

BEPROC 00540

Absence of temporal polyethism in the ponerine ant *Pachycondyla cafraria* (Smith) (Hymenoptera : Formicidae) : Early specialization of the foragers

C. Agbogba

Université Cheikh Anta Diop, Faculté des Sciences: Biologie animale, Dakar, Sénégal

(Accepted 13 December 1993)

Abstract

In the Ponerine *Pachycondyla cafraria* the behaviour of workers is independent of age. They leave the nest to forage a few days after eclosion, and some specialization appears in the young foragers. For the first five days, the callow workers stay in the nest chamber; they remain immobile, or groom themselves, or lick the larvae and pupae, which they transport from one part of the nest to another. Six or seven days after eclosion, some of the young workers remain inside the nest and occupy themselves with inside labour, while others leave the nest to forage, and collect sugar water or hunt for prey. The frequency of some behavioural acts which are performed by the young inside workers increases or decreases with age.

Key words: Ant; Callow; Division of labour; *Pachycondyla cafraria*; Ponerinae; Worker

Introduction

In ants (Hölldobler and Wilson, 1990) the division of labour among members of the colony is based on worker age (temporal polyethism) or anatomical differences (caste polyethism). In general, when the division of labour is based on age, young workers are engaged in brood care and other kinds of labour inside the nest, while the older workers leave the nest to carry out nest construction, defence of the colony, and foraging. *Pachycondyla cafraria* is a carnivorous ant; the hunter workers paralyze their prey by stinging, and transport them back to the nest either on their own or in groups, after having recruited nestmates (Agbogba, 1982, 1984). In this monomorphic ant the division of

labour is known. About a third of the workers are hunters and the other two-thirds are nurses (Bonavita and Poveda, 1970). Two categories of foraging workers were found in this species: hunters and sugar liquid collectors (Agbogba, 1982). In the category of hunters there were two sub-categories: 'stingers' and 'transporters' (Agbogba, 1989; Agbogba and Howse, 1992).

To find out whether this division of labour is based on age, several groups of newly eclosed workers of *Pachycondyla cafferaria* were maintained for 17 weeks, and the behaviour of these young workers was examined.

Materials and Methods

Two colonies of *P. cafferaria*, containing 70 and 98 workers respectively, two queens, pupae, larvae and eggs, were set up in laboratory nests. Each nest, in a sealed Petri dish, was connected to a plastic box (60 × 30 cm and 8 cm deep), which served as a foraging area. The colonies were fed with sugar water and live termites. The newly eclosed workers in each colony were observed for the first part of their lives. Using an entomological needle, the callow workers (2 days old) in each colony were marked with different coloured nail varnish (white = w; pink = p; and red = r) on the thoraxes (th), on the abdomens (ab), or on both. The callow workers (6 or 7 days old), who stayed in the nest and were occupied with inside labour, kept the markings which they received 2 days after their eclosion; the others, who left the nest to forage, received additional colour markings. Many combinations of colour markings were made to permit group recognition (sugar collectors and hunters). The workers kept these colour markings for several weeks, but some of them needed to be marked again.

In each colony, when the newly eclosed workers appeared, observations were carried out three times daily, each observation lasting 2 h, for the first 5 days. When the ants were 6 days old, tests were carried out twice daily, each lasting 3 h, over a period of 16 weeks. During each test, prey freshly killed or still alive, sugar water or sand mixed with sugar water were offered in the foraging area.

Results

In *Pachycondyla cafferaria* several broods were reared until adults (males, females and workers) eclosed. The newly eclosed workers differed from the older ones only in the colouration of the body. They were uniformly light red when they eclosed; the abdomen, thorax and head changed to nearly black after 3 days, the legs, antennae and mandibles being brown. When the ant was 1 week old the whole body become black.

Behaviour of callow workers (from eclosion to 5 days old)

The behaviour of 77 callows (33 in colony 1, and 44 in colony 2) was observed (Table 1). In total, 464 behavioural acts in 5 groups of colony 1, and 645 in 7 groups of colony 2 were observed. This data shows that all the newly eclosed workers stayed in the nest for the first 5 days. They presented 4 kinds of behavioural acts: immobility; self grooming; larval care and pupal care. The proportion of these different acts varies between the group but,

TABLE 1

Behavioural acts of the newly eclosed workers of *Pachycondyla caffraria*, from eclosion to 5 days old

Group	Number of workers	Behavioural acts Number/percentage				Total acts 1 + 2 + 3 + 4
		1	2	3	4	
Colony 1						
wth	6	22	18	30	12	82
		26.8	21.9	36.5	14.6	
pth	5	14	18	28	45	105
		13.3	17.1	26.6	42.8	
rth	8	6	4	35	42	87
		6.9	4.6	40.2	48.2	
wab	6	10	15	32	40	97
		10.3	15.4	33	41.2	
pab	8	5	7	42	39	93
		5.3	7.5	45.1	41.9	
Total	33	57	62	167	178	464
		12.3	13.3	36	38.4	
		25.6%		74.4%		
Colony 2						
wth	8	14	18	28	41	101
		13.8	17.8	27.7	40.6	
pth	5	10	8	37	29	84
		11.9	9.5	44.0	34.5	
rth	7	8	12	32	41	93
		8.6	12.9	34.4	44.0	
wab	5	9	8	30	35	82
		10.9	9.7	36.5	42.6	
pab	6	8	6	31	38	83
		9.6	7.2	37.3	45.7	
rab	6	12	10	37	42	101
		11.8	9.9	36.6	41.5	
wpth	7	18	24	28	31	101
		17.8	23.7	27.7	30.7	
Total	44	79	86	223	257	645
		12.3	13.3	34.6	39.8	
		25.6%		74.4%		

1 = immobility; 2 = self grooming; 3 = larval carrying; 4 = pupal carrying.

globally, the behaviour of callows was essentially oriented towards larval and pupal care (in both colonies, the percentage of acts related to larval and pupal care was 74.4%, and those of other acts was 25.6%).

Behaviour of young workers (from 6 days to 17 weeks old)

The behaviour of *P. caffraria* workers did not shift progressively from nursing to foraging with increasing age as is the case for other ants. In each group, when the newly eclosed

TABLE 2

A behavioural repertory: behavioural acts of the young inside and outside workers of *Pachycondyla caffraria*, from 6 days to 17 weeks old

Behavioural acts	Number and frequency of behavioural acts							
	Colony 1				Colony 2			
	Inside workers		Outside workers		Inside workers		Outside workers	
	N	F	N	F	N	F	N	F
Self-grooming	174	0.06002	216	0.04741	195	0.06130	224	0.04844
Brood carrying								
carry egg	230	0.07933	0	0	244	0.07711	0	0
lick egg	229	0.07899	0	0	243	0.07680	0	0
carry larva	288	0.09934	0	0	319	0.10082	0	0
lick larva	305	0.10520	0	0	334	0.10556	0	0
feed larva	313	0.10796	0	0	349	0.11030	0	0
carry pupa	270	0.09313	0	0	296	0.09355	0	0
lick pupa	282	0.09727	0	0	310	0.09797	0	0
Exploring foraging area	0	0	886	0.19446	0	0	890	0.19247
Food handling inside								
carve prey	241	0.08313	323	0.07089	258	0.08154	336	0.07266
carry prey	250	0.08623	650	0.14266	274	0.08659	659	0.14251
carry sugar food	0	0	394	0.08647	0	0	403	0.08715
Foraging								
collect sugar food	0	0	649	0.14244	0	0	657	0.14420
collect or hunt prey	0	0	1438	0.31562	0	0	1455	0.31466
Cleaning								
clean nest chamber	168	0.05795	0	0	183	0.05783	0	0
throw out food particles	149	0.05139	0	0	159	0.05025	0	0
Total	2899	1.0	4556	1.0	3164	1.0	4624	1.0

N = number; F = frequency.

workers were 6 or 7 days old, some of them left the nest to forage and others, of the same age, remained in the nest. Indeed, in colony 1, 10 young workers out of 33 remained in the nest whilst 23 foraged, and in colony 2, 12 out of 44 remained in the nest whilst 32 foraged. The number of outside young workers was more than double the number of inside young workers.

A behavioural repertory (Table 2) showed that:

- (a) the inside young workers (10 in colony 1, and 12 in colony 2) were occupied with self grooming, egg care (picking the eggs up and putting them on an egg pile, or licking them), larval care (carrying the larvae between nest chambers, licking and feeding them), pupal care (carrying the pupae and licking them), food carving and handling, and with cleaning (cleaning the nest chamber and throwing the dessicated food particles out of the nest). In these young inside workers the frequency of brood care

activities was higher ($f = 0.66$) than those of food handling ($f = 0.17$) cleaning ($f = 0.11$) and self-grooming ($f = 0.06$).

- (b) the outside young workers frequently explored the foraging arena. They were specialized: some of them (5 in colony 1, and 7 in colony 2) collected the liquid sugar water in their crop, or transported grains of sand mixed with sugar water in their mandibles; the others (18 in colony 1, and 25 in colony 2) collected the freshly killed prey or hunted. In each test a choice of sugar water (or sand mixed with sugar water) and prey was offered. The sugar water gatherers showed no interest in the prey, whilst the hunter or the prey collectors showed no interest in the sugar. In the nest they were occupied with self grooming and food handling, but not with brood care or cleaning activities. In these young outside workers, the frequency of foraging activities was higher ($f = 0.65$) than those of food handling ($f = 0.30$) and self-grooming ($f = 0.05$).

None of the inside or outside young workers observed changed their activities during the course of the 16 weeks of observations. The frequency of all behavioural acts was nearly stable. Only the frequency of egg care performed by the young inside workers decreased with age, while those of self-grooming, carrying, licking and feeding larvae, carrying and licking pupae, carving and carrying prey, and cleaning the nest chamber increased.

Discussion

This study shows that the workers of the monomorphic ponerine ant *Pachycondyla cafferaria* do not follow the normal pattern of temporal polyethism which is known to exist in many species of ant, and which has been examined in detail by Hölldobler and Wilson (1990). The behaviour of *P. cafferaria* workers did not change as they grew older, progressing from nursing to foraging. The newly eclosed workers of *P. cafferaria* left the nest at an early age – 6 or 7 days after eclosion – to forage, like the Ponerine ant *Amblyopone pallipes*, but a well-defined division of labour in the latter is unknown (Traniello, 1978, 1982).

This paper reveals an early specialization in *P. cafferaria* outside young workers: some of them collect the sugar food and others collect or hunt for prey, displaying the same behaviour as the older ones previously studied (Agbogba and Howse, 1992). This foraging behaviour observed in the outside young workers cannot be considered as a form of social homeostasis; indeed it was observed in the outside young workers while the older foragers were present in the colony and foraged. This result suggests that the *P. cafferaria* outside young workers grow up very quickly.

On the other hand, the frequency of their activities was more or less the same; they did not change their role during the course of the 16 weeks of observations. Their specialization is therefore stable.

Early specialization of young workers in foraging or predatory activities is unknown in the Ponerinae which was studied previously. In the Ectoninae *Neivamyrmex nigriscens* (Topoff and Mirenda, 1978), early participation by young workers in predatory raids is known, and in the Formicinae *Formica neorufibarbis gelida* polymorphic species (Bernstein, 1976) the small workers are able to forage at an early age.

In the inside young workers, during the course of 16 weeks of observations, the frequency of egg care decreased and those of larval care, pupal care and prey handling increased, suggesting that these workers grow up slowly, and their responsiveness to environmental stimuli may change with age, as is the case with other ants (Topoff et al., 1972; Cammaerts-Tricot, 1974; Jaisson, 1975; Topoff and Mirenda, 1978; Mackay, 1983).

We know that in ants, and other social insects, some flexibility in worker behaviour exists. The future observations and experiments where some of the outside or inside young workers will be taken away may give us more information about the evolution and the possible flexibility of *P. cafferaria* young workers' behaviour.

Acknowledgement

I wish to thank Adèle M. Trickett, teacher at the British Senegalese Institute, for helping me with the English in this manuscript.

References

- Agbogba, C., 1982. Contribution à l'étude de la prédation et de l'approvisionnement de la société chez des fourmis carnivores. Analyse comparative chez des espèces d'Afrique tropicale et du midi de la France. Thèse 3^e cycle, Université de Provence, 132 pp.
- Agbogba, C., 1984. Observations sur le comportement de marche en tandem chez deux espèces de fourmis ponérines: *Mesoponera cafferaria* (Smith) et *Hypoponera* sp. (Hym. Formicidae). *Ins. Soc.*, 31: 264–276.
- Agbogba, C., 1989. Contribution à l'étude des interactions sociales et des activités collectives au cours de l'approvisionnement chez des fourmis prédatrices. Thèse Doct. Sci., Université de Dakar, 238 pp.
- Agbogba, C. and Howse, P., 1992. Division of labour between workers of the ponerine ant *Pachycondyla cafferaria* (Smith) (Hymenoptera: Formicidae). *Ins. Soc.*, 39: 455–458.
- Bernstein, R.A., 1976. The adaptive value of polymorphism in an alpine ant, *Formica neorufibarbis gelida* Wheeler. *Psyche*, 83: 180–184.
- Bonavita, A. and Poveda, A., 1970. Mise en évidence d'une division du travail chez une fourmi primitive. *C.R. Acad. Sc.*, Paris, 270: 515–518.
- Cammaerts-Tricot, M.C., 1974. Production and perception of attractive pheromone by differently aged workers of *Myrmica rubra* (Hymenoptera Formicidae). *Ins. Soc.*, 21: 235–247.
- Hölldobler, B. and Wilson, E.O., 1990. *The Ants*. Belknap/ Harvard University Press, Cambridge, Massachusetts, 732 pp.
- Jaisson, P., 1975. L'imprégnation dans l'ontogenèse des comportements de soins aux cocons chez la jeune fourmi rousse (*Formica polyctena* Först). *Behaviour*, 52: 1–37.
- Mackay, W.P., 1983. Stratification of workers in harvester ant nests. *J. Kansas Entomol. Soc.*, 56: 538–542.
- Topoff, H.R. and Miranda, J., 1978. Precocial behaviour of callow workers of the army ant *Neivamyrmex nigriscens*: importance of stimulation by adult during mass recruitment. *Anim. Behav.*, 26: 698–706.
- Topoff, H.R., Lawson, K. and Richard, P., 1972. Trail following and its development in the neotropical army ant genus *Eciton* (Hymenoptera; Formicidae; Dorylinae). *Psyche*, 79: 357–364.
- Traniello, J.F.A., 1978. Caste in a primitive ants: absence of age polyethism in *Amblyopone*. *Science*, 202: 770–772.
- Traniello, J.F.A., 1982. Population structure and social organization in the primitive ant *Amblyopone pallipes* (Hymenoptera: Formicidae). *Psyche*, 89: 65–80.