

*Departamento de Zoologia, Universidade Estadual de Campinas, Brazil
and Departamento de Zoologia, Museu Paraense Emílio Goeldi, Belém, Brazil
and Lehrstuhl Zoologie II der Universität, Theodor Boveri Institut, Würzburg*

Functional Polygyny, Agonistic Interactions and Reproductive Dominance in the Neotropical Ant *Odontomachus chelifer* (Hymenoptera, Formicidae, Ponerinae)

FLAVIA N. S. MEDEIROS, LUCIANO E. LOPES, PAULO R. S. MOUTINHO,
PAULO S. OLIVEIRA & BERT HÖLLDOBLER

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Abstract

Intracolony aggression among dealated queens of the ponerine ant *Odontomachus chelifer* leads to a dominance order within the colony. Behavioral domination between queens entails an array of stereotyped displays which may escalate from vigorous antennation bouts to full mandibular strikes. In extreme situations a dominant queen may also suspend her subordinate opponent, who remains in pupal posture while being lifted up. As a rule the individual initiating a contest normally wins it. Subordinate queens may assume a crouching posture at the approach of a dominant nestmate from behind, a fact suggesting that chemical cues may also play a role in the establishment of the dominance order. Behavioral performances during domination contests and the rank position of different dealated queens correlated well with the data on individual egg production, ovarian development and other parameters of division of labor within the colony. Therefore, highly-ranked queens laid more eggs, had better developed ovaries and engaged less frequently in foraging activities outside the nest. Inseminated queens occupied the top positions in the dominance structure of the colony, and accounted for most of the aggressive interactions recorded within the nest tubes. Aggression toward egg-laying queens and the destruction of newly-laid eggs were conspicuous behavioral traits in the reproductive dominance of the *O. chelifer* colony. High ranking dealated queens were also the ones more frequently seen attacking alate females. The latter were observed to lay eggs, and some of them had developed ovaries. Our results with *Odontomachus chelifer* are in accordance with the data obtained elsewhere for other ponerine ants, and provide the first demonstration of a dominance structure linked to reproductive status among queens in a functionally polygynous ant colony.

Corresponding author: Bert HÖLLDOBLER, Theodor Boveri Institut, Lehrstuhl Zoologie II der Universität, Am Hubland, W-8700 Würzburg, Germany.

Introduction

The association of two or more inseminated queens during colony founding (pleometrosis) is a widespread phenomenon in colonies of social insects. Among the ants, however, the incidence of pleometrosis within particular species can be a flexible trait which rises under certain environmental conditions, and may be regarded as an optional procedure of the species (HÖLLDOBLER & WILSON 1990). The principal advantage arising in multiple foundress associations is that normally a larger initial brood and worker force can be produced in less time and with less individual weight loss as compared to solitary founding queens (BARTZ & HÖLLDOBLER 1982; TSCHINKEL & HOWARD 1983; RISSING & POLLOCK 1988). It has been shown that young colonies with larger initial worker forces may be more successful at brood raiding and territorial contests against incipient neighboring colonies (BARTZ & HÖLLDOBLER 1982; RISSING & POLLOCK 1987, 1991; SOMMER & HÖLLDOBLER 1992).

The occurrence of multiple inseminated queens in a nest, however, does not lead necessarily to true polygyny and in most cases of pleometrosis studied to date the reproductive activity within the established colony is usually controlled by a single egg-laying queen (secondary monogyny). In several species of social wasps and bees a female's reproductive success is largely determined by her rank position in the hierarchical structure of the colony, with the dominant female inhibiting oviposition by the subordinates through openly aggressive interactions (e.g., PARDI 1948; WEST-EBERHARD 1969, 1978; BROTHERS & MICHENER 1974; RÖSELER 1991). Queen domination leading to functional monogyny is also well documented in ants (e.g., BUSCHINGER 1968; TSCHINKEL & HOWARD 1978 [but see VARGO 1990]; HEINZE & BUSCHINGER 1988; HEINZE 1990; ITO 1990).

Ritualized contests among coexisting queens in young colonies of the ant *Iridomyrmex purpureus* were shown to result in a reproductive rank order which may significantly affect the oviposition rate by young queens (HÖLLDOBLER & CARLIN 1985). As the *Iridomyrmex* colony matures, however, the queens become mutually intolerant and disperse to different parts of the nest, creating a condition of oligogyny (see also HÖLLDOBLER 1962; BUSCHINGER 1974). Primary polygyny, in which groups of founding queens survive and coexist side by side in mature colonies as multiple egg-layers, seems to be a rare phenomenon among ants and is known to occur only in the leafcutter ant *Atta texana* (MINTZER & VINSON 1985; MINTZER 1987) and in *Pheidole morisii* (S. P. COVER, pers. comm.). Secondary polygyny, however, appears to be more common and occurs when additional inseminated queens are added by adoption or fusion with other colonies to an already existing colony started by a single queen (HÖLLDOBLER & WILSON 1977, 1990).

Whatever the process through which a polygynous nest can be formed in nature, the associated queens in mature colonies may not equally gain from the alliance and their fertility may vary widely. The establishment of dominance orders as a result of reproductive competition among colony members has been shown for several taxa of social Hymenoptera (SEGER 1991, and citations within). Among ants, dominance interactions leading to a differential reproductive activity

by individual colony members have already been reported for many species (e.g., WILSON 1974, 1975; COLE 1981; FRANKS & SCOVELL 1983; HÖLLDOBLER & CARLIN 1985; BOURKE 1988; HEINZE & SMITH 1990; HEINZE & LIPSKI 1990).

In the primitive ant subfamily Ponerinae, a series of recent studies have revealed that an array of complex behavioral mechanisms play a major role in the regulation of reproduction within the colony (PEETERS & HIGASHI 1989; OLIVEIRA & HÖLLDOBLER 1990, 1991; ITO & HIGASHI 1991). The present paper reports observations concerning the reproductive division of labor within a polygynous colony of the neotropical ponerine ant *Odontomachus chelifer* Latreille. In this species we find a clear queen-worker dimorphism and we have no indication that gamergates (mated workers: see PEETERS 1991) exist.

The coexistence of several queens within a nest is also known to occur in *O. assiniensis* (LEDOUX 1952) and *O. cephalotes* (PEETERS 1987) and is probably caused by colony fusion and/or adoption of newly-mated queens by an already existing colony (see COLOMBEL 1970a, b, 1972). In the African *O. assiniensis*, the possibility of a division of labor among isolated groups of dealated virgin queens has been mentioned by LEDOUX (1952). We demonstrate here that stereotyped agonistic interactions among coexisting queens in *O. chelifer* lead to the formation of a dominance order in which highly-ranked individuals account for most of the reproductive activity within the colony. Dissections performed on the individuals after our behavioral observations revealed that some dealated queens were inseminated, and that those in the top group of the dominance order had better developed ovaries.

Materials and Methods

The colony of *Odontomachus chelifer* used in this study was collected on 17 March 1990, in a semi-deciduous forest at the Santa Genebra Biological Reserve, Campinas, Southeast Brazil. The nest was located on the ground, next to the roots of a tall tree in the interior forest. The entrance hole measured 5 cm in diameter with a layer of humid leaf litter in its surroundings. Adult ants, pupae, larvae, and eggs, were found all the way down to 1.0 m below the ground surface. The ants were cultured at ambient temperature (15°–32 °C) at the Departamento de Zoologia of the Universidade Estadual de Campinas. The artificial nest consisted of 12 glass test tubes (2.2 cm diameter \times 15 cm length) containing water trapped behind a cotton plug. Nest tubes which represented distinct nest chambers, were placed in a box (40 \times 35 cm) which was connected to a similar-sized foraging arena, where the ants were fed with termites, beetle larvae, frozen fruit flies, diluted honey and synthetic ant diet (BHATKAR & WHITCOMB 1970). The queens and eggs were scattered among the 12 nest tubes. Queens frequently moved from one tube to another, and aggressive interactions were observed in all tubes. We started with our qualitative observation right after the collection of the colony. At that time the colony consisted of 13 dealated queens, 27 alate females, 5 males, approximately 130 workers, and a few eggs, larvae and pupae. The males died within a few days after collection. We did not observe any mating attempts inside or outside the nest. Between Mar. and Dec., 6 of the alate females shed their wings, most probably without having been mated. Two of those females had died by Dec. 1990, when we finally marked all remaining 17 dealate queens with individual patterns of color dots (gloss enamel, Testors, Rockford, Il. USA) on the thorax and/or gaster.

Presumably under natural conditions the alate females would by now have left the maternal nest for the nuptial flight, but it was not obvious to us that the virgin queens made major attempts to depart from the nest. They appeared to be fully integrated in the society. Alate females ($n = 21$) and workers remained unmarked. Egg-laying and agonistic encounters between marked and unmarked ants were recorded in intermittent sessions lasting 1 to 12 h. Behavioral data were gathered both day and night

(under a red lamp) and the results are based on a total of 100 h of observations (from 11 Dec. 1990 to 14 Jan. 1991). Special attention was given to physical attacks (mandibular strikes) and antennation bouts between adult ants. For each of such agonistic encounters, the observer recorded which ant unambiguously initiated the contest and which typically assumed a submissive posture. A matrix of dominance relationships was constructed based on the agonistic interactions between marked dealated queens, and the probability of linearity within the hierarchy was calculated according to the method of APPLEBY (1983). Queens with very low scores (i.e., ≤ 5 interactions) were not ordered with respect to one another within the matrix.

Aggressive displays by marked dealate queens toward other dealate or alate queens in the typical egg-laying posture (gaster curved forward), or toward females carrying newly-laid eggs, were also recorded. In order to evaluate whether the activities of individual queens differed according to their reproductive state and social status within the colony, snapshots of the colony ($n = 106$) were taken at 30 min intervals so as to record which marked queens were either attending eggs in the nest tubes or foraging/patrolling in the arena.

Two weeks after the completion of our behavioral observations, the ovarian development of all marked queens and of a few alate females and workers was determined. Dissections were performed on individuals killed by placing them for a few minutes in a freezer. We recorded the number of visible ovarioles, the number of oocytes and whether or not we could identify sperm in the spermathecae. An oocyte was considered mature, when it measured approximately the size of a freshly laid egg. "Developing oocytes" were all other oocytes which were smaller but clearly yolky. The observer performing the dissections and scoring the results did not know the previous history of individual ants.

Results

Dominance Behavior

Behavioral domination between queens of *Odontomachus chelifer* entails an array of stereotyped displays which may escalate from antennation bouts to typical mandibular strikes, and in extreme cases the subordinate queen may be held aloft by her dominant opponent (Fig. 1). A given agonistic encounter may start or end at any point within this aggressiveness spectrum, and a dominant ant may interchangeably antennate, groom or attack her opponent during a domination contest. Normally the individual initiating a contest wins it. In a typical episode, one queen approaches another frontally and antennates vigorously on the opponent's head and antennae or, more rarely, on the thorax or gaster. The aggressor usually stands over her subordinate who typically lowers and backs her antennae while being antennated; the mandibles are kept closed (Fig. 1A). The whole antennation contest is not continuous and normally occurs at brief intervals; the entire sequence may last from a few seconds to 10–15 min (in which case the aggressor may also groom or bite any part of the opponent's body). Occasionally, however, a subordinate queen may open her mandibles and/or raise her body while being antennated by a dominant individual. In this case the latter ant would escalate to a more aggressive display which typically consisted in the seizure of the subordinate's mandibles (keeping them closed) or head (Fig. 1B). More rarely, the aggressor would also aim her attacks at the opponent's thorax, gaster, petiole or legs and antennae. While tightly seizing the opponent by the mandibles or head the dominant queen usually pulls her; the subordinate's antennae being kept backwards and lowered. Occasionally a subor-

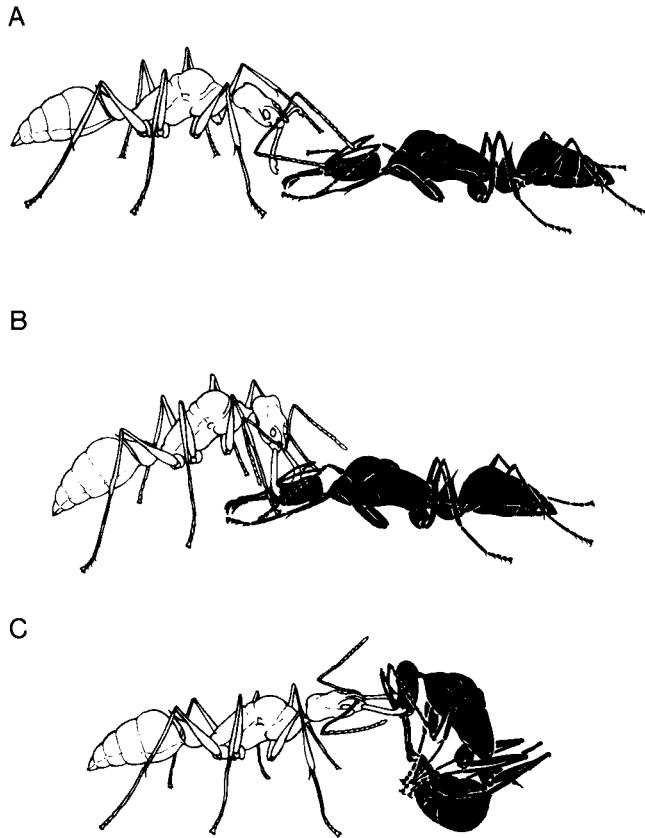


Fig. 1: Ritualized dominance displays between dealated queens of *Odontomachus chelifer*. A. The dominant queen (white) antennates the head of her crouching subordinate (black), who responds by pulling back the antennae and closing the mandibles. B. The dominant queen changes to a more aggressive display, seizing and pulling her subordinate on the head. C. The dominant queen escalates her aggressive behavior by lifting up her opponent, who assumes a pupal posture in an extreme submissive behavior

dinate tries to break free by shaking her body, in which case the dominant queen responds by lifting her opponent up, who assumes a typical pupal posture which is an extremely submissive behavior (Fig. 1 C). When released by her aggressor a subordinate queen may remain in pupal posture for some time before returning to her normal state. The aggression may resume, however, if her previous opponent is still nearby.

Subordinate ants were observed to assume a submissive posture at the simple approach of a dominant queen, no physical contact being required. In the proximity (ca. 3 cm) of a dominant queen, a subordinate ant retreats and lowers its antennae, remaining crouched for several minutes. On more than 30 occasions we observed this submissive behavior taking place even when the dominant ant approached from the rear of the subordinate.

Although queen-worker contests were less common than queen-queen ones, they followed the same behavioral pattern described above. The behavior of lifting up the opponent was particularly common during contests involving dominant dealated queens and winged females, with the latter assuming a pupal posture. Alate females were also observed having their wings seized and pulled from the rear by dominant dealated queens.

Table 1: Dominance order constructed from 394 records (100 h of observation) of agonistic interactions between queens of *Odontomachus chelifer*. The probability of a linear hierarchy occurring by chance is $p > 0.1$ ($K = 0.213$). Note that queen YGR was the most aggressive one, not being attacked by any ant. The last two columns in the matrix refer to aggression by queens toward alate females (ALA) and workers (WKR)

Dominant ants	Subordinate ants																
	YGR	BRE	GOR	GOL	WHI	SGO	YWH	GYE	SYE	SIL	RWH	GSI	GRE	RED	BLU	RGR	YEL
YGR	×	44	54	42	31	50	35		5	5			1	2	1		270
BRE		×	4	19	11	14	13	1	4		1			3			70
GOR			×	4	3			2	13		1						23
GOL				×	1		10	1	2			1	1				16
WHI					×				1	1					2		5
SGO						2	×				1	1					4
YWH				1				×	3								4
GYE									×						1		1
SYE										×							0
SIL											×						0
RWH												×					0
GSI													×				1
GRE														×			0
RED															×		0
BLU																×	0
RGR																	×
YEL																	×
Total	0	44	58	66	48	64	58	4	28	7	3	1	2	5	4	0	2
																	394
																	457
																	108

Queen Domination and Rank Order

Table 1 presents a dominance order based on 394 agonistic interactions between 17 queens of *Odontomachus chelifer* over 100 h of observation. Dominance contests involving any two queens belonging to the top group (YGR, BRE, GOR, GOL, WHI, SGO, YWH) comprised 86 % (338/394) of all the aggressive interactions observed between marked queens. Interactions involving at least one of the 7 queens in the top group comprised 99 % (392/394) of all the contests recorded. These queens were also the ones most frequently seen attacking both alate females and workers (only on three occasions did alate females and workers initiate an agonistic encounter with a marked dealated queen). Queen YGR was clearly the most dominant ant in the colony: besides participating in 69 % (270/394) of all the queen-queen contests recorded, queen YGR was never seen being attacked by any ant (Table 1). Although interacting aggressively with 11 queens

in the colony, queen YGR directed 95 % (256/270) of her attacks toward her most immediate subordinates in the hierarchical structure of the colony (BRE, GOR, GOL, WHI, SGO, YWH). Similarly, the second highest ranking queen (BRE) was never attacked by anybody except queen YGR; she aimed most of her attacks at her immediate subordinates (Table 1). Several queens interacted less than 5 times, and queen RGR was never observed to interact with another queen.

Table 2: Egg production, ovarian development and behavioral correlates in marked queens of *Odontomachus chelifer*. Dissections on queens were performed two weeks after the completion of the behavioral data (100 h of observation). Data on egg attendance, and presence of the queens in the foraging arena, are based on snapshot records (n = 106) of the colony. Vigorous unanswered antennations and/or mandibular strikes toward queens in the typical egg-laying posture or carrying a newly-laid egg were summed as "aggression toward egg-layers". +++ very conspicuous; ++ conspicuous; + weak; – very weak or absent; ? unknown or not visible. Compare with Table 1; see text for further details

Queen	No. of eggs laid	No. of clearly visible ovarioles	No. of mature yolky oocytes	No. of developing yolky oocytes	Aggression toward egg-layers	Times seen in arena	Attendance to eggs	Spermatheca	Fat body	Yellow body
YGR	8	15	10	5	16	6	56	filled	+++	+++
BRE	5	13	3	8	6	1	48	filled	++	+++
GOR	13	12	2	7	3	7	39	?	++	++
GOL	7	10	7	3	0	2	48	?	++	+++
WHI	8	11	4	0	1	3	40	?	++	++
SGO	8	15	5	6	4	1	40	filled	+++	+++
YWH	6	11	2	4	2	9	50	?	++	++
GYE	2	10	0	2	0	14	39	—	++	+
SYE	4	10	3	?	1	12	39	?	?	?
SIL	2	10	2	0	0	15	30	—	++	+
RWH	2	10	0	0	0	18	30	—	++	?
GSI	0	?	0	0	0	68	7	—	?	?
GRE	0	10	1	0	0	20	25	—	++	—
RED	0	10	0	1	0	17	40	—	++	—
BLU	0	10	1	0	0	8	48	—	++	+
RGR	0	10	0	1	0	9	34	—	++	—
YEL	0	10	0	0	0	17	19	—	+	—

Reproductive Activity and Ovarian Development

The results on egg production by individual *O. chelifer* queens during the course of our observations are summarized in Table 2. The queens belonging to the top group in the dominance order were also the ones laying the greatest number of eggs. The rank position of individual queens was significantly correlated with egg-laying activity (Spearman's $r_s = 0.91$; $p < 0.05$). Highly-ranked individuals, but particularly queen YGR, were more frequently seen exhibiting aggressive behavior toward egg-laying queens (Table 2). In such encounters a dominant queen antennates vigorously and/or attacks a subordinate egg-layer (which may be either in the typical egg-laying posture or carrying a newly-laid

egg). The aggression eventually escalates to mandibular strikes toward the subordinate's mandibles and clearly aims at destroying the newly-laid egg. Attacks by dominant queens toward subordinate egg-layers ($n = 33$) resulted in the consumption of newly-laid eggs by the aggressor on 12 occasions. The destruction of a newly-laid egg by an inspecting queen on an unattended egg pile was recorded once.

Several small egg piles were scattered among the nest tubes of the *Odontomachus chelifer* colony, and we were able to follow the development of workers and males out of some eggs. Most marked queens were each seen near an isolated pile of eggs (Table 2). Therefore, attendance to the eggs by a marked queen was not significantly correlated with her rank position (Spearman's $r_s = 0.51$; $p > 0.05$), as opposed to what was shown for *Pachycondyla* colonies whose eggs were all deposited on a single pile (OLIVEIRA & HÖLLDOBLER 1990, 1991; ITO & HIGASHI 1991). Snapshot records of the foraging arena, however, revealed that a queen's rank position was negatively correlated with foraging or patrolling activity outside the nest tubes (Spearman's $r_s = -0.70$; $p < 0.05$; see Table 2).

Table 3: Data on ovarian development of some of the alate females and workers of the colony of *Odontomachus chelifer* from which behavioral data were taken over 100 h. Dissections were performed two weeks after the behavioral observations. ++ conspicuous; + weak; — very weak or absent. See also Table 1

Ant	No. of clearly visible ovarioles	No. of mature oocytes	No. of developing oocytes	Fat body	Yellow body
Alate females					
1	12	1	3	++	+
2	11	0	4	++	+
3	10	3	0	++	+
4	10	2	4	++	+
5	10	1	2	++	+
6	10	1	0	++	+
Workers					
1	7	1	0	++	—
2	7	0	1	+	—
3	6	1	0	+	—
4	6	0	0	++	—
5	6	0	0	+	—

Two weeks after terminating the behavioral observations, all marked dealate queens, as well as a few workers and alate females, were dissected in order to assess the developmental stages of their ovaries. The results are presented in Tables 2 and 3. Dealate queens belonging to the top group in the dominance order were also the ones possessing the best developed ovaries, as expressed by a greater number of visible ovarioles as well as mature and developing oocytes (Table 2). As expected, the rank position of individual queens was significantly

correlated with the number of oocytes in the ovaries (Spearman's $r_s = 0.89$; $p < 0.05$). The presence of yellow bodies was also more conspicuous among highly ranked queens. Sperm was detected with certainty in the spermatheca of three of the queens (YGR, BRE and SGO) in the top group of the hierarchy. In five other highly ranked queens (GOR, GOL, WHI, YWH, SYE) we were not absolutely certain that the spermatheca contained sperm, because these queens had died before the dissections could be performed and some of the internal tissue was already decayed. In any case, the general pattern resulting from the behavioral and physiological data suggests that queen YGR is the highest-ranked individual within the hierarchical structure of the colony, showing greater aggressiveness toward rivals and better developed ovaries (Tables 1, 2).

The results from the dissections of a few alate females and workers of *O. chelifera* (Table 3) revealed differential development in their ovaries, as expressed by the variation in the number of detectable ovarioles and oocytes among the individuals. The presence of yellow bodies in their ovaries indicates that eggs had been produced. In fact, egg-laying by alate females ($n = 21$) and workers ($n \approx 130$) was recorded on 7 and 14 occasions, respectively. Worker eggs, however, were characteristically flaccid and more or less degenerate in form, and were given to queens as trophic eggs. Eggs of virgin queens were similar to those laid by inseminated queens. They were deposited on egg piles. This is remarkable because egg-laying by alate queens seems to have been rarely recorded in ants (HÖLLDOBLER & WILSON 1990).

Discussion

In the more advanced ant societies the reproductive dominance by the morphologically differentiated queen is usually maintained by inhibitory pheromones which prevent the ovarian development and egg-laying in worker nestmates (reviews in PASSERA 1984; FLETCHER & ROSS 1985; HÖLLDOBLER & BARTZ 1985; WHEELER 1986). In addition, reproductive division of labor mediated by stereotyped agonistic interactions among colony members has also been reported for several ant species. Aggression and reproductive dominance were shown to occur among workers (COLE 1981; FRANKS & SCOVELL 1983; BOURKE 1988; OLIVEIRA & HÖLLDOBLER 1990), gamergates (PEETERS & HIGASHI 1989; ITO & HIGASHI 1991), dealated virgin queens (WILSON & BROWN 1984; OLIVEIRA & HÖLLDOBLER 1991), and inseminated queens (FOWLER & ROBERTS 1983; HÖLLDOBLER & TAYLOR 1983; EVESHAM 1984; HÖLLDOBLER & CARLIN 1985; HEINZE 1990; HEINZE & SMITH 1990). The dominance order that is established among competing nestmates results ultimately in differential reproductive activity among them, with one or a few highly-ranked individuals laying most of the eggs. In most cases reported up to date domination results in the complete monopolization of reproduction, which leads either to secondary monogyny or functional monogyny. To our knowledge the current study of *O. chelifera* revealed the first case where a correlation has been demonstrated to exist between aggressive competition and fecundity in a truly polygynous species, in which differential reproductive success of individual queens occurs (e.g. WILSON 1974; MERCIER et

al. 1985 a, b; KELLER 1988; VAN VEEN & SOMMEIJER 1988; BOURKE 1991; SATOH 1991).

The displays observed among *O. chelifera* queens closely match what has been previously described for other ants which establish hierarchies based on behavioral domination (COLE 1981; HÖLLDOBLER & TAYLOR 1983; WILSON & BROWN 1984; HÖLLDOBLER & CARLIN 1985; OLIVEIRA & HÖLLDOBLER 1990, 1991; ITO & HIGASHI 1991). The long duration of the contests in *O. chelifera* (up to 15 min) and the behavior of lifting up a subordinate in pupal posture enhances the pattern of the dominance interactions in this species. Contrary to what was suggested by WILSON & BROWN (1984) for dealated queens of *Eurhopalothrix heliscata*, we found no evidence of physical damage being caused to the queens of *Odontomachus chelifera* as a result of the dominance contests. In the queenless ponerine ant *Diacamma australe*, physical mutilation of the bladder-like vestigial wings (now called gemmae, PEETERS & BILLEN 1991) was shown to be a mechanism of reproductive dominance whereby a gamergate (mated worker) prevents nestmates from mating and reproduction (PEETERS & HIGASHI 1989).

The fact that a subordinate queen of *O. chelifera* will assume a submissive posture at the approach of a dominant nestmate suggests that chemical and/or vibrational cues may also play a role in the establishment of the hierarchy within the colony. Indeed, the possibility of pheromonal signals released by the high ranking queens is strengthened by the fact that subordinate ants behave submissively when dominant ones approach them from the rear. Similar observations are reported by HEINZE & ORTIUS (1991) for *Leptothorax acervorum*.

The consumption of one another's eggs has been demonstrated to be an indicator of reproductive rivalry among nestmates, and has been reported for ants (e.g. WILSON 1974; OLIVEIRA & HÖLLDOBLER 1990, 1991), wasps (WEST-EBERHARD 1969) and bees (RATNIEKS & VISSCHER 1989). Here we show that aggression toward egg-laying queens is a conspicuous part of the reproductive dominance behavior in the *O. chelifera* colony. Since this behavior was clearly most frequently exhibited by highly-ranked *O. chelifera* queens (particularly YGR) and resulted in the destruction of some newly-laid eggs, it probably enhances the differential net production of eggs by differently-ranked individuals, as demonstrated elsewhere for *Pachycondyla* ants (OLIVEIRA & HÖLLDOBLER 1990) and *Polistes* wasps (WEST-EBERHARD 1969). We have not seen *O. chelifera* queens deposit newly-laid eggs on a principal egg pile. Instead, the eggs were scattered among several small piles within several nest tubes and individual queens of *O. chelifera* were usually seen attending and transporting isolated egg piles. In *Pachycondyla obscuricornis* the shuffling and guarding of newly-laid eggs on a communal egg pile has been suggested to play a protective function in situations where the destruction of one another's eggs is associated with reproductive competition among nestmates (see OLIVEIRA & HÖLLDOBLER 1990, 1991). Egg-shuffling was not observed in the *O. chelifera* colony, but the peculiar situation of multiple egg piles may suggest an extreme case of egg-guarding in which individual queens would temporarily protect their own fresh eggs against destruction by competing nestmates. In fact, on six different occasions we recorded egg-laying queens picking up an isolated pile right after having deposited an egg on it;

the pile was guarded and transported between her mandibles for some time. The protective function of this behavior against egg destruction by rivals, however, needs further experimental investigation.

Our results on *Odontomachus* complement those obtained elsewhere for other Ponerinae (PEETERS & HIGASHI 1989; OLIVEIRA & HÖLLDOBLER 1990, 1991; ITO & HIGASHI 1991), and confirm the relevance of behavioral domination for the social organization within colonies of phylogenetically more primitive ant taxa. This type of social structure can be regarded as an ancestral trait, and additional investigation on the reproductive division of labor in phylogenetically primitive taxa may cast further light on the evolution of eusociality in ants.

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