Insectes Sociaux

RESEARCH ARTICLE

Nesting patterns, ecological correlates of polygyny and social organization in the neotropical arboreal ant *Odontomachus hastatus* (Formicidae, Ponerinae)

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Abstract Queen number varies in the population of *O. hastatus* in SE Brazil. Here, we evaluate how nesting ecology and colony structure are associated in this species, and investigate how reproduction is shared among nestmate queens. Queen number per colony is positively correlated with nesting space (root cluster of epiphytic bromeliads), and larger nest sites host larger ant colonies. Plant samplings revealed that suitable nest sites are limited and that nesting space at ant-occupied bromeliads differs in size and height from the general bromeliad community. Dissections revealed that queens in polygynous colonies are inseminated, have developed ovaries, and produce eggs. Behavioral observations showed that reproduction in polygynous colonies is mediated by queen–queen agonistic interactions that include egg cannibalism. Dominant queens usually produced more eggs. Field observations indicate that colonies can be initiated through haplometrosis. Polygyny in *O. hastatus* may result either from groups of cofounding queens (pleometrosis) or from adoption of newly mated queens by established colonies (secondary polygyny). Clumping of bromeliads increases nest space and probably adds stability through a strong root system, which may promote microhabitat selection by queens and favor pleometrosis. Rainstorms that frequently knock down bromeliads can be a source of colony break-up and may promote polygyny. Bromeliads are limited nest sites and may represent a risk for young queens leaving a suitable nest, thus favoring secondary polygyny. Although proximate mechanisms mediating queen number are poorly understood, this study suggests that heterogeneous microhabitat conditions probably contribute to the coexistence of variable forms of social structure in *O. hastatus*.

Introduction

Ants are dominant social insects that can markedly affect the ecology and dynamics of animal and plant populations with which they interact, and which themselves can also generate habitat modification via nest construction and ecosystem engineering (Blüthgen and Feldhaar, 2010). The Formicidae as a whole present a broad array of nesting and feeding habits, hunting strategies, modes of social communication and colony organization, and life-history traits (Hölldobler and Wilson, 2008). Ants are especially dominant in the tropical region where they are remarkably diverse both on the ground and on vegetation. Among the arthropods living in the canopy of tropical rainforests, ants comprise over 90% of the individuals sampled (Tobin, 1995). Compared to ground, however, the forest canopy presents some major constraints that arboreal ants need to overcome in order to be successful. These may include nest site limitation, decreased availability and diversity of food resources, low humidity, as well as frequent forager displacement and nest damage caused by strong winds and rainstorms (Davidson, 1997; Floren and Linsenmair, 1997; Dejean and Corbara, 2003).

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Arboreal nesting is a derived feature in ants (Hölldobler and Wilson, 1990). The ant subfamily Ponerinae is a quite heterogeneous group; most species make their nests at variable depths in the ground, with elaborate galleries and chambers, or in pre-existing structures (Peeters, 1997). Very few ponerine species have arboreal nests and probably the best documented cases belong to the genera *Pachycondyla*, *Odontomachus*, and *Platythyrea* (e.g., Davidson and Epstein, 1989; Corbara and Dejean, 1996; Blüthgen et al., 2000; Djiéto-Lordon et al., 2001; Rico-Gray and Oliveira, 2007, and references therein). Due to difficulties in accessing ant nests and ant foragers up in the tridimensional forest canopy, field studies on the behavioral ecology of tropical ponerines have focused mostly on ground-nesting species, although some of these may hunt both on the ground and on foliage (Hölldobler and Wilson, 1990).

Species in the so-called 'poneroid' complex of ants display a variety of life-history traits, modes of colony organization, and reproductive systems (reviewed by Hölldobler and Wilson, 2008). One such variable feature within this group is the number of reproductive females in the colony, which here are referred to as queens (usually winged) and that are morphologically distinguishable from the wingless workers (see Steiner et al., 2010, for details on the identity of female reproductives in ants). When colonies are founded independently (i.e., without the aid of workers), queens may attempt to start the colony singly after the nuptial flight (haplometrosis) or form groups of two or more queens that cooperate in founding and brood rearing (pleometrosis) (Hölldobler and Wilson, 1977). A main advantage of cooperative over solitary colony foundation is that in the former strategy a larger initial worker force is produced more quickly, thus shortening the risky phase during which the queens and the brood are more vulnerable to predation (see Tschinkel, 2006 and included references). This is especially important in the subfamily Ponerinae, where queens do not have large wing muscles and risk themselves outside the nest to bring prey to feed initial larval brood (Peeters, 1993). Additionally, due to nest site limitation newly mated queens can be better off joining a resident queen instead of risking to search for another empty nest site (Herbers, 1986; Nonacs, 1988), and the nest owner may gain by accepting the joining queens at a risky stage of colony foundation (Leal and Oliveira, 1995; Trunzer et al., 1998). Most pleometrotic associations, however, do not result in true polygyny and after the eclosion of the first workers queen number is often reduced to a single egg-laying queen (secondary monogyny) (Herbers, 1993; Peeters 1993). In contrast to primary polygyny, secondary polygyny is well documented in nature and consists in the adoption of inseminated queens by an already established colony started by a single queen (Hölldobler and Wilson, 1977). Whatever the origin of polygynous nests, egg-laying queens are known

to coexist with or without antagonistic behavior in various ant taxa, including ponerines (reviewed by Bourke and Franks, 1995; Hölldobler and Wilson, 2008).

Ecological setting and study organism

In tropical forests, where arboreal nesting habits are widespread among ants (Hölldobler and Wilson, 1990), ponerine species frequently construct their nests associated with epiphytes that grow in the forest canopy (Davidson and Epstein, 1989). Among these, tank bromeliads are often inhabited by ant species that opportunistically form their colonies in the basket-like leaf structure, within root clusters, or in spaces between the epiphyte and the host tree (Dejean et al., 1995; Blüthgen et al., 2000). The arboreal perches occupied by epiphytic bromeliads, however, are inherently unstable sites due to periodic windstorms and heavy showers that often knock down the plants to the forest floor, and frequently cause death (Hietz, 1997; Pett-Ridge and Silver, 2002). Thus the canopy habitat is formed by a mosaic of suitable and unsuitable microhabitats for tank bromeliads, mediated by factors such as branch diameter, angle or height, bark texture, microclimate, relative position in the tree, and firmness of root attachment (Zotz and Vollrath, 2002; Winkler et al., 2005). As a consequence, from an ant colony's standpoint, life inside an epiphytic bromeliad can be risky and colony longevity may depend on the plant's capacity to withstand the harsh conditions of the canopy environment.

The arboreal ponerine *Odontomachus hastatus* is a large and aggressive ant species that commonly nests among roots of epiphytic bromeliads in tropical rainforests of Central and South America (Brown, 1976; Gibernau et al., 2007). In the sandy forest at Cardoso Island in Southeast of Brazil, nest size may vary with the dimension of the epiphyte clump: larger groups of bromeliads have bigger root clusters and hence provide more nesting space for the ant colony (Fig. 1). Annual rainfall at Cardoso Island is extremely high (Barros et al., 1991) and rainstorms frequently knock down bromeliads (and their ant inhabitants) to the inundated forest floor (Camargo, 2002). Thus competition for firmly attached bromeliads as potential nest sites can be a relevant limiting factor mediating the ecology of colony foundation and colony survival in *O. hastatus*, and may favor polygyny if suitable nest sites are in limited number. Although correlates of nesting ecology, queen number, and social organization are well established for small myrmicines (e.g., Herbers, 1986; Foitzik and Heinze, 1998), they remain poorly documented in ponerines. Because monogynous and polygynous colonies of *O. hastatus* coexist in sympatry at Cardoso Island (Camargo, 2002), this species is particularly interesting to investigate the causes and correlates of social structure variation. In the current study we use field and
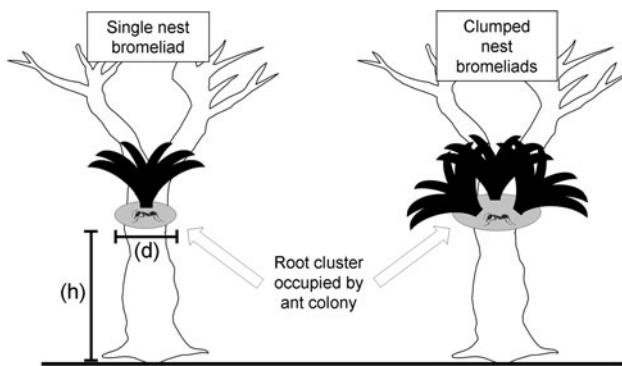
Fig. 1 General outline of single and clumped epiphytic bromeliads used as nest sites by *Odontomachus hastatus* at the sandy forest of Cardoso Island, SE Brazil. The greatest diameter of the root cluster occupied by the colony (*d*), and the height of epiphyte attachment to host tree in relation to the ground (*h*) were recorded for each nest site. The number of clumped bromeliads and the diameter of the root cluster on a tree are positively correlated (Pearson's $r = 0.32$; $P < 0.0001$, $N = 214$ plants)

laboratory data to evaluate how nesting ecology and colony structure (i.e., number of functional queens, and colony size) are associated in *O. hastatus*, and further investigate how reproductive activity is partitioned among egg-laying queens within captive colonies.

Materials and methods

Study area

Fieldwork was carried out from August 1999 to October 2001 in the sandy plain forest of the State Park of Cardoso Island (22,500 ha, altitude 0–800 m a.s.l.), located off the coast of São Paulo State, southeast Brazil (25°03′S; 47°53′W). The forest has an open canopy formed by 5–15 m tall trees growing on poor sandy soil, and abundant bromeliads growing both on the ground and as epiphytes (Barros et al., 1991). Mean annual temperature and rainfall are 20.9°C and 3,000 mm, respectively (Barros et al., 1991). The climate is generally hot and wet along the whole year, but may be divided into two seasons: a cool and less rainy period (winter) from April to August (minimum temperature 13°C, rainfall ca. 500 mm), and a warm and rainy period (summer) from September to March (maximum 32°C, rainfall up to 2,600 mm) (Funari et al., 1987).

Nest plants and colony structure

Initial observations showed that *O. hastatus* nests among roots of epiphytic bromeliad species at Cardoso Island. Nest bromeliads ($N = 19$) were tagged after following loaded workers attracted to sardine baits, and the following main

characteristics were recorded for 16 of such ant-occupied plants: bromeliad species, number of plant individuals (single or clumped), greatest diameter of root cluster occupied by the colony, and height of epiphyte attachment to host tree (relative to ground). The composition of 19 *O. hastatus* colonies (i.e., number of queens, males, workers, and brood) was determined in the field, immediately after the collection of the nest bromeliads. Colonies were then transported to the laboratory and were cultured at 23–26°C in plastic boxes containing plaster galleries (30 × 20 × 8 cm), which were covered with glass plates to maintain high internal humidity. The ants were fed with freshly killed fruit flies, beetle larvae and termites, and synthetic ant diet (Bhatkar and Whitcomb, 1970). One week after the collection of the colonies, all dealated queens from seven colonies were dissected to record the number of visible ovarioles, the number of oocytes, and whether or not the spermatheca was filled with sperm. An oocyte was considered mature if it measured approximately the size of a freshly laid egg; developing oocytes were smaller but clearly yolky. Dissections were performed on freshly frozen individuals.

Use of epiphytic bromeliads for nesting: are nest sites limited?

The density of *O. hastatus* nests was estimated within a 13,350 m² plot in the sandy forest. In this area, all epiphytic bromeliads were checked for the presence of *O. hastatus* colonies. To facilitate the location of ant-occupied plants, we followed loaded workers departing from sardine baits distributed on vegetation. A total of 45 epiphytic bromeliads containing an *O. hastatus* colony were found, and the following characteristics were recorded: number of plant individuals used as nest (single or clumped), greatest diameter of root cluster occupied by the colony, and height of epiphyte attachment to host tree (relative to ground) (Fig. 1).

To investigate whether the characteristics of the bromeliads used as nests by *O. hastatus* differ from the general bromeliad community at the sandy plain forest of Cardoso Island, we sampled epiphytic bromeliads along two 350 m transects in the same plot where ant-occupied plants were sampled. At every 10 m, epiphytic bromeliads found within 1.5 m off each transect were recorded and characterized as described above for ant-occupied plants.

Queen–queen interactions and reproductive activity

In order to investigate how reproductive activity is partitioned among coexisting egg-laying queens within nests, three *O. hastatus* colonies were used for behavioral studies in captivity, each containing one (colony #4), two (colony #7), or six egg-laying queens (colony #10) (see Table 1).

Table 1 Colony composition and species of nest bromeliads occupied by the ant *Odontomachus hastatus* in the sandy forest of Cardoso Island, Brazil

Colony code	Date of collection	Dealated queens	Workers	Winged females	Males	Pupae	Larvae	Eggs	Nest bromeliad
1	24 Aug 1999	5	320	4	0	1	10	17	–
2	25 Aug 1999	1	76	0	0	1	0	0	–
3	26 Aug 1999	12	420	20	2	0	3	0	–
4	04 Apr 2000	1	306	0	1	45	21	0	*Vriesea procera*
5	05 Apr 2000	1	100	0	0	30	8	10	*Vriesea procera*
6	06 Apr 2000	1	437	15	1	57	14	1	*Vriesea procera*
7	06 Apr 2000	3[a]	356	0	1	95	52	0	*Quesnelia arvensis*
8	17 Aug 2000	2	256	10	0	0	0	0	*Vriesea procera*
9	18 Aug 2000	10	536	0	0	0	2	57	*Vriesea procera*
10	19 Aug 2000	7[a]	440	0	1	3	0	0	*Vriesea* sp.
11	21 Feb 2001	0	35	0	2	10	11	0	*Vriesea procera*
12	21 Feb 2001	1	275	0	4	105	20	0	*Aechmea* sp. 2
13	05 Oct 2001	7	532	2	0	3	18	20	*Vriesea procera*
14	06 Oct 2001	8	502	1	0	46	13	26	*Aechmea* sp. 1
15	06 Oct 2001	1	170	0	0	8	11	20	*Vriesea procera*
16	06 Oct 2001	1	123	0	0	9	2	0	*Vriesea procera*
17	06 Oct 2001	8	282	0	0	14	17	0	*Aechmea cylindrata*
18	07 Oct 2001	1	52	0	0	0	3	10	*Vriesea procera*
19	07 Oct 2001	2	315	0	0	22	33	22	*Vriesea procera*

All queens from colonies #13 to #19 were dissected to describe ovarian development and to check for the presence of sperm in the spermatheca (see Table 2). Colonies #4, #7, and #10 were used for behavioral studies in captivity

– no data

[a] One queen died during transportation of the colony to the laboratory

Colonies were reared as described above, and queens in each colony were marked with individual patterns of color dots on the thorax (Enamel paint, Testors, Rockford, Il, USA). Behavioral observations involving queens and workers in each colony began 1 month after the settlement of the colonies, at which time eggs and larvae produced in the laboratory were already detectable. Behavioral data were gathered at daytime in continuous sessions lasting 1–4 h, and results are based on a total of 50 h of observation for each colony (from October and December 2000). Egg-laying activity by marked queens was monitored in all observation sessions, with special attention to hostile behavior toward egg-layers and egg cannibalism. Newly laid eggs were observed for 1 h after deposition on the egg pile. A matrix of dominance relationships was constructed based on queen–queen agonistic interactions recorded in each colony. Most especially, based on previous experience with dominance behavior among *Odontomachus* queens (Medeiros et al., 1992), we recorded antennation bouts and mandibular strikes between queens and annotated which ant unambiguously initiated the contest and which typically assumed a submissive posture.

In order to evaluate whether the activities of individual queens differed according to their reproductive state and social status within the colony, instantaneous samplings (snapshot records) of the colony were taken at 5 min intervals (Altmann, 1974) to record which marked queens were either attending the eggs, or somewhere else in the nest area. One week after the termination of the behavioral observations, the ovarian development of all marked queens from each colony was determined as described above. The observer performing the dissections and scoring the ovarian development did not know the previous history of individual ants.

Results

Nest plants and colony structure

Table 1 presents the composition of the *O. hastatus* colonies collected in nest bromeliads at Cardoso Island. Nearly half of the collected colonies had more than one dealated queen, and the number of workers per colony was positively correlated with the number of queens (Spearman's $r = 0.69$; $P = 0.001$; $N = 18$ colonies). The nest plant most commonly inhabited by the ants was *Vriesea procera*, although other bromeliad species in the genera *Aechmea* and

Quesnelia more rarely also hosted ant colonies. Indeed, *V. procera* accounted for 73% (33/45) of the bromeliad individuals occupied by *O. hastatus* colonies within the sampled area. Among the overall epiphytic bromeliad community, *V. procera* accounted for 80% (172/214) of the plants sampled through transects. Thus *O. hastatus* uses *V. procera* bromeliads opportunistically, in accordance with its frequency of occurrence in the forest ($G = 1.06$; $df = 1$; $P = 0.32$).

Nest site availability, and the occupation pattern by ant colonies

Samplings of the epiphytic bromeliads revealed that *O. hastatus* colonies occur at a density of nearly 33.7 nests/ha, and that the characteristics of the plants used as nests are quite distinctive. Compared with the general bromeliad community of the study area, the bromeliads housing *O. hastatus* colonies had larger root clusters (i.e., nest space) and were located at increased heights on host trees (Figs 1, 2). The occupation pattern of bromeliads by *O. hastatus* suggests that suitable nest plants are limited in the study area.
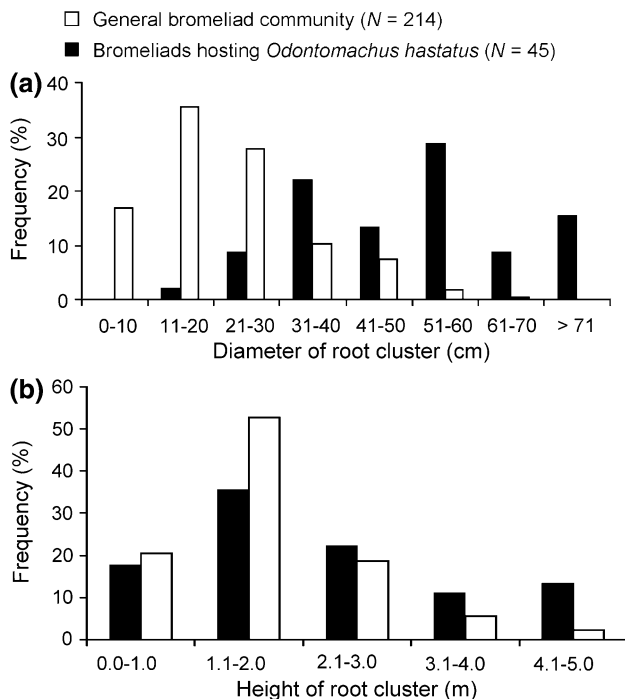

Fig. 2 Occupation pattern of epiphytic bromeliads by colonies of *Odontomachus hastatus* at Cardoso Island, SE Brazil. Plants occupied by the ants differ from the general bromeliad community in **a** size ($G = 109.64$; $P < 0.0001$) and **b** height ($G = 12.03$; $P = 0.01$) of nesting space (root cluster). Size and height of nesting sites are independent variables (Pearson's $r^2 = 0.0014$; $P = 0.58$; $N = 214$ plants). See also Fig. 1

Correlates of queen numbers and nest traits

Polygyny is associated with nest space in the *O. hastatus* population at Cardoso Island. Measurements of nest bromeliads indicate that the number of queens per colony is correlated with the diameter of the root cluster hosting the colony, and the size of the worker force follows the same trend (Fig. 3).

Most of the dissected queens (colonies #13 to #19; see Table 1) had the spermatheca filled (23/28) and presented yolky oocytes, suggesting that *O. hastatus* colonies with more than one dealated queen are functionally polygynous
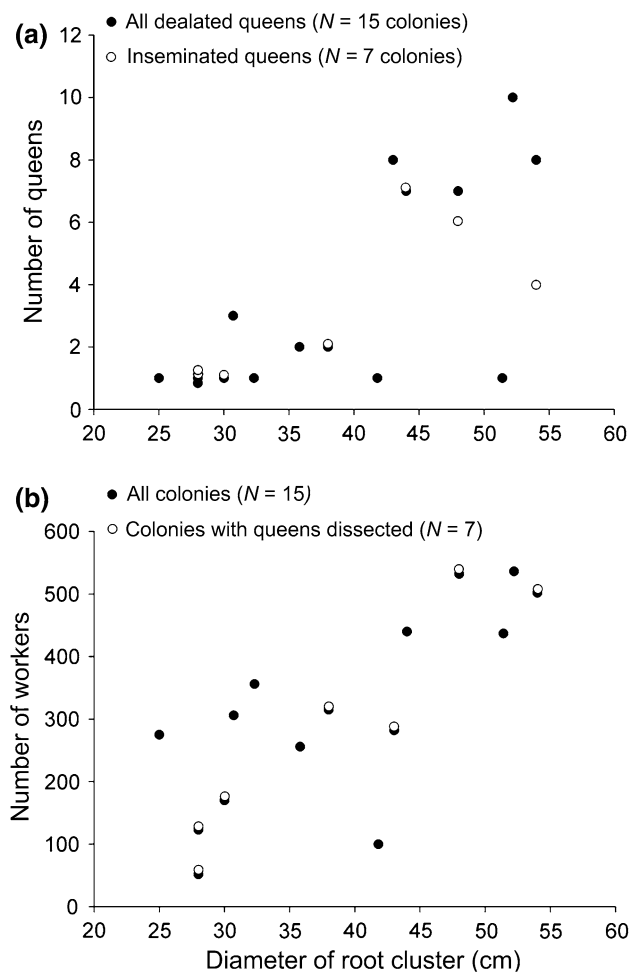
Fig. 3 Relationship of queen and worker number per colony of *Odontomachus hastatus*, and nesting space (root cluster diameter) provided by epiphytic bromeliads at Cardoso Island, SE Brazil. Data results from all 15 colonies whose composition and nest traits were obtained in the field (Table 1), seven of which had the dealated queens dissected to check for insemination status (Table 2). **a** Dealated queens$_{total}$: Spearman's $r = 0.68$; $P = 0.0047$. Dealated queens$_{inseminated}$: Spearman's $r = 0.82$; $P = 0.0023$. **b** Workers (all colonies): Spearman's $r = 0.77$; $P = 0.0008$. Workers (colonies with queens dissected): Spearman's $r = 0.92$; $P = 0.0034$. Symbols from colonies with the same number of queens or workers are slightly displaced to improve clarity. See also Fig. 1

Table 2 Reproductive condition of *O. hastatus* queens a week after the colonies were settled in the laboratory

Colony code	Queen code	Spermatheca	No. of mature oocytes	No. of immature oocytes	Yellow bodies	No. of visible ovarioles
13	A	Filled	0	33	+++	14
	B	Empty	0	3	−	12
	C	Filled	0	15	++	14
	D	Filled	0	28	++	14
	E	Filled	0	14	+	14
	F	Filled	0	20	+	14
	G	Filled	0	27	+	14
14	H	Empty	0	3	−	12
	I	Filled	0	7	−	14
	J	Empty	0	8	−	14
	K	Empty	0	4	−	14
	L	Empty	0	2	−	14
	M	Filled	0	18	+	14
	N	Filled	0	30	++	14
	O	Filled	1	27	+++	14
15	P	Filled	0	12	+	14
16	Q	Filled	1	39	++	14
17	R	Filled	0	20	+++	14
	S	Filled	1	21	+++	14
	T	Filled	0	23	+++	14
	U	Filled	0	7	++	12
	V	Filled	0	26	++	14
	X	Filled	1	11	++	14
	W	Filled	0	23	+	12
	Y	Filled	0	25	+++	14
18	Z	Filled	1	26	++	14
19	AA	Filled	1	29	+++	14
	BB	Filled	1	40	+++	14

Symbols for yellow bodies: +++ very conspicuous, ++ conspicuous, + weak, − very weak or absent. Colony codes as in Table 1

(Table 2). Ovarian development as expressed by quantity of developing oocytes and yellow bodies varied greatly among inseminated queens of the same colony, which suggests unequal reproductive activity by queens. The ovaries of virgin queens had few developing oocytes and no detectable yellow body (Table 2).

Queen–queen interactions and dominance behavior

Agonistic interactions among coexisting queens of *O. hastatus* (colonies #7 and #10) entailed a series of stereotyped displays ranging from antennation bouts to overt aggression with typical mandibular strikes; the ant initiating the encounter normally won it. An aggressive encounter usually begins with the frontal approach by one queen (dominant) followed by a sequence of vigorous antennal drumming on the head, antennae or legs of the opponent (subordinate). The dominant queen usually stands over the opponent who typically lowers the body, backs the antennae, and closes the mandibles (Fig. 4). The contest may last from a few seconds

Fig. 4 Ritualized domination between dealated queens of *Odontomachus hastatus*. The dominant queen (*black*) vigorously antennates the head of her crouching subordinate (*white*), who responds by backing the antennae and closing the mandibles. Contests may escalate to overt aggression, especially during egg-laying, and may lead to egg cannibalism

to 4 min, and typically terminates with the subordinate queen walking away in the opposite direction as the aggressor vigorously antennates its gaster. More rarely, however, the contest may escalate to a true fight and rival queens may lock their mandibles or even pull one another by the antennae, which on one occasion caused mutilation of the appendage. Most queen–queen agonistic interactions

Table 3 Dominance order constructed during 50 h of intermittent sessions recording agonistic interactions between six marked queens in colony #10 of *Odontomachus hastatus*

Dominant queens	Subordinate queens						Total	Workers
	KB	YL	OR	PK	RD	GR		
KB	X	16	22	15	42	13	108	149
YL		X	3	2	12	5	22	112
OR		2	X	2	15		19	41
PK		3	2	X	5	4	14	51
RD		4	1	2	X	3	10	42
GR			1		2	X	3	17
Total		25	29	21	76	25	176	412

Numbers refer to queen–queen and queen–worker contests

occurred near the egg pile, with the subordinate queen typically leaving the surrounding area after the contest.

Aggression by queens towards workers were observed in both the monogynous colony (#4) and the two polygynous colonies (#7 and #10), and followed the same behavioral pattern described for queen–queen contests. Normally the workers assumed a submissive posture by lowering the body and withdrawing the antennae and mandibles. Queen–worker contests generally occurred when workers were manipulating the egg pile in the presence of a nearby queen.

The two egg-laying queens of colony #7 engaged in 55 contests over 50 h of observation, and queen BA dominated queen IS in all aggressive encounters. Queen BA also dominated workers more often than queen IS, accounting for 71% of all queen–worker contests recorded ($N = 145$).

Table 3 presents a matrix of dominance relationships between the six queens of colony #10 based on 176 contests recorded over 50 h. Aggressive interactions involved all queens but most especially queen KB, which participated in 61% of the queen–queen contests recorded (108/176). Aggression towards workers was performed most frequently by queens KB and YL, which together accounted for 63% of the queen–worker contests recorded (261/412).

Contrary to the monogynous colony #4, egg-laying events generally were a major cause of aggression in the polygynous colonies #7 and #10. In the latter case, dominant queens were conspicuously aggressive toward other queens in the typical egg-laying posture or carrying a newly laid egg. In such cases aggression typically involved vigorous antennation followed by mandibular strikes aiming at pulling the egg directly out of the queen's gaster, or from her mandibles. On one such occasion, the dominant queen succeeded in robbing and eating the recently laid egg. Despite open hostility toward egg-laying queens, these were generally successful at depositing their eggs on the pile. Queen–queen aggression in the vicinity of eggs occasionally persisted for some time after deposition. Although queens frequently inspected the egg pile with the antennae, they were never seen destroying newly deposited eggs. On several occasions, in both the monogynous and polygynous colonies, workers were seen depositing queen-laid eggs on the pile. Flaccid, worker-laid eggs were given to queens as trophic eggs.

Reproductive activity and ovarian development

After terminating the behavioral observations, we dissected the queens from the monogynous and polygynous colonies in order to assess the developmental stages of the ovaries, and compare with data on egg production. The results are given in Table 4. All queens from the three colonies were inseminated, presented developing oocytes, and contained conspicuous yellow bodies indicating past egg production. As expected, the single queen in the monogynous colony #4 spent most of her time near the egg pile and presented a large egg production over 50 h. In colony #7, the greater aggressiveness of queen BA during contests corresponded with her better developed ovaries, increased egg production and higher levels of egg attendance compared to rival queen IS. In colony #10 all but one queen laid eggs, with three queens accounting for 86% (25/29) of the eggs laid over 50 h (Table 4). Although queens in colony #10 differed significantly in both egg production ($G = 12.89$, $df = 5$, $P = 0.03$) and egg attendance levels ($G = 48.38$, $df = 5$, $P < 0.0001$), no correlation was found between these parameters and the rank position of individual queens in the dominance matrix (Spearman's $r = -0.03$; $P = 0.957$; see also Table 3).

Discussion

Although there is general consensus that certain ecological circumstances may promote polygyny in ants, few studies have assessed how queen number is affected by specific environmental characteristics (Herbers, 1986; Seppä et al., 1995; Pedersen and Boomsma, 1999; Foitzik et al., 2004). Arboreal species nesting in pre-existing sites serve as ideal models to study ecological correlates of social structure variation because nest plants are easily defined, nesting spaces can be measured, and the quantity of available nest sites can be determined in a given habitat (e.g., Feldhaar et al., 2000; Dalecky et al., 2005). Our field data with bromeliad-nesting *Odontomachus hastatus* at Cardoso Island showed that queen number varies widely among colonies and is positively correlated with nesting space (root cluster), and that larger nest sites host larger ant colonies. Samplings of epiphytic bromeliads further showed that suitable nest sites are limited and that ant-occupied plants differ in two traits (size and height of nesting space) from the general

Table 4 Ovarian development, egg production and behavioral correlates in marked queens of *Odontomachus hastatus*, after 50 h of intermittent sessions recording intracolonial interactions

Colony code	Queen code	Spermatheca	No. of mature oocytes	No. of immature oocytes	Yellow bodies	No. of eggs laid	Attendance to eggs (%)
4	MA	Filled	1	32	+++	13	97.2
7	BA	Filled	2	18	+++	7	88.2
	IS	Filled	0	13	++	3	5.2
10	KB	Filled	0	30	++	8	23.0
	YL	Filled	0	35	++	7	15.3
	OR	Filled	0	30	++	0	6.7
	PK	Filled	0	21	++	3	44.5
	RD	Filled	0	25	++	1	21.2
	GR	Filled	0	24	+++	10	16.2

Data on egg attendance are based on instantaneous samplings of marked queens ($N = 600$ snapshot records); each colony had only one egg pile. Colony codes as in Table 1

Symbols for yellow bodies: +++ very conspicuous, ++ conspicuous

bromeliad community. Dissection data revealed that several (if not all) nestmate queens in polygynous colonies of *O. hastatus* are inseminated, have developed ovaries, and produce eggs. Observations in captivity strongly suggest that egg production per queen in polygynous colonies tends to be lower compared to a solitary queen in a monogynous colony. Indeed behavioral data further confirmed that reproduction is unequally shared in polygynous colonies, and is mediated by stereotyped queen–queen agonistic interactions that may escalate to overt aggression, particularly toward egg-layers, and destruction of newly laid eggs. Those queens with better performances during domination contests usually produced more eggs. While opening the nest plants we found no evidence that dealated queens of *O. hastatus* were spaced out within root clusters (i.e., located in different cavities), which supports our observations of rival queens sharing the same chambers in captivity and suggests that oligogyny may not occur in this species (see Hölldobler and Wilson, 2008). Such a social structure based on behavioral domination has been repeatedly reported among different ant taxa and most especially in species of the subfamily Ponerinae, a group characterized by diverse modes of colony organization and reproductive systems (see Heinze, 1993; Peeters, 1993, 1997; Hölldobler and Wilson, 2008, and references therein).

Our study confirms previous observations on social structure in *Odontomachus* ants, which report the occurrence of multiple queens within colonies (Ledoux, 1952; Colombel, 1972; Peeters, 1987; Medeiros et al., 1992; Ito et al., 1996). So far we are not certain whether polygyny in this species results from groups of cofounding queens (pleometrosis) or from adoption of newly mated queens by established colonies (secondary polygyny). Indeed both mechanisms can reasonably occur in facultatively poly-

gynous *O. hastatus*: when nest sites are limited, queen number can increase through a rise in queen adoptions by established colonies (e.g., Herbers, 1986; Hannonen et al., 2004), or through an increase in foundress associations (e.g., D'Ettorre et al., 2005; Feldhaar et al., 2005).

In August 2002 we found an incipient colony of *O. hastatus* with only 3 workers, 6 eggs and a single dealated queen, indicating that this species establishes new colonies through haplometrosis as also reported by Gibernau et al. (2007) in French Guiana. The fact that queen number and colony size (number of workers) were positively correlated in *O. hastatus* may suggest that inseminated queens are added as the colony ages (e.g., Pedersen and Boomsma, 1999; Blatrix and Jaisson, 2001). Indeed Colombel (1972) reported that small colonies of *O. troglodytes* were always monogynous whereas large colonies (~250 workers) were polygynous due to adoption of newly mated queens by mature colonies. Although Ito et al. (1996) found no correlation between the number of queens and workers in colonies of *O. rixosus*, the fact that new colonies are always founded independently by solitary queens and that numerous queens are found in mature colonies indicate that functional polygyny in this species results from queen adoption. In the case of *O. rixosus* whose colonies may contain >70 inseminated queens, lack of correlation between queen and worker numbers may stem from recent addition of young queens that might not have yet produced workers, or that might have left the colony with workers to found a new one by budding (see Peeters and Ito, 2001).

Colony foundation through foundress associations have already been recorded in ponerine ants (Dejean and Lachaud, 1994; Leal and Oliveira, 1995; D'Ettorre et al., 2005) and may also lead to permanent polygyny (Trunzer

et al., 1998). For instance in the termite-hunting ant *Pachycondyla marginata*, over 80% of the colony foundations were performed by associated queens, and survival of incipient colonies were shown to be positively correlated with the number of cofounding queens (Leal and Oliveira, 1995). It is possible that such enhanced colony survival in pleometrotic ponerine colonies may stem from increased initial worker force compared to haplometrotic colonies, as shown for the ant *Pachycondyla villosa* (Trunzer et al., 1998) and other ant species (e.g., Rissing and Pollock, 1991). Similarly, by producing more workers earlier than other competing colonies, pleometrotic colonies of *O. hastatus* may benefit from securing suitable nest bromeliads that are in limited supply at Cardoso Island, and in addition may increase food intake and survival at a vulnerable colony stage. In such case one could also expect queen and worker numbers to be associated in mature colonies. Intraspecific brood raiding among neighboring colonies, a behavior known to favor pleometrosis in ants (Tschinkel, 2006), has not been recorded in *O. hastatus*.

Irrespective of the mechanism leading to functional polygyny in *O. hastatus* (pleometrosis or secondary polygyny), a number of factors seem to promote communal breeding in this species given the ecological setting at Cardoso Island (see Herbers, 1993; Bourke and Franks, 1995; Seppä et al., 1995, and references therein). The clumping of epiphytic nest bromeliads creating increased nesting space due to merged root clusters likely promote microhabitat selection by queens, which may favor pleometrosis (associated or not with oligogyny, see Nonacs, 1992; Herbers, 1993). Thus strict microhabitat requirements (i.e., big bromeliad clumps) may be a driving force leading to pleometrosis in *O. hastatus*, as revealed for desert ant species showing strong habitat selection (Tschinkel and Howard, 1983; Rissing et al., 1989). Since clumping of epiphytic bromeliads may cause strong intraspecific competition for space, pleometrotic colonies may be favored by producing a large worker force in the shortest time (Tschinkel, 2006, and included references). Indeed, large initial worker force in *O. hastatus* colonies may also be important to secure more suitable nest plants against other bromeliad-nesting ant species found at Cardoso Island (Cogni and Oliveira, 2004).

According to Hölldobler and Wilson (1977), fragility of nest sites can favor polygyny by minimizing the risk of queen loss in nest fragments after physical disturbance: colonies with multiple queens would ameliorate the harmful effects of orphaning by making nest fragments more likely to possess a mated egg-layer. Fragility of nest sites is an important factor mediating colony structure in small myrmicine *Leptothorax* ants, which rely on ephemeral cavities produced by other insects such as rotten sticks, hollow acorns, hazelnuts or grass stems (Foitzik and Heinze, 1998).

The short life of such nest cavities (half-life of as little as 10 weeks in the summer) causes a constant exchange of nesting sites and increased competition among colonies for empty cavities, and may even lead to colony usurpation by founding queens and takeovers by mature colonies (Foitzik and Heinze, 1998). Indeed, by manipulating nest site availability Herbers (1986) has demonstrated that shortage of nest cavities markedly affects *Leptothorax* colony structure, such that the degree of polygyny is correlated with the availability of nesting chances for newly mated queens (Herbers, 1986). Although probably not as ephemeral as the nest cavities used by *Leptothorax* ants, we believe that epiphytic bromeliads may constitute fragile nest sites for *O. hastatus* in view of the periodical rainstorms that frequently knock down loosely attached plants to the inundated forest floor at Cardoso Island, as reported for epiphytic bromeliads in other tropical forests (Hietz, 1997; Pett-Ridge and Silver, 2002). Although epiphyte knock down was not quantified, our observations of fallen bromeliads after heavy showers suggest that physical disturbance of nest plants can be a source of colony break-up, supporting nest fragility as a potential promoter of polygyny in *O. hastatus*. Clumped bromeliads that are firmly attached to host trees by their merged root systems likely constitute more stable and long-lasting nest sites for *O. hastatus* (see Zotz et al., 2005; Winkler et al., 2005; see also Feldhaar et al., 2003, on ant-inhabited *Macaranga* plants). Indeed, clumping has been shown to have a positive impact on stability and growth rates of epiphytic bromeliads (Zotz et al., 2005). Nest bromeliads at increased heights were more frequently occupied by *O. hastatus* colonies than plants at lower positions on host trees. Since this ant species is a generalist predator of arthropods in the forest canopy (Camargo, 2002; Gibernau et al., 2007), it is possible that nest plants at higher locations on tree trunks provide more immediate access to foliage-dwelling arthropod prey (see also Dejean et al., 1995). Whether the observed occupation pattern of epiphytic bromeliads by *O. hastatus* represents differential preference by founding queens or differential survival of ant colonies awaits further investigation.

The main ecological factors favoring polygyny are those that make attempting to found colonies alone relatively risky, including heavy predation of sexuals during and after nuptial flights and decreased survival of incipient colonies (e.g., Herbers, 1993; Bourke and Franks, 1995). Moreover, habitat saturation, habitat patchiness, or nest site limitation can also decrease the probability of successful colony foundation by a solitary queen (Herbers, 1986; Seppä et al., 1995). Besides occurring in limited number, epiphytic bromeliads are discrete nest sites that can be scattered apart by nearly 50 m in tropical forests (Dejean and Olmsted, 1997; Camargo, 2002). Particularly in inundated habitats such as the sandy forest at Cardoso Island, shortage of

bromeliads suitable for nesting may represent a limiting factor for ant reproduction, as remarked for Mexican flooded forests (Dejean et al., 1995). Thus it is possible that the search for potential nest bromeliads in the tridimensional canopy environment represents a risk for young queens leaving a suitable nest, and which may fail to locate another appropriate and unoccupied nest site (Herbers, 1986; Rosengren et al., 1993).

Variation in the number of reproductive females within colonies is a common trait among ant species, providing opportunities for comparative investigation on communal breeding in ants (Bourke and Franks, 1995). Although the proximate mechanisms mediating queen number variation in ants remain poorly understood, our study with bromeliad-nesting *O. hastatus* suggests that variation in micro-environmental conditions (i.e., size of epiphyte clumps) at Cardoso Island probably contribute to the coexistence of variable forms of social structure in this species (see Reber et al., 2010). Recent studies have demonstrated that a range of ecological factors in addition to nest site limitation can interact to influence social organization in ants, such that responses in queen number per colony can be far more complex than previously realized (Foitzik et al., 2004; Dalecky et al., 2005; McGlynn, 2010). Although challenging, such difficulty should inspire further investigation linking colony organization, natural history, and ecology of social insects at variable environmental settings.

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