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Short communication

Division of labour between foraging workers of the ponerine ant *Pachycondyla caffraria* (Smith) (Hymenoptera: Formicidae)

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Summary

Two categories of foraging worker were found in *Pachycondyla caffraria* from Senegal. One specialises in hunting and the other in collecting sweet liquid food. In the category of hunters there are two sub-categories: "stingers" and "transporters". When the workers were offered a group of live termites (20–30 *Microcerotermes sp.*), two types of behaviour were observed: some workers stung and paralysed the prey, while others transported the termites back to the nest. While on a foraging raid, the two roles are undertaken by two distinct groups of workers, and the roles are not interchanged during the course of the raid. The number of hunters, liquid collectors and transporters of prey are highly correlated with colony size.

Introduction

Division of labour in ants has been surveyed in detail by Hölldobler and Wilson (1990), who distinguish between temporal polyethism, in which the tasks of workers vary with their age, and caste polyethism, in which morphologically defined castes have differing sets of tasks. Ponerine ants, with the exception of members of the genus *Megaponera*, are unusual in that the worker caste is not polymorphic. In ants in general, tasks are divided into nest duties: caring for the queen and brood, and foraging. Some flexibility exists. In the carnivorous ponerine ant *Pachycondyla caffraria*, Bonavita and Poveda (1970) found that about a third of the foragers were "hunters" and the rest were "nurses", engaged in brood care. Hunters that were removed were quickly replaced by nurses which changed their role. In *Tapinoma erraticum* (Lenoir, 1979) and *Pachycondyla* (*Neoponera*) *apicalis* (Lachaud & Fresneau, 1987) an intermediate subgroup of workers is present which can replace lost nurses for foragers. In colonies of the latter species, the replacements switched back to their original tasks after 10 days in another role, suggesting that the polyethism is not primarily age-dependent.

The behaviour of the hunters of *Pachycondyla caffraria* was examined and evidence found for a further division of labour.

Methods

Six colonies of *P. caffraria* were collected from the field in Senegal and set up in laboratory nests, each containing 60–127 mature workers, two queens and larvae. Each nest in a sealed petri dish was connected to a plastic box 60 × 30 cm and 8 cm deep. This served as a foraging arena. Each colony was fed with sugar-water and live prey (termites). The foraging workers were marked, as a group, on the abdomens (sugar-water collectors), or on the thoraces (hunters) with different coloured paint or nail-varnish.

In the first experiment, to investigate whether or not the members of the sugar-water group changed, daily observations were made for 20 weeks. Tests were carried out three times a week, each over a period of 2 hours. In the second experiment live termites were placed one at a time in the foraging arena. The hunting workers that took the prey were then marked.

In the third experiment a small piece of the carton nest of *Microcerotermes* containing 20–30 live termites was placed in the foraging arena of each colony. This was done twice a week over the same 20 weeks as the previous experiment, and observations lasted for one hour in each instance.

Results

Experiment 1

During the first two days of observation, workers that were recruited to the sugar-water were marked. These amounted to 25–32% of the foraging population (Table 1). In each test a choice of sugar-water and prey was offered. No food was offered between tests. The sugar-water gatherers were recruited only to the sugar-water and

Table 1. Distribution of the foraging workers in the functional subcategories in the ant *Pachycondyla caffraria*. Numbers of hunter workers in group A and B after change of role are given in parentheses (see text)

Colony	Numbers of workers in each colony	Total number of foraging workers	Numbers of sugar-water collectors (and %)	Numbers of hunter workers		
				Total number (and %)	Workers of group A	Workers of group B
1	88	78	21 27%	57 73%	26 (30)	31 (27)
2	127	115	29 25%	86 75%	25 (30)	61 (56)
3	68	54	17 31%	37 69%	4 (9)	33 (28)
4	60	49	15 31%	34 69%	23 (24)	11 (10)
5	75	68	19 28%	49 72%	30	19
6	60	47	15 32%	32 68%	20	12

Table 2. Correlation between total number of ants in the colony and numbers of ants in functionally separate categories

Category	Correlation coefficient (r)	Probability (ANOVA)
Sugar-water collectors	0.99	$P < 0.00001$
Group A hunters		
– before change of role	0.32	$P > 0.5$
– after change of role	0.53	$P < 0.3$
Group B hunters		
– before change of role	0.93	$P = 0.007$
– after change of role	0.95	$P = 0.004$

showed no interest in the prey. No other foragers fed from the sugar-water during the tests. The number of sugar-water collectors in the colony was closely correlated with the total size of the colony ($r = 0.99$, $P < 0.00001$: Table 2).

Experiment 2

After three days of observation with live termites, only the marked workers (hunters) were observed to forage for the live prey. They comprised between 50% and 75% of the foraging population (Tab. 1). None of the hunters were recruited to sugar-water or honey when it was offered.

Experiment 3

Two kinds of behaviour were observed in the hunters, when offered 20–30 live termites. Those of one group (A) stung and paralyzed their prey and then left them in the arena. Those of the other group (B) transported the paralyzed prey back to the nest. All group B workers were then marked. The proportions of groups A and B were very variable among the different colonies, 6–40% for group A and 18–48% for group B (Tab. 1), but the proportion of prey transporters was closely correlated with the total size of the colony ($r = 0.93$, $P = 0.007$), while the number of attackers was uncorrelated ($r = 0.32$, $P > 0.5$). After eight weeks, some group B workers in four colonies adopted group A behaviour. They now engaged exclusively in capturing and stinging termites. This shift was observed in four colonies, in which 4 out of 31, 5 out of 61, 5 out of 33, and 1 out of 11 workers changed their roles.

Discussion

In this study, high correlations were found between (a) the numbers of foraging workers in the colony (around 90%) and colony size, b) the number of hunters and

the number of sugar-water gatherers (approximately 3:1) and c) the number of transporters of paralyzed prey and the total number in the colony (approximately 32%). On the other hand, the number of workers that attacked and stung termites is not correlated with colony size. Workers that changed their role during the course of the 20 week observation period actually improved the correlation between numbers of transporters and colony size (from $r = 0.93$ to $r = 0.95$), and between the numbers of attackers and colony size ($r = 0.32$ to $r = 0.53$). These results suggest that each colony has precise requirements for carbohydrates and protein, which are met by a division of labour between hunters and sugar-water foragers, which occur in relatively fixed proportions. Specialisation occurs among the hunters, and it appears that the most important factor is the supply of protein, which determines the proportion of transporters. Interestingly, the only changes of role observed were from transporters to attackers, suggesting that transporters that return to the nest without food may then gradually change their behaviour, perhaps by a lowering of thresholds to kairomones produced by potential prey.

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