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Research article

Facultative polygyny in *Ectatomma tuberculatum* (Formicidae, Ectatomminae)

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Summary. Polygyny, the presence of several mated queens within the same colony, is widespread in insect societies. This phenomenon is commonly associated with ecological constraints such as limited nest sites. In habitats where solitary nest foundation is risky, monogynous colonies can reintegrate young daughter queens (secondary polygyny). We studied the reproductive structure (i.e. queen number) of the ectatommine ant *Ectatomma tuberculatum* from Bahia State, Brazil. This species was found to present facultative polygyny: out of a total of 130 colonies collected, 39.2% were monogynous, while 43.8% were polygynous. Polygynous colonies had significantly more workers than monogynous ones. Queen number in polygynous colonies ranged from 2 to 26, with an average of 4 ± 4 queens per colony. All nestmate queens were egg-layers with no apparent dominance hierarchy or agonistic behavior. Non-nestmate queens were adopted by monogynous colonies suggesting that polygyny is secondary, originating through queen adoption. This species is characterized by an open recognition system, which probably allows a switch from monogynous to polygynous colonies. The behavioral acts of queens showed that resident queens remained frequently immobile on or near the brood, contrarily to alien or adopted queens and gynes. In addition, monogynous queens showed no behavioral or physiological (i.e. by ovarian status) differences in comparison with polygynous ones. Secondary or facultative polygyny, probably associated with queen adoption, may have been favored in particular environmental conditions. Indeed, by increasing colony productivity (i.e. number of workers) and territory size (by budding and polydomy), polygyny could uphold *E. tuberculatum* as a dominant species in the mosaic of arboreal ants in Neotropical habitats.

Key words: Queen adoption, queen behavior, ant, egg-laying, Neotropical.

Introduction

The occurrence of multiple mated queens in the same colony (i.e. polygyny) is known in many ant species, and queen number usually varies between and within species (Hölldobler and Wilson, 1990; Bourke and Franks, 1995). The origin of polygynous colonies can either be primary by pleometrotic colony foundation (e.g. *Iridomyrmex purpureus*: Hölldobler and Carlin, 1985; Carew et al., 1997; *Pachycondyla villosa*: Trunzer et al., 1998; Heinze et al., 2001) or secondary, generally by the reintegration of recently inseminated daughter queens (e.g. *Gnamptogenys striatula*: Giraud et al., 2000; *Leptothorax* cf. *andrei*: Rüppell et al., 2001).

In polygynous ants, egg-productivity per capita tends to decrease as queen number increases (e.g. *Plagiolepis pygmaea*: Mercier et al., 1985; *Solenopsis invicta*: Vargo, 1992). According to Keller and Nonacs (1993), lower individual reproduction in polygynous colonies does not results from direct pheromonal inhibition, but rather is the consequence of workers regulating queens' reproductive output in response to pheromonal queen signals. Worker regulation of queen fecundity would maximize colony efficiency by adjusting egg production to the current brood rearing capacity of the colony. Even though polygyny can lead to reproductive competition among queens, a new queen would still benefit from seeking adoption into an existing colony if the costs of founding a colony solitarily are high (Hölldobler and Wilson, 1977; Rosengren et al., 1993; Heinze, 1993; Bourke and Heinze, 1994). The adoption of young queens in established colonies (i.e. secondary polygyny) is also associated with ecological factors such as limited nest sites (e.g. Herbers, 1986; Bourke and Heinze, 1994; Pedersen and Boomsma, 1999). Ecological features play an important role in shaping the social system where ant populations will locally adopt out of the many possible (Bourke and Franks, 1995). The evolutionary forces affecting the evolution of polygyny

are closely linked to those affecting the evolution of euso-ciality itself. As a result, studying either of these matters will provide a better understanding of the others (Bourke and Franks, 1995).

The recently designed subfamily Ectatomminae (Bolton, 2003) comprises many polygynous queenright species such as *Ectatomma permagnum* (Paiva and Brandão, 1989), *E. ruidum* (Lachaud et al., 1999), and *Gnamptogenys striatula* (Blatrix and Jaisson, 2001), as well as the genus *Rhytidoponera* where colonies are queened by several mated workers (e.g gamergates: Ward, 1983). All these species were previously considered as Ponerinae belonging to the tribe Ectatommini. *E. tuberculatum* was until recently considered to be strictly monogynous in Mexican populations (e.g. Weber, 1946; Champalbert, 1986; Garcia-Perez et al., 1991; Villet and Fénéron, 1998), with a large queen well-differentiated from the workers, and a semi-claustral mode of colony foundation (Dejean and Lachaud, 1992). In fact, other reproductive strategies such as polygyny seem to have evolved in this species in both Brazilian (Itabuna, Bahia State: Delabie, 1990) and Mexican (Apazapan, Veracruz State: Hora et al., 2001) populations. In both studies, however, no queen behavior was presented. Cook (1905) found colonies with several queens in a Guatemalan population, though it is uncertain whether the females were mated queens or gynes (i.e. young unmated queens). He also observed colony division, i.e. queens and workers leaving to found a new colony, but remains unclear whether it represented budding or colony fission (sensu Peeters and Ito, 2001). The presence of microgynes associated with normal queens (or macrogynes) was demonstrated in an Apazapan population (Hora et al., 2001), and these small queens are now considered as parasitic inquiline queens (Hora et al., submitted).

The nest of *E. tuberculatum* is always established underground at the base of a tree. The nest consists of a single vertical tunnel following the main root and reaching a depth of approximately 1.50m onto which open one to five horizontal chambers at intervals of about 20 cm. The entrance at the base of the tree trunk is extended by a typical 10–30 cm long chimney made of soil and plant material (Delabie, 1990). This species forages almost exclusively on the tree where the nest is established as well as on the surrounding vegetation in contact with tree's canopy. It also presents the ability to collect homopteran honeydew (Weber, 1946; Delabie, 2001). Because of its foraging habits and the remarkable stability and aggregation of its populations, this species is considered as one of the more characteristic elements of the mosaic of dominant arboreal ants in cocoa plantations of Bahia, Brazil (Majer et al., 1994). Such plasticity in the life-history traits of *E. tuberculatum* could partially explain its notable ecological and adaptive success.

We investigated here the reproductive structure (i.e. queen number) of *E. tuberculatum* populations from Bahia State (Brazil) in order to better understand the mechanisms underlying facultative polygyny in this species. Our findings suggest that polygyny may play an important role in maintaining *E. tuberculatum* as an ecologically dominant species in the mosaic of arboreal ants in Neotropical habitats.

Material and methods

1. Colony collection and rearing conditions

A total of 130 colonies of *E. tuberculatum* were collected in Bahia State, Brazil, in three different localities – Itabuna, Buerarema, and Uruçuca – during different fieldwork trips (1996, 1997, 1999, and 2001). *E. tuberculatum* nests are easy to locate because of the typical chimney entrance at the base of the trunk. Although most nests were found under cocoa trees (*Theobroma cacao* L.; Sterculiaceae), a large number of other trees and shrubs belonging to various families were used as nest sites. After collection, we scored an immediate census of queens, workers, gynes (i.e. unmated queens), males, and brood.

Nest density was estimated in 10 areas (25 × 25 m). In each area, we monitored the total number of suitable trees as well as the number of trees associated with an *E. tuberculatum* nest. Suitable trees were defined in Bahia as those used by *E. tuberculatum* to nest and which belong to the plant families Caesalpiniaceae, Euphorbiaceae, Fabaceae, Melastomataceae, Meliaceae, Moraceae, Solanaceae, Sterculiaceae, Ulmaceae and Urticaceae. Furthermore, *E. tuberculatum* is usually found nesting at the base of plants with a diameter ranging from 0.03 to 0.19 m (J. Delabie and R.R. Hora, unpubl. data). Thus, both characteristics (i.e. plant species and diameter) were used as parameters to define suitable nest sites. In order to determine whether or not polygyny is related to nest density, the number of queens was checked in 30 colonies collected in 2001.

Colonies were reared in the laboratory in a controlled environment room (T = 27–28 °C; RH = 60–80%; light/dark cycle = 12 h :12 h) and kept in artificial plaster nests (26 × 18.5 cm) connected to a foraging arena (25 × 24 cm). During behavioral observations, nests were kept in the dark by using a red glass while foraging arenas were under the alternating light/dark cycle. Food consisting of a honey-apple mixture, mealworms, crickets, and flies was provided daily.

2. Queen behavior and queen adoption

The scan sampling method (Altmann, 1974) was used to characterize the behavioral profile of queens from monogynous and polygynous colonies. We carefully monitored the behaviors of six queens from monogynous colonies (n = 6) and 36 from polygynous ones (n = 6). The polygynous colonies studied contained 2 to 14 mated queens (Table 1). In addition, two of these colonies also contained gynes (10 and 5 respectively). A total of 23,712 scans were performed (416 scans per individual over a period of 8 consecutive days). All queens and gynes were individually marked with enamel paint or numbered labels glued on their thorax (Fresneau and Charpin, 1977).

To test whether or not monogynous colonies are able to adopt conspecific queens, we introduced one alien queen into each of the six monogynous colonies studied above. These colonies had been in the laboratory for 13 ± 8 months (mean ± SD; range: 7–24). All alien queens came from polygynous colonies belonging to the same population as their respective recipient colonies and had spent 7 to 9 months (mean ± SD: 8 ± 0.6) in the laboratory. Furthermore, all of them were winged but inseminated when collected (see Results). They were placed directly in the foraging area. A queen was considered adopted if she was not the target of agonistic interactions from workers and/or the resident queen. The behavioral acts of resident queens were studied using the scan sampling method described above before and after adoption while those of alien queens were studied after their adoption (during 8 consecutive days).

At the end of the observations, we estimated the reproductive condition of both queens by measuring ovarian development (i.e. total number of ovarioles, yolky oocytes, and presence/absence of yellow bodies) and mating status (i.e. filled or empty spermatheca).

Two Factorial Correspondence Analyses (FCA; software SPAD; see Lebart and Fénelon, 1971 for details of the method) allowed us to compare the behavioral profile of (1) monogynous queens, polygynous queens, and gynes, as well as of (2) alien and resident queens before and after adoption. To verify independence between the groups, we used

Col.	Site collected	N of workers ($\cong$)	N of queens	N of gynes	Brood* (eggs, larvae and cocoons)	Origin of alien queen introduced**
A	Buerarema	70	1		+ + –	Buerarema
C	Uruçuca	120	1		+ + –	Uruçuca
D	CEPLAC	120	1		+ + +	CEPLAC
E	CEPLAC	260	1		+ + +	CEPLAC
F	CEPLAC	65	1		+ + +	CEPLAC
G	Buerarema	75	1		+ + –	Buerarema
H	CEPLAC	80	2		+ + +	
I	CEPLAC	190	3		+ + +	
J	CEPLAC	150	2	10	+ + +	
K	Buerarema	150	12	5	+ + +	
L	Buerarema	170	3		+ + +	
M	Uruçuca	200	14		+ + +	

Table 1. Composition of six monogynous and six polygynous colonies of *E. tuberculatum* studied in the laboratory

* (+) = presence; (–) = absence. ** All alien queens were winged when collected.

Hoteling's test, which compares the three series of points on the basis of their coordinates on the first two axes.

Results

1. Field work

Out of the 130 colonies collected, 51 (39.2%) were monogynous, 57 (43.8%) polygynous, and 22 (16.9%) queenless. A total of 728 queens (286 mated and 442 unmated) were dissected. Polygynous colonies were present in all three sites. The average number of mated queens in polygynous colonies was 4±4. The number of mated queens in polygynous colonies ranged from 2 to 26. Five colonies were highly polygynous, containing respectively 10, 15, 16, 19, and 26 mated queens. Queens (n = 45) from 11 colonies fully or partially retained their wings even though they were inseminated.

Polygynous colonies contained more workers than monogynous ones (Mann-Whitney U test, $U = 1052.5$, $n_{mono} = 51$, $n_{poly} = 56$, $p < 0.02$; Fig. 1), and queen number was correlated with the number of workers (Spearman, $r_s = 0.24$, $p < 0.02$; $n_{mono} = 51$, $n_{poly} = 56$). However, in polygynous colonies there was no correlation between queen number and colony size as measured by the number of workers ($r_s = 0.10$, $p = 0.45$, $n = 56$; Fig. 2).

In the 10 areas studied, nesting sites were not limited since only 11% (range: 4–17%) of the all trees suitable for *E. tuberculatum* actually had a nest. There was no correlation between queen number and nest density ($r_s = 0.02$, $p = 0.88$, $n = 30$).

2. Queen behavior

Queens from monogynous and polygynous colonies exhibited similar behavioral profiles as shown in the FCA analysis (Fig. 3; Hoteling's test: $F_{(2,39)} = 2.65$, $p > 0.05$). In contrast, gynes clearly constituted a separate group (monogynous queens *vs.* gynes: $F_{(2,18)} = 1.45^{E+13}$, $p < 0.001$; polygynous
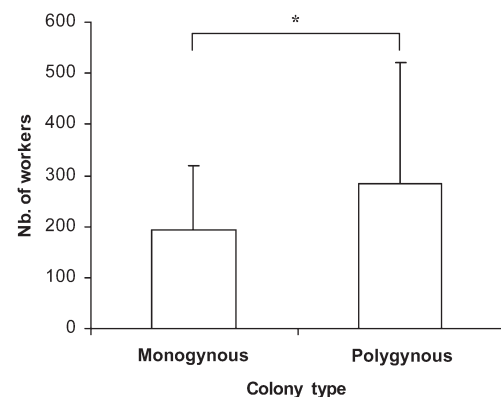

Figure 1. Number of workers (mean ± SD) in monogynous and polygynous colonies of *E. tuberculatum*. Number of colonies in brackets
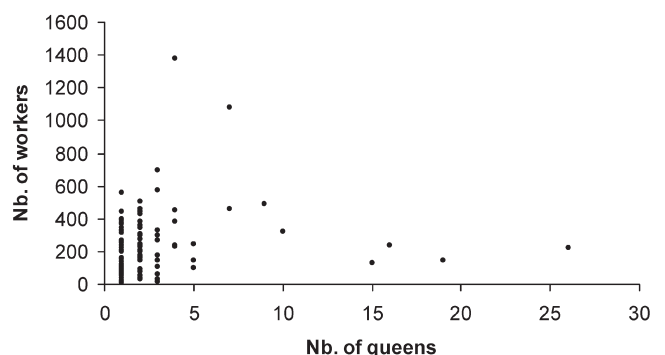

Figure 2. Number of workers in monogynous (n = 51) and polygynous (n = 56) colonies of *E. tuberculatum*. Number of queens in polygynous colonies ranged from 2 to 26

queens *vs.* gynes: $F_{(2,48)} = 1.34^{E+13}$, $p < 0.001$). Unlike mated queens, gynes patrolled in the foraging area and while in the nest stayed less frequently immobile on the brood: 0.75 ± 1.32% of all behavioral acts in comparison with mated queens in monogynous (45.19 ± 14.5%) and polygynous (32.28 ± 14.87%) colonies.
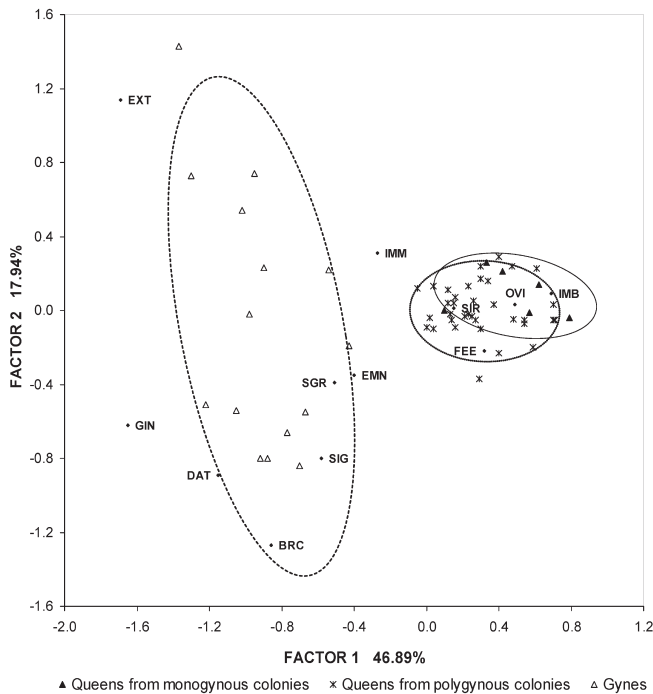
Figure 3. Factorial correspondence analysis (FCA) on the first two axes of behavioral data obtained from scan samplings of queens from monogynous (n = 6) and polygynous colonies (n = 36) and gynes (n = 15). BRC (brood care), DAT (domestic activities), EMN (exploring and moving inside the nest), EXT (extranidal activities), FEE (feeding on prey), GIN (guarding inside the nest), IMB (immobility on brood), IMM (immobility), OVI (oviposition), SGR (self-grooming), SIR (social interactions received), and SIG (social interactions given)

There was no significant difference in the number of eggs laid by queens in monogynous and polygynous colonies ($U = 74.5$, $n_{mono} = 6$, $n_{poly} = 36$, $p = 0.23$). In polygynous colonies, nestmate queens exhibited no significant differences in both egg-laying behavior (except in colony L) and number of oocytes (except in colony H; Table 2). No agonistic behavior was observed between queens, even during oviposition. Furthermore queens apparently did not engage in oophagy. The only observed case of oophagy occurred when a mated queen ate a gyne's freshly-laid egg. In one colony, gynes laid unfertilized male-yielding eggs (n = 9), which were commonly eaten by larvae (n = 7) or queens (n = 1).

The ovarian status of queens from monogynous and polygynous colonies was similar: the number of yolky oocytes was not significantly different ($U = 74.5$, $n_{mono} = 6$, $n_{poly} = 35$, $p = 0.26$), and all queens presented conspicuous yellow bodies at the base of each ovariole.

3. Queen adoption

All six monogynous colonies studied adopted the alien queen experimentally introduced into the foraging area. In five cases the resident workers pulled and transported the queen from the foraging area to the nest. In one colony the alien queen walked and entered the nest alone (i.e. without being transported by workers). The alien queen was the target of neither attacks nor agonistic interactions from the resident workers and queen in each monogynous colony. Alien queens clearly constituted a separate group as shown in the FCA analysis on

Table 2. Reproductive status of queens from monogynous (before and after alien queen adoption) and polygynous colonies. Alien queens adopted by monogynous colonies are also shown. All queens possessed yellow bodies at the basis of their ovarioles

	Colony	Eggs laid by resident queens		χ^2 (exact p-value)[a]	Eggs laid by alien queens	χ^2 (exact p-value)	Yolky oocytes		χ^2 (exact p-value)
		Before adoption	After adoption				Resident queens	Alien queens	
Mono-gynous colonies	A	21	18	0.23 (0.74)	6	6.00 (0.022*)	62	48	1.78 (0.21)
	C	9	16	3.00 (0.12)	3	8.89 (0.004*)	45	38	0.59 (0.51)
	D	12	9	1.20 (0.36)	17	2.46 (0.16)	13	24	3.27 (0.09)
	E	13	18	0.80 (0.47)	12	1.20 (0.36)	39	45	0.42 (0.58)
	F	4	0	4.00 (0.12)	10	10.0 (0.002*)	16	36	7.69 (0.007*)
	G	9	16	3.00 (0.12)	10	1.38 (0.32)	28	62	12.84 (0.0004*)

		N of queens	Eggs laid (Median)				Yolky oocytes (Median)		
Poly-gynous colonies	H	2	8	1.00 (0.45)			60.5		7.94 (0.006*)
	I	3	7	3.31 (0.19)			52		1.88 (0.39)
	J	2	5.5	0.81 (0.54)			54.5		0.08 (0.84)
	K	12	10	15.82 (0.15)			42.5		14.09 (0.22)
	L	3	11	7.02 (0.029*)			44		1.94 (0.36)
	M	14	7.5	12.72 (0.46)[b]			32		13.73 (0.31)[b, c]

[a] Comparison between resident (after adoption) and alien queens.   [b] Asymptotic p-value.   [c] Data from 13 queens.
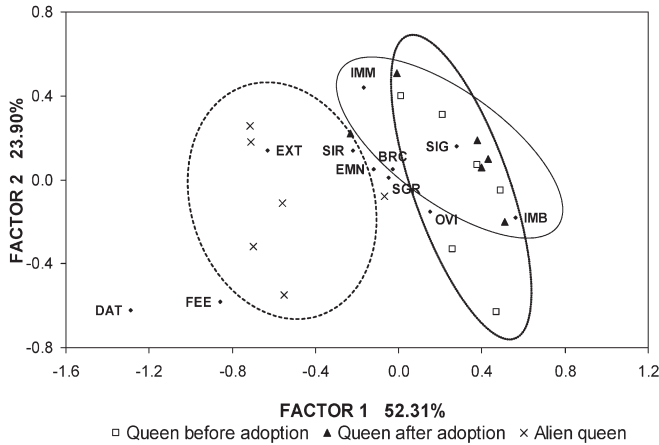
Figure 4. Factorial correspondence analysis (FCA) on the first two axes of behavioral data obtained from scan samplings of queens before and after adoption (n = 6) and alien queens after adoption (n = 6)

behavioral profiles (Fig. 4; alien queens *vs.* resident queens before adoption: $F_{(2,9)} = 25.81$, p < 0.001; alien queens vs. resident queens after adoption: $F_{(2,9)} = 18.68$, p < 0.001). Alien queens stayed less frequently immobile on the brood (Mann-Whitney *U*-test, U = 3, p < 0.05) and engaged more in feeding activities than resident queens (U = 1, p < 0.01). In contrast, resident queens showed no differences in their behavioral profiles before and after alien queen adoption (Fig. 4; $F_{(2,9)} = 0.48$, p = 0.63).

In three colonies resident and alien queens differed significantly in the number of eggs laid (Table 2). Except in two colonies, resident and alien queens presented similar fecundity as measured by the number of oocytes (Table 2).

Discussion

We have shown that, at least in some Brazilian populations, *E. tuberculatum* is characterized by facultative polygyny, that is, monogynous and polygynous colonies are found in the same population. In polygynous colonies, all queens can lay fertilized eggs, exhibiting functional polygyny.

Aggression, competition, and dominance among nestmate queens in mature colonies occur in several ant species (e.g. Heinze et al., 1992, 1998; Medeiros et al., 1992). In the ponerine *Odontomachus chelifer* for example, queen rank is significantly correlated to egg-laying activity and the degree of ovarian development. Individuals at the top of the hierarchy frequently exhibit aggressive behavior toward low rank egg-laying queens (Medeiros et al., 1992). In contrast, there is no evidence of the formation of a dominance hierarchy in multiple-queen colonies of *E. tuberculatum*. In polygynous colonies of the ponerine *Odontomachus rixosus*, queens differ in their behavioral act frequencies, which are clearly correlated with their reproductive condition. Gynes and mated queens having less developed ovaries exhibit worker-like behavior, while fertile queens frequently stay near brood piles (Ito et al., 1996). *E. tuberculatum* queens perform none

of the tasks typical of *E. tuberculatum* workers (Fénéron et al., 1996) and tend to remain immobile, mainly on or near the brood. This suggests that mated queens guard the brood, in contrast to gynes and adopted queens. This could indicate that adopted queens are not be completely integrated into the colony.

Monogynous and polygynous colonies of *E. tuberculatum* coexist in all three Brazilian populations surveyed, suggesting that colonies may switch from one to multiple queens. This could also explain the straightforward adoption of foreign queens by monogynous colonies. In *Formica truncorum*, a species exhibiting facultative polygyny, workers from experimentally dequeened monogynous colonies accept nestmate queens but do not tolerate non-nestmate ones (Sundström, 1997). Interestingly, the presence of resident queens does not seem to affect conspecific queen acceptance in *E. tuberculatum*, reflecting high tolerance towards non-nestmates, at the very least as an immediate response during the limited period of our study (8 consecutive days). An open recognition system, with no aggressive behavior toward heterocolonial workers, was suggested by Fénéron et al. (1999) in Brazilian populations of *E. tuberculatum*. Although such a phenomenon seems characteristic of polygynous societies (Bourke and Franks, 1995), queen adoption in *E. tuberculatum* may also be influenced by both the uniform laboratory conditions and the relatively long period during which (recipient and alien) colonies remained in the laboratory, as these factors are known to reduce aggressiveness (e.g. Stuart, 1987). On the other hand, monogynous colonies of *E. tuberculatum* freshly collected in the field (a few days) are able to quickly accept alien queens from the same population without hostility at all (R.R. Hora, pers. obs.). Since all alien queens studied in this work were mated and had active ovaries we may presume that queen adoption could be associated with a queen fertility signal that might influence worker behavior, as it is known in other species of ants (e.g. Ortius and Heinze, 1999; Strätz et al., 2002). Furthermore, such results indicate that *E. tuberculatum* colonies from Brazilian populations might be vulnerable to usurpation by conspecific queens (e.g. Strätz et al., 2002).

Polygyny could be favored because additional queens would raise colony productivity and/or survivorship (Bourke and Franks, 1995). We found that, in polygynous societies of *E. tuberculatum*, all queens are reproductively active and thus contribute to colony productivity. Moreover, the higher number of workers in polygynous colonies in comparison with monogynous ones supports the fact that multiple queens lead to an increase in the worker force.

Environmental factors could also underlie the evolution of polygyny in *E. tuberculatum*. This species is considered ecologically dominant in the arboreal ant mosaic of cocoa plantations in Bahia, Brazil, because of the high worker biomass and the tendency of this species to monopolize large contiguous blocks of the canopy (Majer et al., 1994; Medeiros et al., 1995). The occurrence of polydomous colonies in *E. tuberculatum* is suggested in populations from Mexico (Garcia-Perez et al., 1991) and French Guiana (F.-J. Richard, pers. comm.). The typically aggregated distribution of colonies in patches in Bahia (Delabie, 1989; 1990), as well as the

possibility of foreign queen adoption presented here, support the existence of polydomous colonies in such populations. In that case, the high number of queenless colonies collected (16.9%) could represent satellite nests. Nevertheless, queenless colonies may also result from the loss or death of the queen. *E. tuberculatum* as well as the dolichoderine *Azteca chartifex spiriti*, a species in which the distribution of polydomous nests supports the large expansion and territory maintenance abilities (Medeiros, 1992), can exert a strong influence on the number and size of workers of other species occurring in their areas of almost exclusive foraging (e.g. Majer et al., 1994). Consequently, the evolution of polygyny and polydomy in this species might have been favored in such particular ecosystems as are cocoa plantations. Indeed, by increasing the worker force, such process would allow the maintenance of *E. tuberculatum* in its dominant status.

Several authors have discussed the evolution of polygyny as an ecologically flexible trait lead by environmental factors (e.g. Hölldobler and Wilson, 1977; Nonacs, 1988; Keller, 1995). According to Nonacs (1988), queen number may constitute an ecologically plastic feature resulting from the interaction of several factors and not solely related to specific habitats. As a result, different strategies would be favored in different habitats. Colony foundation in monogynous populations of *E. tuberculatum* was described as semi-claustral, (Lachaud and Fresneau, 1985; Dejean and Lachaud, 1992): queens found a colony solitarily and often leave the nest to forage until the first workers emerge. Our results suggest that in populations presenting facultative polygyny queens may employ an alternative strategy of colony foundation. As observed in this work, supernumerary queens could result from the adoption of queens, similarly to what occurs in the two closely related species *E. permagnum* (Paiva and Brandão, 1989) and *E. ruidum* (Lachaud et al., 1999). Another interesting fact is the occurrence of inseminated alate queens, suggesting that these ones may not have engaged in nuptial flight. In other words, mating could be intranidal or take place near the nest entrance, as is the case in *Linepithema humile* (Cariou-Etienne and Passera, 1993; Aron et al., 1994), *Camponotus nawai* (Satoh, 1989), *Formica lugubris* (Cherix et al., 1991), and in ant species with wingless females (reviewed in Peeters, 1991). The lack of correlation between the number of workers and the number of queens in polygynous colonies could stem from the recent integration of young queens (particularly in polygynous colonies with more than 10 queens). These queens might not have yet produced workers or might leave the colony with workers to found a new one by budding (Peeters and Ito, 2001), that is, newly adopted queens and workers could leave their mother colony to found a new colony close by and might maintain contact with the original colony. The budding hypothesis is supported by the fact that (1) most polygynous colonies contain only 2 to 3 queens (i.e. 40 out of 57 polygynous colonies collected) and (2) worker exchanges between different nests are known in other populations (e.g. Garcia-Perez et al., 1991).

Nest site limitation is an ecological parameter selecting polygyny (e.g. *Leptothorax longispinosus*: Herbers, 1986; *Myrmica sulcinodis*: Pederson and Boomsma, 1999). However, in the populations of *E. tuberculatum* studied here, nesting sites are not limited, since only 11% of suitable trees are associated with a nest of *E. tuberculatum*. Competition between arboreal species is certainly a factor affecting the availability of nesting sites, that is, each potential tree might not be available because its canopy is already occupied by another dominant species. Polygyny would allow *E. tuberculatum* to warrant its perennial position inside the mosaic of arboreal species despite lower population, weaker recruitment strategies, lower fecundity and aggressiveness compared to other dominant species of the Dolichoderinae or Myrmicinae subfamilies (e.g. *Azteca*, *Crematogaster* and *Wasmannia*: Majer et al., 1994). *E. tuberculatum* would clearly benefit from polygyny as a means to maintain a stable territory formed by an array of permanent nests. Therefore polydomy in conjunction with low competition and aggressiveness between conspecifics would play a crucial role in preventing another dominant species from settling.

In conclusion, polygyny in *E. tuberculatum* appears to be favored in particular ecosystems such as cocoa tree plantations, which are characterized by interspecific competition and territoriality. The adoption of queens may constitute a strategy to increase both worker force and territory size. Additional studies are necessary to clarify the polygynous structure of this species as well as the adaptive values related to its occurrence in different conditions.

Acknowledgements

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