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# Polyethism in the Ponerine Ant *Odontomachus troglodytes*: Interaction of Age and Interindividual Variability

by

Alain Dejean<sup>1,2</sup> & Jean-Paul Lachaud<sup>3,4</sup>

## ABSTRACT

Data from ten *Odontomachus troglodytes* colonies artificially formed, each with one queen, 30 workers and abundant brood, enabled us to study the successive tasks performed by 91 workers from emergence until 7 weeks-old. The principal stages of ethogenesis in *O. troglodytes* were: inactivity, care of eggs, care of larvae and pupae, intermediate activities (nursing + cleaning + construction + necrophoric activity), and finally specialization in activities outside the nest.

This age polyethism was characterized by great interindividual variability. At each stage we found that some workers were very active but others were much less so. Workers of the same age could develop different subspecializations: among nurses some become receivers of honey droplets, whilst workers carrying out intermediate activities could specialize in construction or necrophoric activities, and some workers outside the nest specialized as hunters. Furthermore, some workers even remained as "inactives", "nurses" or "intermediates" all their life.

The percentage of 35 day old workers involved in outside activities is nearly that found in colonies composed of mature adults. As in these latter colonies, foragers are subdivided into weakly specialized foragers and efficient hunters. The fact of performing guarding behavior at nest entrance and the evolution of aggressiveness linked to this function appear as the basic factors involved in the predatory behavior ontogenesis.

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## INTRODUCTION

Polyethism in eusocial insects is based on three main factors: polymorphism, age and individual variability (Wilson, 1971). Most species of ponerine ants have monomorphic workers, although *Megaponera foetens* (Arnold, 1915; Van Boven, 1970), *Pachycondyla* (= *Termitopone*) *laevigata*, *P.* (= *T.*) *marginata* (Wheeler, 1936) and sometimes *Brachyponera senaarensis* (Dejean *et al.*, 1990) are exceptions. In the Ponerinae, therefore, only age and individual variability can influence the division of labor (Lachaud and Fresneau, 1987a; Jaisson *et al.*, 1988).

Age polyethism, in which each worker passes through different behavioral specializations as it ages, has been particularly well studied in the subfamilies considered most highly evolved: Myrmicinae (Weir, 1958a, b; Wilson, 1976; Smeeton, 1982; Calabi *et al.*, 1983; Dejean, 1985), Dolichoderinae (Lenoir, 1979a), and Formicinae (Otto, 1958; Lenoir, 1979b). In all cases, the main role of the youngest workers is brood care. Older workers, having passed through several stages, become foragers outside the nest.

Among ants, age polyethism is a widespread phenomenon. With the apparent (and unclear, see Lachaud *et al.*, 1988) exception of *Amblyopone pallipes* (Traniello, 1978), it is found in all ponerine species in which it was looked for (Colombel, 1969; Bonavita and Poveda, 1970; Fresneau and Lachaud, 1984; Corbara *et al.*, 1987; Dejean *et al.*, 1990). However, very detailed studies embracing both age polyethism and the added dimension of social behavior ontogeny have only been made on *Ectatomma tuberculatum* (Champalbert and Lachaud, 1990; Dejean *et al.*, 1989) considered one of the more evolved ponerines (Brown, 1958; Fresneau *et al.*, 1982).

In this work, we propose to study age polyethism in another highly evolved ponerine (Brown, 1976; Lachaud and Dejean, 1990): *Odontomachus troglodytes*. The general biology of this species is well known (Colombel, 1969) as is the predation behavior (Dejean and Bashingwa, 1985; Dejean, 1988) and carbohydrate collection behavior (Lachaud and Dejean, 1990) of adults. Our main aim is an investigation of ethogenesis and the factors determining predation behavior.

## METHODS

Worker ants of the genus *Odontomachus* are characterized by long and powerful mandibles that can open to  $180^\circ$  (Fig. 1). During exploration these mandibles are held fully open whereas in the nest they are kept closed. When capturing prey the mandibles are closed suddenly through the operation of a trap-jaw mechanism. The same phenomenon occurs if the ants are highly excited. In some cases, the shock occurring during mandibles closure on the substrate propels the workers backwards. These shocks are the origin of the name "tic-ants" given to *Odontomachus* spp. (Brown, 1976).

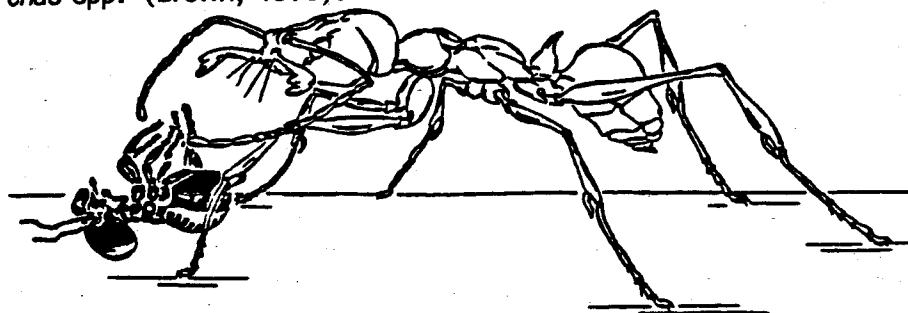


Fig. 1. *Odontomachus troglodytes* predatory behavior. A worker, mandibles wide open, is antennating a dead termite. Sudden closure of the mandibles is released when the bristles on their inner margins come in contact with the prey.

*Odontomachus troglodytes* is common in anthropogenic habitats, on the forest edge, or along the edges of paths. Most colonies contain fewer than 1000 workers (Colombel, 1969). The foragers hunt both underground and on the surface. Their main prey are termites (Dejean and Bashingwa, 1985) but they may also collect liquids largely sugary like honeydew and juices extruding from fruits or from extrafloral nectaries (Evans and Leston, 1971; Lachaud and Dejean, 1990).

Our study was carried out in Kikwit (Bandundu Region, Zaire), on 10 colonies whose original composition was artificially limited to one queen, 30 workers, 20 pupae, 30 larvae and numerous eggs. The ratio of larvae to workers was set at 1:1. After three weeks, the colonies produce numerous young larvae. Over the same period, workers progressively emerged from the pupae present initially, maintaining the minimum worker:larvae ratio at 1:1.

The colonies were reared in artificial nests of the Chauvin type. A test tube of 2.5x22cm, the bottom serving as a drinking trough, opened onto a foraging arena of 20x30cm. Each colony was fed five times a week with honey, termites and grasshoppers (either whole or cut into pieces). The amount of food provided was adjusted so that none of the food or very little remained unconsumed.

The workers were individually marked with Enamel paint and coded so that the original workers could be immediately distinguished from those that emerged in the artificial nests. Newly emerged workers are translucent and were marked only after their cuticle had hardened.

Observations were made on each colony for seven weeks between January and April.

#### Developmental stages in age polyethism

This analysis takes into account data from mature workers present in the nest at the beginning of the study (Lot I) and callow workers from the total of 200 pupae initially present in the experimental nests (Lot II).

The workers' behavior was checked between three and seven times each week. On the basis of its behavior, each worker was assigned to one of the six behavioral sub-castes defined below:

##### Inside the nest

- Inactives: Their predominant characteristic is their inactivity. They feed themselves on prey and honey. Receive honey through pseudotrophallactic exchanges. Groom themselves. Receive grooming from nestmates but rarely return it.

- Nurses: Their behavior is mainly brood orientated, involving antennation, manipulation and transport, licking and feeding. Grooming nestmates is frequent. The activities described for inactives occur sporadically.

- Cleaners: Predominantly occupied in cleaning activities in the nest. They occasionally participate in brood care but merely by resting near the brood.

##### Mixed activities

- Intermediates: Involved in tasks inside and outside the nest. Carry dead nestmates out of the nest (necrophoric behavior) and similarly dispose of prey remains and cotton wool from the drinking trough. Build screens of prey and cocoons remains to

block light filtering into the nest (construction activity). Act as "guards" at the nest entrance.

#### Outside the nest

- Preforagers: Explore the foraging area but do not collect honey. Appear very timid and easily frightened. Recoil and flee when they encounter prey. Are often transported back towards the nest by foragers that encounter them in the foraging area.

- Foragers: Collect and transport honey between the mandibles. Scavenge for the remains of dead insects. Hunt and capture living prey.

#### Ontogenesis of the hunting behavior

Because of our particular interest in the development of predatory behavior in *O. troglodytes* workers, we analyzed the behavioral modifications that occurred as ants passed through the stages defined above.

The aggressiveness of workers at the nest entrance was tested in the 10 experimental colonies. A worker termite, *Cubitermes* (about 5mm long) mounted on a copper wire attached to the handle of a thin paint brush, was lowered a few millimeters in front on the ants. Aggressiveness in other situations was tested in three colonies used for foraging studies. In these cases a *Cubitermes* worker was lowered in the same way in front of ants at more than 40cm from the nest in the 110x110cm foraging arenas used with these three colonies. Similar tests were also carried out on ants inside the nests of these colonies by removing the lids of the plastic boxes containing their nests.

Worker responses were classified as:

- a) escape
- b) no reaction
- c) aggressiveness (closure of the mandibles propelling the worker backwards or simply opening of the mandibles inside the nest)
- d) attack (closure of the mandibles and seizure of prey)
- e) attack with use of the sting

## RESULTS

### Social organization of mature workers (Lot I)

When the colonies were originally collected in the field, most

of the workers normally performing outside activities were out foraging. The 30 workers removed at random from each field colony to form the experimental colonies, therefore, were mainly those working inside the nest and performing inside and mixed activities. The experimental colonies were therefore in a phase of social regulation necessitated by the need to replace the foraging workers. In *Pachycondyla* (= *Neoponera*) *apicalis* (Lachaud and Fresneau, 1987b) and in *O. troglodytes* (= *O. haematodes*) (Colombel, 1969) social regulation of this type can restore the proportions of workers engaged in each task within a week, that is, without a great increase in the total number of workers.

To establish a reference point for our study we therefore recorded the proportions of workers in each behavioral sub-class after one week of laboratory maintenance. These figures defined the structure characteristic of mature *O. troglodytes* colonies.

There was very little variation between the ten experimental colonies as experimental conditions were relatively homogeneous. We have therefore analyzed the data from the workers in all ten colonies as a whole rather than calculating mean values for each colony.

After one week of laboratory maintenance, the organization of the experimental colonies was similar (see Colombel, 1969) to that of undisturbed mature colonies. The brood was separately stocked: eggs piled together, most larvae clinging to the inner wall of the tube by their dorsal hairs, and pupae in a group distant from the drinking trough.

The queen occasionally participated in brood care but, unlike what is normal in more evolved ant genera, also made excursions outside the nest. She was recorded in the foraging arena on 35 observations made over the seven weeks of the experiment and, on six occasions, a queen was observed scavenging fragments of dead insects. In the laboratory, in addition to provisioning the nest with prey, workers also forage for honey. The honey is either consumed by the forager or brought back to the nest in droplets held between the forager's mandibles. As is common in ponerines (Hölldobler, 1985), honey is distributed inside the nest by pseudotrophallactic exchange among nestmates frequently having first been passed from the forager to a worker that acts as a receiver or "receptionist worker" for honey (see Lachaud and Dejean, 1990). The droplets of honey may also be stored on the walls

of the nest galleries and are then fed upon by workers as the need arises.

Workers involved in construction activities may occasionally gather honey or fragments of dead insects (12 observations). They were never observed to capture prey, however.

The 300 workers in the experimental nests at the beginning of the study were distributed as follows (Fig. 2):

- . 12 (4%)inactives
- . 138 (46%)nurses + cleaners
- . 67 (22.3%)intermediates
- . 53 (17.7%)workers gathering sugary substances and prey
- . 30 (10%)hunters that rarely stop near honey

Thus, of the original 300 workers in Lot I, 83 were recorded as foragers one week after the start of the experiment. This

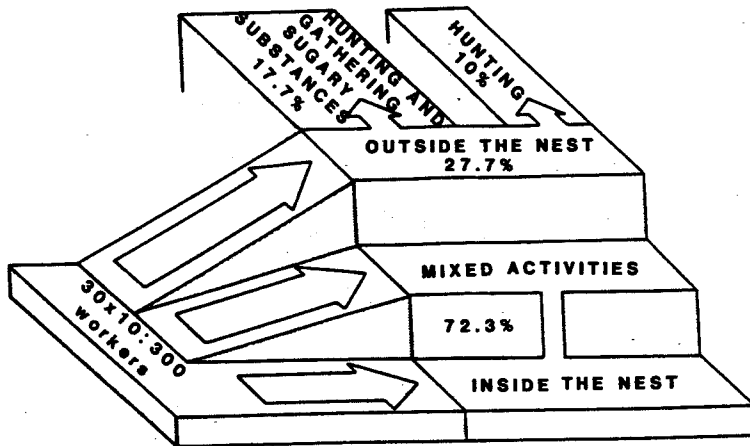


Fig. 2. Distribution of 300 *Odontomachus troglodytes* adult workers (lot I, see text) among the three main behavioral categories (activities inside the nest, mixed activities, or activities outside the nest), one week after installation in artificial nests.

number varied very little later on, and only decreased as the older workers died. After the first week, few ants changed from working inside the nest to working outside it: only 14 cases were recorded in the period extending from the 3rd to the 6th week.

#### Ontogenesis of social behavior in workers (Lot II)

One alate female and 91 workers emerged from the 200 pupae initially present in the experimental nests.



Table 1: Age polyethism and interindividual variability influences on the distribution among behavioral sub-castes of *Odontomachus troglodytes* callow workers (Lot II). For each one, the number of workers is expressed as a percentage of the original total number of callow workers.

Behavioral sub-castes	Behavioral categories (activity)	Number of day after emergence						
		1st-4th	5th	11th	16th	20th	35th	48th
inactive	in nest	100	81.3	29.7	20.9	12.1	10.0	10.1
nursing	in nest		18.7	70.3	73.6	59.3	40.0	40.4
nursing + necrophoric behavior	mixed				2.2	5.5	1.1	0.0
idem + construction	mixed				1.1	13.2	20.0	20.2
guarding behavior	mixed				2.2	4.4	0.0	0.0
preforaging	outside nest					5.5	0.0	0.0
foraging	outside nest						22.2	18.0
hunting	outside nest						6.6	11.2
Total number of workers		91	91	91	91	91	90	89

Callow workers were brownish, only becoming black with the development of full pigmentation after a week. During the first four days after emergence all the workers remain inactive (Table 1 and Fig. 3). They moved about very little and were very timid. Their status is almost that of the brood.

After five days, the young workers began to move around the nest. They usually took up station above the pile of eggs. Those that approached the nest entrance were transported back by nurses and dropped near the brood. Some of these workers (18.7%) began to antennate and manipulate larval brood. By day 11 after emergence, 70.4% of workers had participated in brood care activities.

From day 12 onwards behavioral differentiation was increasingly evident as ants took up first mixed activities and then activities outside the nest.

- Day 12: first cleaning in the nest

- Day 14: first observation of a worker leaving the nest to throw prey remains near the nest entrance (necrophoresis)
- Day 15: first participation in construction activities (building a cover obstructing the nest entrance)
- Day 16: first guarding behavior
- Day 17: first preforaging behavior
- Day 19: from this age onwards workers (initially classified as preforagers) were observed to consume honey and the haemolymph oozing from prey fragments
- Day 21: first occurrence of scavenging (pieces of grasshopper) by a 2-day preforaging worker
- Day 22: first attempts to gather sugary liquids with the mandibles (see Lachaud and Dejean, 1990)
- Day 23: first capture of a living termite

Under the conditions of our experiments, the shift from one behavioral sub-caste to another slowed down considerably after day 35.

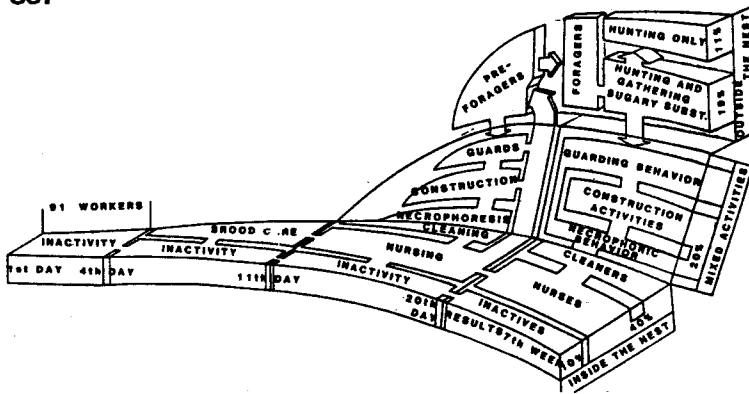


Fig. 3. Age polyethism and changes in the distribution of 91 callow workers (lot II, see text) among the various behavioral sub-castes during the seven weeks of the experiment.

Besides this general sketch accounting for age polyethism, there was considerable variability between individual ants in the age at which they took up particular behaviors as shown by the differences in the successive distributions of workers among the various behavioral categories and their specialization on different subfunctions (Table 1 and Fig. 3).

Activities inside the nest. All 91 workers in Lot II passed through this stage and 45 (49.5%) remained at it. Of these 45, 9 workers remained inactive for all seven weeks of the experiment. The ontogenesis of social behavior in all 82 (90.1%) workers that ever took any part in a task, started with brood care: initially care of eggs, then care of larvae. Of these 82 workers, 15 were never observed to care for pupae, whereas some others frequently were. Concurrently with brood care, many workers groomed nestmates and performed cleaning activities. Temporal specialization as "receptionist worker" for honey (see Lachaud and Dejean, 1990) occurred in 22 ants and 40 workers were never seen to lick or feed the queen.

Mixed activities. A total of 46 (50.5%) workers passed through this stage, and the behavioral development of 19 (20.9%) progressed no further. Six workers switched to specialized guarding behavior straight away, but all the others displayed at least one of the three main functions more or less associated with guarding behavior: necrophoresis, construction, or disposal of debris. While some workers rarely (or never) showed necrophoric behavior, 16 specialized in this behavior. A further 21 workers were recorded displaying efficient construction behavior (building of a cover or screen against light), and 3 showed unspecialized behavior and were involved in all tasks.

Activities outside the nest. Only 27 of the 91 original callow workers (29.7%) became foragers by the end of the seventh week. Foraging behavior was preceded in all 27 workers by preforaging behavior. This initial stage lasted from 1 to 5 days and appeared to be indispensable for the subsequent development of true foraging. After preforaging behavior, workers began to collect honey and scavenge for dead prey. Their efficiency as foragers was highly variable. Of the 27 foragers, 13 specialized in collecting honey with their mandibles while 10 eventually stopped being attracted by honey and specialized in hunting behavior. Four workers performed the both tasks in an efficient way.

#### Ontogenesis of hunting behavior

Only four workers from Lot I displayed provisioning behavior (with honey and dead prey) from the second day of the experiment onward. All the other workers that became foragers appeared

to be very timid during their first excursion in the foraging arena. This behavior persisted in Lot I for 1 to 3 days and in Lot II for 2 to 5 days.

Workers' first excursions were short. They stayed near the nest entrance and their excursions lasted only a few minutes. They frequently failed to detect honey or prey remains even from very short range. When food was detected, early foragers showed escape behavior, running away from the food (mainly toward the nest). During escape, ants held their antennae stretched forward and their mandibles closed, whereas during normal foraging or patrolling, the antennae are held wide apart and the mandibles are open 180° (Dejean, 1988). Experienced foragers obviously recognized preforagers (perhaps through cuticular hydrocarbons, see Bonavita-Cougourdan *et al.*, 1987). Foragers manipulated preforagers encountered in the foraging arena and carried them back to the nest (78 observations for 23 preforagers) in the way typical of *Odontomachus* (Möglich and Hölldobler, 1974). Later, preforagers became attracted by honey and dead prey and licked them. They only became foragers after a few days.

Among the original 83 workers from Lot I that became foragers, 14 never captured live prey (significantly different from callow workers in Lot II: chi-squared test, Yates' correction,  $X^2 = 4.21 > 3.84$ ,  $p < 0.05$ ). However, these workers efficiently foraged for dead prey or honey. Twelve workers could also be classified as poor hunters, capturing only 7-10 prey in seven weeks. It is probable that these workers became foragers under the effect of social regulation but, under normal non-experimental conditions, would have continued to work inside the nest or to display mixed activities all their life.

When confronted with living prey inside the nest (Table 2), callow workers less than four days old did not react. When faced with a termite, they turned away whereas, in the same conditions, young nurses 10-13 days old were aggressive and attacked (A1-A2). Older nurses were even more aggressive (A2-A3) but less so than workers engaged in mixed activities (A3-A4).

All workers likely to leave the nest (preforagers, foragers and workers displaying mixed activities) were equally aggressive (A4-A5, A5-A6, A4-A6) when acting as guards (or at least, when located at the nest entrance). Foragers, however, used their

Table 2: Responses of *Odonotomachus troglodytes* workers to prey (*Cubitermes* worker 0.5 mm in length) according to their behavioral sub-caste and location (inside the nest, at the nest entrance, in the foraging arena, far from the nest entrance). Statistical comparisons: (chi-squared test, Yates' correction). For:  $p=0.05$ ,  $\chi^2=3.84$ ;  $p=0.01$ ,  $\chi^2=6.64$ ;  $p=0.001$ ,  $\chi^2=10.83$ . "without reaction + escape" / "other cases": A1-A2:  $\chi^2=7.08$ ,  $p<0.01$ ; A2-A3:  $\chi^2 \sim 7.6$ ,  $p<0.01$ ; A3-A4:  $\chi^2=4.26$ ,  $p<0.05$ ; A4-A5:  $\chi^2=0.73$ , N.S.; A4-B4:  $\chi^2=15.99$ ,  $p<0.001$ ; A5-B5:  $\chi^2=36.86$ ,  $p<0.001$ ; B4-B5:  $\chi^2=1.61$ , N.S.; B5-B6:  $\chi^2=32.4$ ,  $p<0.001$ . "attack + attack-sting" / "other cases": A'4-A'5:  $\chi^2=3.21$ , N.S.; A5-A6:  $\chi^2=1.66$ , N.S.; A'5-A'6:  $\chi^2=2.4$ , N.S.; A4-A6:  $\chi^2=0.001$ , N.S.; A'4-A'6:  $\chi^2=6.55$ ,  $p<0.05$ . "without reaction + aggressiveness" / "other cases": A6-B6:  $\chi^2=5.24$ ,  $p<0.05$ .

	(Code)	Number of workers	Number of facts	inside the nest			at the nest entrance			outside the nest			
				wr-es	ag	at	wr-es	ag	at	wr-es	ag	at	
Workers less than 4-days old	(1)	10	30	-	-	-	-	-	-	-	-	-	
Nurses 10- to 13-days old	(2)	10	30	23	5	2	-	-	-	-	-	-	
Nurses more than 30-days old	(3)	3	12	3	5	4	-	-	-	-	-	-	
Mixed activities workers 18-days old	(4)	5	28+ 8	-	-	-	1	11	16	-	6	1	1
Foragers 18- to 22-days old	(5)	10	30+35	-	-	-	3	16	9	2	31	4	-
Foragers 30- to 35-days old	(6)	10	30+30	-	-	-	2	10	11	7	4	-	22

Code for statistical comparisons	A			A			B		
	wr-es	ag	at	wr-es	ag	at	wr-es	ag	at
(1)	-	-	-	-	-	-	-	-	-
(2)	23	5	2	-	-	-	-	-	-
(3)	3	5	4	-	-	-	-	-	-
(4)	-	-	-	1	11	16	-	6	1
(5)	-	-	-	3	16	9	2	31	4
(6)	-	-	-	2	10	11	7	4	-

wr-es : without reaction or escape  
 ag : aggressiveness  
 at : attack  
 st : attack-sting

stings more frequently than workers specialized in mixed activities (A'4-A'5).

Workers displaying mixed activities were rarely found more than 40cm from the nest entrance. Like preforagers, they were not very aggressive when offered prey in the foraging arena (B4-B5). Foragers were much more aggressive (B5-B6) and attacked and captured all the termites they encountered. Preforagers and mixed activity workers, although timid when they encountered prey in the foraging arena, were aggressive in the nest and near the nest entrance (A4-B4; A5-B5). Their aggressiveness depended therefore on the area in which they encountered prey. More subtle differences existed among foragers. In the foraging arena they displayed predatory behavior, and encounters with insects led in every case to their capture as prey, whereas at the nest entrance they often displayed a typical attack-retreat sequence (A6-B6).

#### DISCUSSION

One week after the installation of colonies in the artificial nest, the proportion of *O. troglodytes* workers in each behavioral category were: 50% inside the nest, 22.3% engaged in mixed activities, and 27.7% outside the nest. These values were similar to those obtained by Colombel (1969) using a slightly different method. It is noteworthy that, among workers that emerged in the laboratory, the proportion of 35 day olds displaying behavior outside the nest was near that found in adult colonies. The ratios of foragers to all workers were:  $83/300=0.276$  in Lot I, and  $27/91=0.296$  in Lot II, and these were not significantly different (Chi-squared test, Yates' correction,  $X^2=0.19 < <3.84$ ).

The timing of age-related behavioral specialization in *O. troglodytes* is very close to that recorded for *Ectatomma tuberculatum* (Champalbert, 1986; Champalbert and Lachaud, 1990) and so the chronology of age polyethism in these species can be seen as common for ponerine ants. In *O. troglodytes*, however, interindividual variability in the duration of behavioral specializations appears surprisingly strong.

Within any behavioral sub-caste, the existence of a link between interindividual variability and age polyethism inevitably arises when workers of the same age perform different subfunctions. For

example, among numerous species belonging to different sub-families (Formicinae: Kill, 1934; Otto, 1958; Dolichoderinae: Lenoir, 1979a; Myrmicinae and Ponerinae: Agbogba, 1981), the foragers are divided into two sub-groups: collectors of sugary substances and hunters. In *Aphaenogaster senilis* there was an additional third sub-group of foragers that both hunt and collect sugars (Agbogba, 1981). In the ponerine ant *Ectatomma ruidum*, workers outside the nest fell into three categories: those strongly attracted to proteinaceous food, those with an aversion to it, and those indifferent to any type of food (Lachaud *et al.*, 1984). On the other hand, in another ponerine species *Pachycondyla* (= *Neoponera*) *villosa*, the same authors showed that the daily period of foraging activity varied between individuals. In *O. troglodytes*, similar interindividual variability occurred in all behavioral sub-castes. Among nurses, individuals specialized in larval care, pupal care or care of the queen associated with reception and sharing of food. Workers carrying out mixed activities mainly specialized in brood care associated with cleaning or in cleaning associated with construction. Finally, some foragers specialized in prey capture. In addition, in various instances some workers could remain locked in one behavioral sub-caste for a long period of time. If there is no disruption within the society, leading to social regulation, many workers probably remain in one behavioral subcaste until their death. Thus, certain workers remain "inactives", others "nurses", and others "intermediates". Such an overlap between age polyethism and interindividual variability occurs in *Tapinoma erraticum* and *Lasius niger* (Lenoir, 1979a, b). In the latter species, most workers are first nurses and then foragers; some, however, remain nurses all their life whereas others become foragers without previously being nurses. Strong interindividual variability therefore can be superimposed on age polyethism, and some workers never develop into foragers. Nevertheless, interindividual variability does involve not only the quality of the task performed but also the level of activity (low, moderate or high) exhibited by the workers. High activity was characteristic of 6 of the 10 workers of Lot I that became hunters, particularly as they passed into the mixed activity category and in the previous stage. In contrast, the 36 workers that were still nurses on the 48th day after emergence were, on average, not highly active.

Internal physiological state appears to be one of the main factors responsible for interindividual variability. Mercier (1982) showed that in *Pachycondyla apicalis*, workers with well developed ovaries can be distinguished from those whose ovaries are on the decline. Workers with well developed ovaries, under the influence of social regulation, are capable of brood care and can be considered as a reservist group for nursing and activities inside the nest (Lachaud and Fresneau, 1987b). Those with declining ovaries, may undertake exploration outside the nest and correspond to a reservist group for activities outside the nest. Similarly, there is a close link between some ovarian characteristics (number of oocytes per ovariole and length of the basal oocyte) and the frequency of brood care behavior performed by *Ectatomma tuberculatum* workers (Fénéron *et al.*, 1989), together with a great variability in the behavior of same-aged individuals (Fénéron, personal communication).

Environmental cues also influence behavioral variability between individual workers, and these influences cannot be neglected. In *Ectatomma tuberculatum*, familiarisation processes have been proved of major importance in the ontogenesis of brood care (Champalbert and Lachaud, 1990) and of predation (Dejean and *et al.*, 1989). In the latter case, any change in the perception of the social environment (either inside or outside the nest), had an obvious effect on behavioral differentiation between individuals.

Contact with the environment outside the nest is progressive. As they age, workers approach the nest exit more frequently, eventually assuming the function of "nest guards". This categorization includes ants of three different types: a) those receiving food (receptionist workers for honey or prey) and sharing it inside the nest; b) those about to take up either activities outside the nest or mixed activities; and c) those already displaying activities outside the nest (mainly preforagers) or mixed activities. The workers generally become more aggressive the longer they act as "guards" although there is a great interindividual variability. During this time, they become increasingly familiar with the environment outside the nest.

The duration of the subsequent preforager stage varies considerably between individuals. As preforagers, workers learn to recognize food, capture prey and to orientate successfully. In these respects, this preforaging behavior characteristically corresponds



to that of *E. tuberculatum* (Dejean *et al.*, 1989). It is probably also similar to that of *E. ruidum* where workers performing activities outside the nest may display exploratory behavior without collecting prey (Lachaud *et al.*, 1984). Only after a comparatively long time do young *O. troglodytes* foragers begin to venture further away from the nest. In becoming foragers they exhibit three successive subfunctions: The first is honey collection and scavenging for dead prey, followed by the addition of hunting living prey and, finally, concentrating on scavenging and hunting. Here again, age polyethism and interindividual variability interact. Some workers can remain in the first or second subfunction. A similar set of subfunctions: honey collecting, prey capture, predation and collection, is described for the myrmicine *Aphaenogaster senilis* (Agbogba, 1981). In this case, however, no clear relationship with age polyethism was indicated.

The progressively more efficient predatory behavior of *O. troglodytes* parallels the development of aggressiveness in successive behavioral sub-castes. In this species, aggression and prey capture may be correlated because both involve use of the sting and of the powerful mandible closing mechanism. Nevertheless, results from research on workers of *Smithistruma* spp. (Dejean, 1985) (which have the peculiarity of standing immobile before attacking their principal prey, Collembola), suggest that aggression and predation are really distinct. Efficient predatory behavior arises through the inhibition of aggression, so that the prey can be successfully seized by one of its appendages.

*Odontomachus* spp., with their long and powerful mandibles, seize the bodies of prey. The difference between predation and aggression is thus more subtle than in *Smithistruma*. It is noteworthy that the behavior of nest guards is very homogeneous even though they comprise different sub-castes. Their behavior in the foraging arena differs greatly, however, depending on their status as either intermediates or preforagers. Aggression in *O. troglodytes*, as in *Myrmecia gulosa* (Robertson, 1971), increases the nearer workers are to the nest entrance. The difference between aggressiveness and predation becomes more evident when we consider the behavior of foragers near the nest entrance. Here, attack-retreat behavior occurs in 10 of 30 cases whereas it is absent in the foraging arena where prey seizure is necessary. This behavior does occur, however, during attacks on large prey

that are potentially dangerous (Dejean and Bashingwa, 1985).

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