (queen no. 4)		20	+0.70 ± 0.29	0.0129–0.0248	0.0004–0.1216	0.0010–0.1426
C2b (queen no. 5)		20	+0.32 ± 0.45	<0.0001–0.0006	0.0004–0.1216	0.0001–0.1216
C2b (queen no. 6)	Male no. 1	20	−0.24 ± 0.48	—	—	—
	Male no. 2		0.56 ± 0.20	—	—	—
C2b (queen no. 7)		20	−0.32 ± 0.20	<0.0001–0.0001	0.0004–0.1216	0.0001–0.1217

*Estimated according to Pedersen & Boomsma (1999a), assuming a range of possible paternity skew of 0.6–0.9.

from one to another). The fission stopped on 31 January in the morning after lasting at least one full day. No ant was found in the original nest site 7 days later. The two new nests were collected (colonies I2a and I2b). Because one of the two directly observed moves led to a colony fragmentation, we assume this is a frequent phenomenon.

Population structure

Tests of population differentiation between Ibicarai, Itabuna, Ceplac and Branco da Vitoria were significant for all loci, and the global test was highly significant ($P < 0.0001$). The F_{ST} value between the four locations was 0.172. The number of migrants per generation was estimated to between 0.07 and 0.26. Tests of population differentiation between each pair of locations were also highly significant ($P < 0.0001$).

Investigations of isolation by distance were made for the group C2, which contained nine close nests (Fig. 1). The test was significant ($P = 0.048$). This indicates that the nearest nests were the most similar for group C2.

Estimation of the number of matings per queen

All eggs analysed were heterozygous for at least one locus, indicating that they were all diploid. The genotypes of the progeny of the queens analysed were consistent with a single mating for 13 queens and with a double mating for four queens (Table 1). For the 13 queens where only one mate was detected, the probabilities that a second father was not identified by the analysis of mother–offspring combinations were estimated, assuming a possible paternity skew range of 0.6–0.9 (a paternity skew of 0.6 is defined here as one father contributing to 60% of the offspring and the second father to 40% of the offspring). These probabilities were very low (Table 1). The probabilities of non-identification of a second male were 0.0001–0.0657 for a hypothetical paternity skew of 0.6 for the different mothers. The probabilities of non-identification were higher for a paternity skew of 0.9 (0.0166–0.1455), but the contribution of second fathers with a paternity share of 10% is very low, so that the genetic consequences for the colony relatedness would be limited.

The upper limit of double mating in the population was estimated by using the observed proportion of double-mated queens (0.23), corrected using the above non-identification probability range, as indicated in Pedersen & Boomsma (1999a). This gave a range of maximal frequency of double-mated queens in the population of 0.23–0.26.

Relatedness between mates

The regression analysis of relatedness between the 17 queens and their mates yielded highly variable values:

Table 2 Relatedness (*R*) between males having inseminated queens from the same nest

Nest	*R* (± SE)
I2h	−0.37 ± 0.49
B1c	−0.25 ± 0.21
C3c	0.06 ± 0.35
C2b	0.37 ± 0.23

R ranged from −0.65 to +0.77 (Table 1), with a mean ± SE of +0.04 ± 0.49. As the standard error interval includes zero, the mean relatedness between mates is not significantly different from zero. The mean relatedness among males who had inseminated queens of the same nest was also not significantly different from zero (0.04 ± 0.33; Table 2).

When population allelic frequencies were used instead of local allelic frequencies, relatedness estimates were found to be even lower.

Discussion

Population structure and mode of colony foundation

Differentiation tests between colonies from Ibicarai, Itabuna, Ceplac and Branco da Vitoria were highly significant and the estimated number of migrants was low, although the estimations of the number of migrants based on F_{ST} should be viewed with caution (Whitlock & McCauley 1999). These results indicate that there is a limited gene flow at the scale of several kilometres. Isolation by distance was weak, but significant for the C2 group of nests. These results reveal a limited dispersal on a large scale, and a certain population viscosity at the scale of a few metres. This suggests that new nests are founded close to their natal nest, most probably by division of existing ones. Similar population viscosity has indeed been found in polygynous ant species with such a mode of colony foundation (Pamilo 1983; Seppä & Pamilo 1995; Pedersen & Boomsma 1999b), including ponerines (Crozier *et al*. 1984; Tay *et al*. 1997). That nests are produced by budding in *Gnamptogenys striatula* is further supported by the divisions of colonies observed in field, and by the low fat levels in queens (Rumsaïs Blatrix, personal observation). Indeed, in species where new colonies are produced by budding, queens have a lower level of fat than in species with mating flights (Bourke & Franks 1995, pp. 258–298). Reproduction by colony division is correlated with the presence of gamergates in ponerine species (Peeters 1993), but usually only colonies headed by gamergates reproduce by budding (Ward 1983; Peeters 1993). What is most remarkable in *G. striatula* is that even the colonies with differentiated queens seem to have this mode of reproduction, because isolation by distance and colony migrations and fissions were observed for queenright colonies. This may be linked to the arid habitats in which *G. striatula* often live. It has indeed been suggested that both the existence of gamergates and reproduction by budding may be linked to resource-poor habitats (Ward 1983; Bourke & Franks 1995, pp. 277–278).

Finding population viscosity at the scale of a few metres raises the question of colony boundaries. Does each nest represent a separate colony, or do daughter nests remain socially connected after fission, forming polydomous colonies? Viscosity at the fine scale has also been found in polydomous ant species (e.g. Pamilo & Rosengren 1984; Boomsma *et al*. 1990; Chapuisat *et al*. 1997; Pedersen & Boomsma 1999b). The fact that workers have been recaptured in a nest other than the one in which they were marked suggests that *G. striatula* could be polydomous. However, wide-scale worker migrations have been reported in a ponerine species (Pamilo *et al*. 1985; Tay *et al*. 1997), and may explain the presence of workers originally marked in different nests. Therefore, the hypothesis of polydomy requires testing with additional field and genetic studies.

Outbreeding

The relatedness between the queens and their mates was highly variable, indicating that some matings may take place in or around the nest, while others imply a long-distance migration by at least one sex. However, the mean relatedness is not significantly different from zero, indicating no evidence of inbreeding in *G. striatula*. Inbreeding is rare in ants (Gadagkar 1991), including ponerines (Ward 1983; Crozier *et al*. 1984), due to dispersal of at least one sex, or to incest avoidance. This is probably connected to the damaging effects of inbreeding in Hymenoptera, which results in diploid males. Diploid males are usually sterile (e.g. Cook 1993), although some fertile diploid males have occasionally been reported (e.g. Krieger *et al*. 1999). Experiments have been conducted to test for incest avoidance by females in *G. striatula*, but no such behaviour has been detected (Rumsaïs Blatrix, unpublished data). The lack of evidence for inbreeding, together with the lack of incest avoidance, suggest that most females do not mate within the nest, as they do in several other polygynous species (e.g. Passera *et al*. 1988; Keller & Passera 1989; Keller & Passera 1990; Keller 1993). No nuptial flights have been reported for this species, nor were any observed during the two months of collecting, although males and queens are winged. Population structure and field observations suggest limited dispersal of females, but males may disperse more than queens. They may disperse and mate with females near the female's nests of origin,

as has been reported for several ponerine species (Ward 1981; Crozier *et al*. 1984; Peeters 1991). Observations in laboratory colonies are in agreement with this hypothesis: females display sexual calling behaviour near their nests, and males leave the nest after emergence and remain outside (Rumsaïs Blatrix, personal observation). A greater dispersal capacity among males has been found in several polygynous species (Bourke & Franks 1995, pp. 390–391), and, in a future study of *G. striatula,* this could be investigated by using mitochondrial markers to compare the structures revealed by the nuclear and the mitochondrial genomes. However, the strong population structure found at the scale of several kilometeres and the weak estimated number of migrants show that even males do not disperse over large distances.

Mating frequency

The maximal frequency of twice-mated queens in the population was estimated at 0.23–0.26. These values are low and constitute the upper limit of double-mating. We can therefore conclude that the majority of queens mate only once in *G. striatula*, and that mating frequency is low in this species.

Low mating frequencies have been found in other ponerines (Cole 1983; Ward 1983), and it seems to be the rule in most ant species (Boomsma & Ratnieks 1996; Crozier & Pamilo 1996). A low mating frequency has a special relevance in *G. striatula*, because of polygyny and the presence of gamergates. Not participating in direct reproduction must confer some indirect fitness for workers as they are able to mate, but do not when queens are present. Evidence that queens are usually single-mated to unrelated males may begin to explain how the kin structure will lead to understanding the social organization of *G. striatula* colonies.

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