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Semi-claustral colony foundation in the formicine ants of the genus *Polyrhachis* (Hymenoptera: Formicidae)

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Summary

Polyrhachis laboriosa and *P. militaris* are two tree-inhabiting ant species, belonging to the subgenus *Myrma* common in Cameroon forest. While *P. laboriosa* live on pioneer trees on the edge of forest tracks, *P. militaris* inhabit dense equatorial forest. Foundation of societies is independent in these two species. Founding queens of *P. laboriosa* made small cells under leaves, while foundresses of *P. militaris* made cells in soil, hollowed dead branches, or old termitaria. The queens left their cells daily to forage. They collected water, sugared juices, and prey. They were also observed "grazing" the surface of leaves. *P. laboriosa* queens also collected vegetal matter which was then used to build their founding cells under leaves. This behavior was observed in both the field and the laboratory. This article is the first description of semi-claustral foundation in a formicine ant. It may be related to the fact that these ants are protected from predators by mandrels (hooks) on the thorax and the petiole. Bright yellow coloration of the gaster may also serve as an aposematic warning signal for potential predators. Prey capture was studied in the two species by offering both small (isolated or in group) and large prey to the foundresses. Hunting behavior of *Polyrhachis* queens was similar to that of workers, and was identical in the two species.

Introduction

In Cameroon we studied two tree-inhabiting *Polyrhachis* species: *P. laboriosa* F. Smith and *P. militaris* (Fabricius) (see Bolton, 1973). The nests of *P. laboriosa* are generally built between two living leaves connected with fibers of vegetal origin. Contrarily to reports by Ledoux (1958), of the larvae of this species were not seen weaving the nest, like *Oecophylla*. *P. militaris* nest in treetops, branch bifurcations, and organic matter at the base of epiphytes. It was commonplace in the forest to observe dealated females of these two species foraging on the surface of the ground or on leaves. Since these observations were so frequent, we could hypothesize that these queens were foundresses leaving their cells to forage, and that foundation was semiclaustral in these species. As semi-claustral foundation is considered to be the most primitive form of foundation, and so far it is not known in the formicine ants

(Hölldobler and Wilson, 1977, 1990), we decided to study this aspect of *Polyrhachis* biology more closely.

Material and methods

All observations took place in Cameroon between November 1987 and December 1991 at five sites: Ndupé forest; a track between Matomb and Pan Pan (respectively 125 km and 65 km from Yaoundé in the direction of Douala); Ottotomo forest (50 km South of Yaoundé); Ebodjié forest (near Campo); and the campus of the Yaoundé University. *P. laboriosa* lives in the forest on the border of tracks and inhabit pioneer trees or shrubs which have numerous nectaries: e.g., *Alchornea cordifolia* (Euphorbiaceae), *Macaranga* (ibid), and *Albizia zygia* (Mimosaceae). *P. militaris* live in dense equatorial forest in the tops of high trees. They were observed mainly in Ndupé, Ottotomo, and Ebodjié.

For laboratory experiments, dealated females or young societies collected in the field were placed in artificial nests made of a glass tube (20 cm length, 4.5 cm diameter). The closed end of each tube was filled with water plugged with cotton to provide humidity and wrapped in black paper to assure darkness. The tubes were left open to leave the females free to forage in the laboratory. 31 *P. laboriosa* and 8 *P. militaris* queens were reared in these conditions. Some of the females left their tubes after a few days and moved to another more suitable place: a crevice in the wall or in the furniture; or a tree branch hollowed by xylophages. A small *Alchornea cordifolia* plant was available in one of the rooms to provide nectar. All the ants were completely free to move their nest and to forage everywhere. The main problem was their predation by Salticidae spiders and accidental death provoked by people entering the laboratory. At certain sites we regularly provided water, sugar containing liquid, and vegetal fibers (cotton or palm cotton). Each female was observed daily for at least one month.

The predatory behavior of these queens was studied by offering them dead insects of various species. Observations were made according to the method of Dejean (1980). During each attempt at prey capture, the sequence of acts and the respective position of the ant and its prey were recorded.

Statistics. The data were analyzed by calculating frequency distributions, and by comparing them with the Chi square test.

Results

The foundation of the societies in the field:

At Yaoundé alate *Polyrhachis* females were captured regularly in small quantities during the morning in November–December (for *P. laboriosa* 3 captures in 1988, 4 in 1989 and 4 in 1990; for *P. militaris* a single capture in 1990). At Ebodjié 6 alate females of *P. militaris* were captured using a UV lamp, and one was observed on the ground in November and December 1991. As large nuptial flights were never

observed, we assume they may be nocturnal in these species, but this has to be confirmed. In the laboratory one nuptial flight of *P. laboriosa* was observed in June 1990 at midnight (6 females and 5 males), and later dealate females foraged on the ground. Burnat and Godzinska (pers. comm.) observed two nuptial flights in a captive colony of *P. laboriosa* kept in the laboratory in Warsaw: on 8 December (13 females and 5 males) and on 11 December 1991 (3 females and 2 males). Both flights took place in the morning; while the nest was kept in near darkness (less than 2 lux of daylight). In the first case, exposure to daylight of about 140 lux stopped the flying activity of alates within 1 hour. In the second case, the ants were exposed to artificial white light of 3000 lux, which stopped their flying activity within a few minutes.

29 foundations were collected in the field and sampled. They were found during the period October to February. All of the 18 foundations of *P. laboriosa* were found under leaves: 9 on *Alchornea cordifolia;* 5 on *Macaranga sp.* (two Euphorbiaceae); 3 on *Jateoriza macrantha* (Menispermaceae); and one on an undetermined shrub. All the nests were made of vegetal matter forming a small dome with a hole. Two foundations contained two associated queens, indicating that pleometrosis could be possible in that species, at least part of the time. The foundations of *P. militaris* (in total 11) were collected either on the ground (2 in dead wood and 3 in a *Cubitermes fungifaber* termitarium) or on trees (2 in hollowed dead wood on the trees, 2 under a *Platycerium* epiphyte, and 2 in a palm crown at the basis of petioles). One foundation was also discovered in a small chamber in the soil, but it was not sampled. Isolated females were found during three months, from October to December, indicating that swarming occurs during a relatively long period. The first cocoons appear at the end of November, and the workers in February. These data should be considered only as indicative because more sampling is necessary to have a complete view of the timing of foundations in the field.

Development of young societies in the laboratory:

Three *P. laboriosa* females collected after nuptial flight were observed for four months. The first egg appeared 4 or 5 days after collection. After three weeks the society contained about ten eggs. The first larvae appeared one week later and ate the majority of the eggs. The first cocoons appeared after 7 weeks, and the first worker after 10 weeks. After 3.5 months the society had 4 or 5 workers, and the first worker started to forage. A few days later the queen stopped foraging and from then on she stayed permanently in the nest. In the case of *P. militaris*, only one female was observed, and the development of the society was identical.

Daily pattern of foraging:

In the forest, foraging (observed during the period October to the end of January) occurred mainly during the morning until 10 or 11 a.m. ($n > 100$). *P. militaris* females were sometimes seen after noon, but not as a rule.

In the laboratory all the females, except one *P. militaris*, were mainly active in the morning, generally until 10 or 11 a.m., but sometimes until 2 or 3 p.m. Some females did not forage every day and stayed inside their nests for a few days. 14 *P. laboriosa*

queens were also active at sunset (18 h–18 h 30) on some days. It was the only activity period for one exceptional *P. militaris* female.

Retrieval of vegetal fibers and other building material:

In the field, the females of *P. laboriosa* retrieved various material (blades of grass, vegetal fiber, feather, silk of old moth cocoon) which was used to build their cells under leaves. *P. militaris* females nested in small cavities in wood or in soil and they closed them. Hence they did not need to transport building material.

In the laboratory all the females of *P. laboriosa* started to build immediately during the first day of semi-captivity. They used any material which could be torn to pieces: dry leaves, cotton, paper, moth cocoons, string, sponge, feathers... Cotton of the oil palm tree *(Elaeis guinensis)* was very attractive for the foundresses: they extracted its fibers with coordinated movements of the mandibles and the forelegs. The cotton was held between the other four legs and the gaster. Finally, a ball was made and held in the mandibles for transport (n = 80). The size of the ball was very variable, up to 10 mm in diameter. In the laboratory, females of *P. militaris* only closed their cells, using cotton, paper, or wood fibers.

Water provisioning:

Water retrieval by the females of the two studied species was observed in the field. This phenomenon was observed only twice in *P. militaris*, but it was very frequent in *P. laboriosa*. It occurred during the entire period of foundress foraging, but it is typical for the dry season (from the end of December to the end of February). During the morning the females foraged on the surface of leaves where they licked the dew. Foraging for water stopped at 9 h–9 h 30, 10 h 30 in shaded places.

In the laboratory, the females of both studied species behaved in the same way, they searched for wet places. One *P. militaris* female made 15 trips to retrieve water during a single day.

Sugared juice provisioning:

In the field, the females of *Polyrhachis* were frequently observed collecting nectar from extrafloral nectaries of various trees and shrubs (mostly *Alchornea cordifolia* for *P. laboriosa*). Sometimes they were observed on the leaves just under groups of Homoptera, licking the falling honeydew. Such behavior, sometimes called "grazing", was observed close to the following plant/plant lice associations: *Chromolaena odorata* (Composaceae)/*Aphis citricola*, *Bridelia micrantha* (Euphorbiaceae)/Coccidae. Direct exploitation of honeydew was never observed. *P. militaris* female were observed twice licking a fruit (once an undetermined fruit and once a fruit of the parasol tree *Msusanga cecropioides*). In the laboratory, *Polyrhachis* queens were also observed drinking the nectar of *Alchornea cordifolia* leaves which were collected for them daily, and licking honey and fruits.

Table 1. Number of observations of *Polyrhachis* foundresses retrieving prey in the field

Prey	*P. laboriosa*	*P. militaris*
Interdeterminate	1	18
Arthropod parts	2	19
Termite workers	8	4
Caterpillars		
– < 10 mm	7	10
– > 10 mm	2	1
Tettigonidae		
– < 10 mm	7	1
– > 10 mm	1	–
Acrididae < 10 mm	1	1
Grillidae	–	1
Heteroptera	1	–
Blattidae	–	3
Diptera	5	22
Coleoptera (larva)	1	5
Formicidae (male)	1	–
Total	37	85

"Grazing" of leaves and substratum:

In the field, the dealated females of the two species were frequently seen "grazing" the surface of leaves ($n > 15$). In the laboratory, they showed the same behavior towards fresh leaves. They also lick places where insects had been crushed. "Grazing" was a very frequent activity of *Polyrhachis* workers, but less frequent in the case of queens.

Prey provisioning:

Numerous observations were made of a female returning to its nest with a prey (Table 1).

Predatory behavior:

In the laboratory, we investigated predatory behavior of the *Polyrhachis* queens by offering them isolated or grouped prey. The queens proved capable of attacking prey of various size, including large orthopterans (Tettigonidae) up to 30 mm of length.

As a rule, prey was detected by queens at a distance of 3 to 10 mm from the apex of their antennae, followed by antennal contact (Figs. 1, 2). Sometimes prey was also detected accidentally by direct contact (DC). Large prey (more than 10 mm long) was always (in 100% of the cases) detected from some distance (Fig. 2B, C, D). In contrast, only 73.7% (*P. laboriosa*) and 85.3% (*P. militaris*) of small prey (less than 10 mm) was detected at distance. The difference related to the prey size was significant for *P. laboriosa* ($X^2 = 28.9$, $P \ll 0.001$), but not for *P. militaris* ($X^2 = 2.5$, NS). This may indicate that *P. militaris* is a more efficient hunter than *P. laboriosa*. Sometimes the prey was abandoned. This tendency dependend on prey size. Very

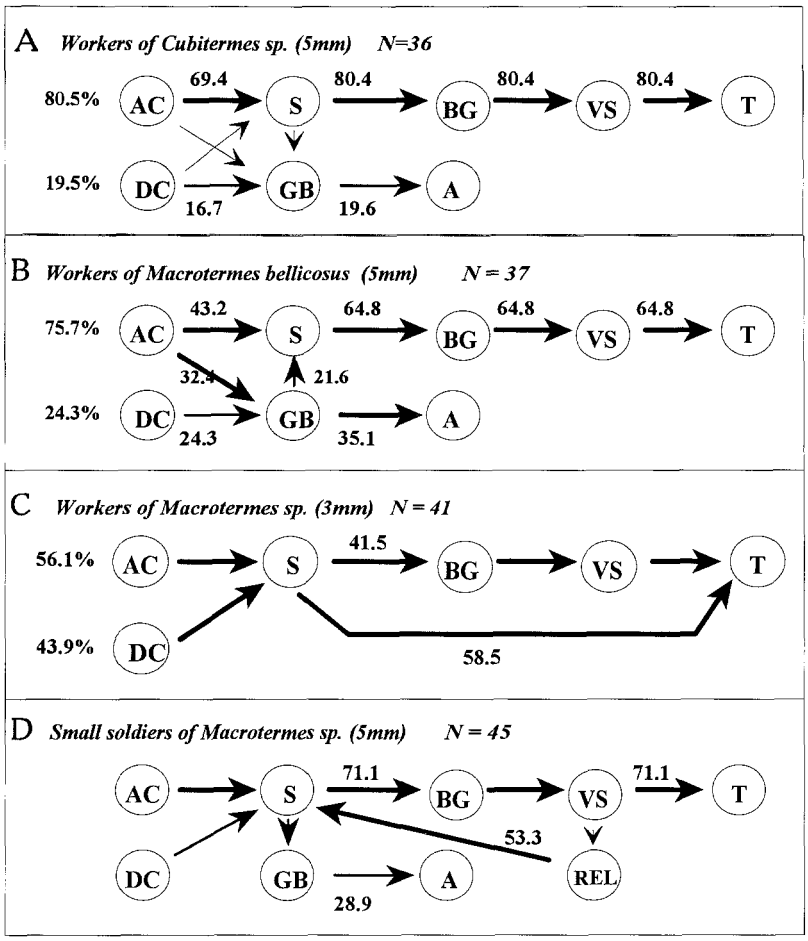

Figure 1. Predatory behavior of founding *Polyrhachis laboriosa* queens towards isolated termite prey. AC = antennal contact, DC = detection by contact, S = seizure, GB = going back, VS = venom spraying, A = abandonment, T = Transport, REL = release of the prey

small prey (3 mm long *Macrotermes* workers and small Tettigonidae) were never abandoned (Fig. 1 C). In contrast, 5 mm long termite workers were not very attractive: 19.6%, 35.1% and 28.9% of them were abandoned (Fig. 1 A, B, D). Very large prey (such as the 22 mm Tettigonidae) were abandoned very frequently (in 56% of the cases – Fig. 2 D) compared with 13.8% *(P. laboriosa)* and 12.5% *(P. militaris)* for small preys; the percentages increased with prey size (> 22 mm: 48%). The difference between small and large prey was highly significant ($X^2 = 16.9$, $P < 0.001$). This indicates that *Polyrhachis* queens prefer easily transportable prey. Different attractiveness of termites and Tettigonidae of similar size may be related to the composition of insect fauna available for a predator in the trees. In that habitat, termites are rare, but grasshoppers are common.

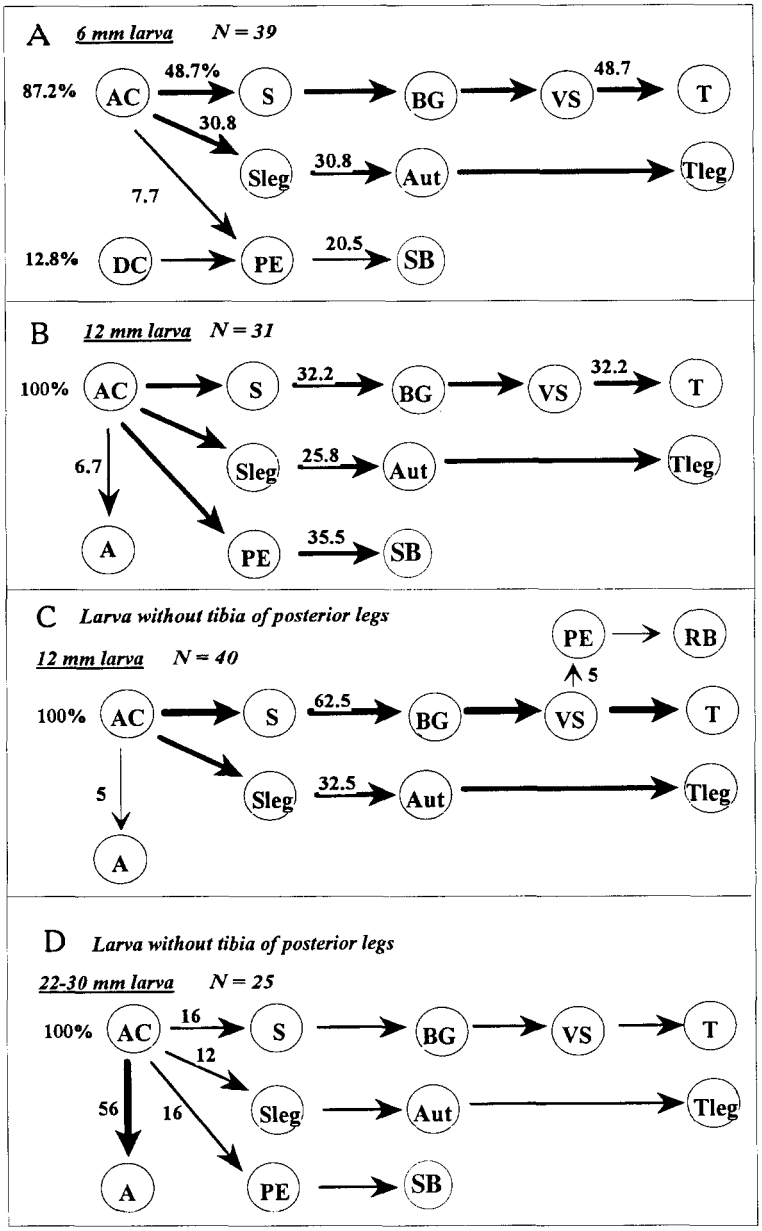

Figure 2. Predatory behavior of founding *Polyrhachis laboriosa* queens towards isolated Tettigonidae prey. Sleg = Seizure of the posterior leg, PE = Prey Escape, Aut = Autotomy of the sized leg, SB = Searching Behavior. See Fig. 1 for other abbreviations

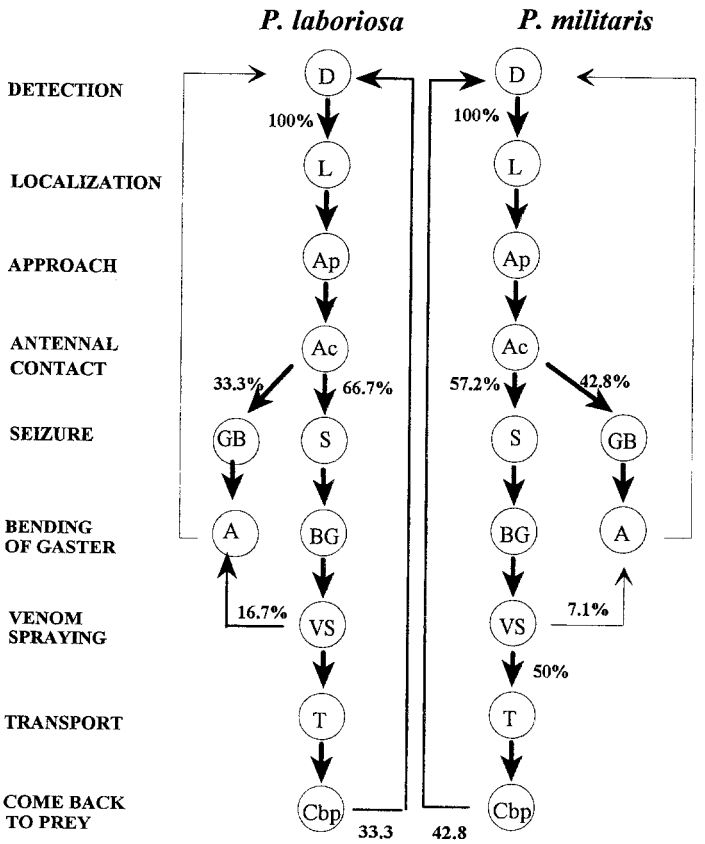

Figure 3. Predatory behavior of *P. laboriosa* and *P. militaris* queens toward 5 grouped workers of *Macrotermes bellicosus*. A = abandon, GB = going back

In the Tettigonidae, the seizure of a posterior leg was generally followed by reflex autotomy (Fig. 2). In such a case the ant retrieve the leg to its nest and the prey was safe; it could jump and escape. The escape of the prey was followed by a particular searching behavior of the queen: she moved quickly along a sinuous trajectory, with spread antennae and open mandibles (Fig. 2 A, B, D). This behavior was different from the exploratory behavior of these ants. Such behavior has already been described and is called "reserve behavior" in other predatory ants by Dejean (1988).

When the prey was provided in groups of 5, hunting behavior of the *Polyrhachis* queens was similar (Fig. 3). In some cases the queen killed two prey successively, transported the second prey and came back to retrieve the first one. Some queens made up to 6 or 8 trips in one hour.

Discussion

Independent foundation with partial claustration is not rare in some ant subfamilies. It is frequent in the Myrmeciinae and most of the Ponerinae have adopted this type of

foundation. It also exists in some Myrmicinae (see reviews by Wilson, 1971; Dumpert, 1981; Lachaud and Dejean, 1991). In all these species foraging involves prey capture. In contrast, semi-claustral foundation is not known in the Formicinae (Lenoir et al., 1988). Hence, it seems that our field and laboratory observations of the semi-claustral foundation in two species of *Polyrhachis* are the first observations of this phenomenon in formicine ants. We would like to stress that *P. laboriosa* and *P. militaris* are both of the subgenus *Myrma*, of which very little is known. Even though the presence of "silk" has been seen in some species of this subgenus, all known truly weaving species belong to the other subgenera (see Ofer, 1970; Yamauchi et al., 1987; Dorow et al., 1990; Yi and Jue, 1990). Semi-claustral foundation and the absence of larval weaving seem to be associated with the subgenus *Myrma*.

In *Polyrhachis*, semi-claustral foundation of societies might be favored by the presence of powerful hooks (mandrels) on the thorax and the petiole of these ants. The efficiency of these antipredatory defense weapons has not been investigated directly, but it seems reasonable to suppose that the presence of mandrels may play a role in protecting foraging foundresses from predators (Dumpert, 1981). Thus, the evolution of the mandrels may act as a factor stabilizing the semi-claustral foundation of societies in *Polyrhachis*. These ants also posses striking yellow pilosity on the gaster (Bolton, 1973), which may be aposematic. The aposematic coloration may also have enhanced the semi-claustral foundation of the queens, protecting foraging foundresses through its warning effect on potential predators (see Guilford, 1990). We must note, however, that some worker specimens of various species of *Polyrhachis* are known only from samples collected from frog stomachs (Wheeler, 1922). All these ants were workers, and they might have been eaten at night when their aposematic coloration no longer protected them. Queens never forage at night!

Queen foraging involves prey capture in all known species with semi-claustral foundation. In both *Polyrhachis* species we studied, foraging also involved predation. We observed that predatory behavior of the queens is similar to that of their workers (Dejean et al., in prep.). This study also provides the first report of the particular searching behavior in ant queens after the escape of the prey.

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Note of proof:
semi-claustral foundation has been recorded once in *Cataglyphis niger* (Fridman S. and Avital E., 1983, Foraging by queens of *Cataglyphis bicolor nigra* (Hymenoptera: Formicidae): an unusual phenomenon among the Formicinae. *Israel J. Zool. 32*: 229–230). This observation has never been confirmed (see for discussion Lenoir et al., 1988).