

## Social organization of *Platythyrea lamellosa* (Roger) (Hymenoptera: Formicidae): II. Division of labour

M.H. Villet

Department of Zoology, University of the Witwatersrand, P.O. Wits, 2050 Republic of South Africa

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Although colonies of *Platythyrea lamellosa* were found to be consistently queenless, the division of labour amongst workers resembled the pattern generally characteristic of ants. Mated workers were involved only with reproduction and tending larvae. The behaviour of virgin workers was influenced by their age. Although they showed a degree of individual variation in behaviour, they were clearly organized into three roles: nursing eggs and larvae; tending cocoons and domestic tasks; and foraging. Behaviours sharing a common focus (e.g. larvae or prey) were highly associated. The integration of individual variability into a relatively precise pattern at the level of the colony was not merely a statistical artifact, but probably involved the way that tasks were spatially localized within the nest, as well as the changing physiological state of individual ants. Nest structure is probably important in this regard.

Alhoewel kolonies van *Platythyrea lamellosa* deurgans koninginloos is, het die verdeling van werk onder die werkers dieselfde patroon gevolg as by ander miersoorte. Bevrugte werkers was net gemoeid met reproduksie en die versorging van larwes. Die gedrag van onbevrugte werkers is deur hul ouderdom beïnvloed. Alhoewel hulle 'n mate van individuele verskille getoon het, was hulle duidelik in drie rolle georganiseer, naamlik, die versorging van eiers an larwes; die versorging van kokonne en die nes; en prooi jag. Take waar daar met dieselfde soort materiale (soos larwes of prooi) gewerk is, was sterk geassosieerd. Die intergrasie van individuele verskille in 'n taamlik presiese patroon op die vlak van die kolonie was nie 'n statistiese artefak nie, maar is waarskynlik beïnvloed deur die ruimtelike plasing van take binne die nes, sowel as die veranderende fisiologiese toestand van individuele miere. Nesstruktuur is waarskynlik belangrik in hierdie verband.

Division of labour in social insects can be studied at a number of complementary levels. The behaviour of a colony as a whole can show how ecological and social contingencies are met; this can be done without reference to the identity of specific workers. Alternatively, the mechanisms underlying these patterns can be explored by understanding the additive effects of responses of individual workers. While one approach emphasizes the structure of labour in a colony, the other focuses on the organization of the workforce (Jeanne 1986). An understanding of the mechanisms governing the behaviour of individual ants is needed to explain the characteristics of the whole colony (Corbara, Lachaud & Fresneau 1989), which in turn contributes to ecological and evolutionary explanations of social behaviour. In ants these mechanisms are usually related to age, size and reproductive status (Brian 1979; Sudd 1982).

Division of labour has been studied in some detail in several groups of closely related species of ponerine ants, especially of the tribes Ponerini (Dantas de Araujo, Fresneau & Lachaud 1988; Fresneau 1984; Fresneau, Garcia-Perez & Jaisson 1982; Fresneau & Dupuy 1988; Perez-Bautista, Lachaud & Fresneau 1985; Villet 1989, 1990) and Ectatommini (Corbara *et al.* 1989; Fresneau *et al.* 1982; Rubin, Lachaud & Fresneau 1989). Most of these studies have involved species that have a queen caste. In many species of ponerine ant the queen caste is absent and inseminated workers have taken over the social function or role usually filled by the queen caste (Fukumoto, Abe & Taki 1989; Peeters & Higashi 1989; Villet 1989, 1990; Ware, Compton & Robertson 1990), but detailed studies of their division of labour have not been published.

The genus *Platythyrea* belongs to the tribe Platythyreini

and contains several queenless species, including *P. lamellosa* (Villet, Hart & Crewe 1990a), *P. sp. A* (Villet 1989) and *P. schultzei* (Villet 1991), *P. lamellosa* was chosen for an investigation of division of labour because of the absence of a queen caste.

### Materials and Methods

Four colonies, including foragers, of *P. lamellosa* were collected at Tosca (25°53'S/23°58'E), northern Cape, South Africa. Notes about nest structure, foraging habits and other behaviours were made in the field at Tosca, and at Esigodini (20°17'S/28°55'E), Zimbabwe and Dunstable Farm, 30 km west of Hoedspruit, (24°28'S/30°43'E), South Africa. Colonies were taken to the laboratory where they were housed and fed as described by Villet *et al.* (1990a). The arena was covered with sheets of glass to prevent the ants being disturbed by breathing during observations (Lachaud, Fresneau & Corbara 1988). Every ant was marked with enamel modelling paint and numbered uniquely using a fine drafting pen. This allowed the association of different sets of data collected from the same ant. The behavioural studies focused on one colony, containing 33 ants, some eggs, 23 larvae, 49 cocoons and no males.

A behavioural catalogue was compiled by *ad libitum* sampling (Altmann 1974) in the laboratory during forced nest translocations and other observations of behaviour. Focal animal sampling (Altmann 1974), in which a 30-min sequence of behaviours was recorded from each ant, was used to assemble data for an ethogram of one colony. A log-Poisson distribution was used to estimate the completeness of the behavioural catalogue from the ethogram (Fagen & Goldman 1977). The structural relationships of behaviours

were also analysed from the focal animal samples, using a behavioural transition analysis that generated a hierarchical dendrogram by a centroid-linking algorithm (Chilko 1983).

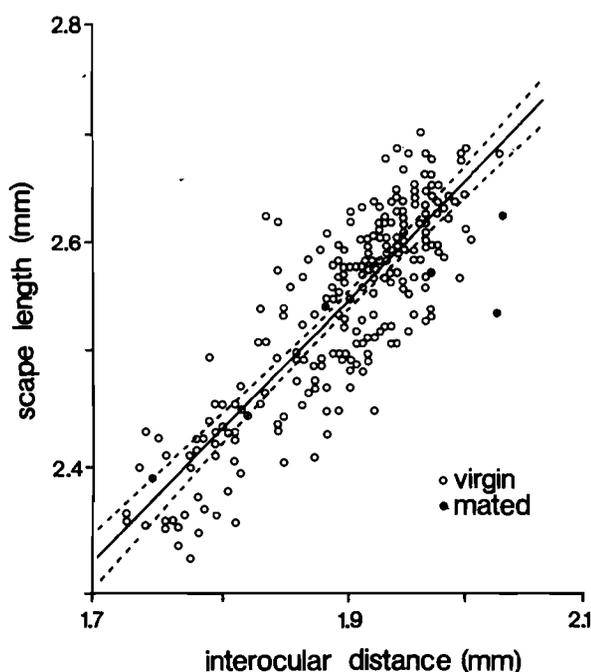
To examine the organization of workers into roles, as distinct from the clustering of behaviours into tasks (Jeanne 1986), a centroid-linking hierarchical cluster analysis was performed on scan samples (Altmann 1974) of 50 acts collected from each worker over five days. The resulting dendrogram compared the similarity of these behavioural profiles. Histograms were used to interpret the groups.

The reproductive status of workers was established by dissection of their reproductive organs, using the anatomical criteria of Villet *et al.* (1990a). Size variation in workers was quantified by measuring the smallest distance between the eyes (interocular width) and the length of the scape, excluding the radicle, of all the ants in four nests, using a Wild M3 stereo microscope and an Olympus OSM optical micrometer. To investigate the relationship between body size and behaviour, a repertoire was compiled for each ant from the *ad libitum*, scan and focal animal samples, and an analysis of variance performed on these data. A least-significant-difference (LSD) criterion was used to compare the interocular widths of ants between each pair of behaviours (Herbers & Cunningham 1983).

## Results

### Morphological differentiation

Workers were monomorphic (Figure 1). The range of interocular width of virgin workers covered 0,3 mm, and the coefficient of variation was 3,57% ( $n = 253$ ). The distribution of worker sizes was slightly skewed ( $G_1 = -0,631$ ) towards larger workers, and scape length was allometrically related



**Figure 1** Plot of scape length against interocular width for 253 workers of *Platythyrea lamellosa* from four nests. The least-squares regression line and its 99% confidence interval are superimposed.

( $r^2 = 0,72$ ;  $F = 637,4$ ;  $p = 0,0001$ ) to interocular width by the following equation (including standard deviations):

$$\text{scape length} = 1,500 (\pm 1,021) \text{ interocular width}^{0,825 (\pm 0,033)}$$

### Organization of behaviour

From the focal animal samples of 28 different behaviours and 1697 acts, it was estimated that the complete repertoire of virgin workers of *P. lamellosa* contained 30 (95% C.I. =  $\pm 4$ ) behaviours. Another ten behaviours were seen in the field or the laboratory, bringing the total observed to 38 behaviours (Table 1). This implies that the repertoire was adequately characterized.

Only one of the behaviours was unusual for an ant. Workers were seen carrying small stones (WS), up to 2 mm in diameter, from the area around the nest, and piling them on the mound around the nest entrance, both in the field and in the laboratory. Field observations showed that very few of the stones were brought up from inside the nest. The behaviour of milking larvae seen in other *Platythyrea* species (Villet 1989) was not observed in *P. lamellosa*; the sternal abdominal tubercle from which the adults of other species appear to lick a secretion is poorly developed in larvae of this species (Hanrahan, Villet & Walther 1987; Villet, Hanrahan & Walther 1990b). Males tended to rest together in the laboratory nests, and were usually found in groups during excavations. First instar larvae were not removed from amongst the eggs when they hatched, but were later separated from them. They remained stuck to one another until much older.

Nestmates were recruited to new nest sites by being carried by the neck with their bodies aligned over the back of the ant carrying them. The hind legs of the ant being carried tended to stick out, rather than being folded against the body.

Workers foraged alone and never recruited nestmates. In the field they returned to the nest with the remains of dead insects such as cockroaches, beetles and bugs, spider skins and recently dead lepidopteran larvae. The latter were actively hunted and killed by ants in laboratory colonies. Among the identifiable remains found within nests in the field were a pamphagid grasshopper nymph, several grasshopper legs, parts of beetles and ants, and the stones of *Berchemia zeyheri* berries.

Analysis of the transitions between behaviours produced three major groups of behaviours (Figure 2): care of eggs (EA, EC, EG, ER), care of cocoons (CA, CC, CG, CR) and a group containing care of larvae (LA, LC, LG, LR) as a very distinct subgroup linked to personal behaviour (FA, FF, NR, RA, SG, WI), social interactions (WA, WG) foraging (WO) and maintenance of the nest (FC, NC, ND, NL). The linkage between larval care and other types of behaviour was formed through personal behaviours with which they are both commonly associated; they were otherwise unrelated.

The ethogram of a single, entire colony of *P. lamellosa* is presented in Table 1. The sample represents a catalogue fraction (Fagen & Goldman 1977) of 0,96, and had a sample coverage (Fagen & Goldman 1977) of 0,9993. These indices mean that the ethogram is representative of the behaviour of the colony (Fagen & Goldman 1977). Brood received some

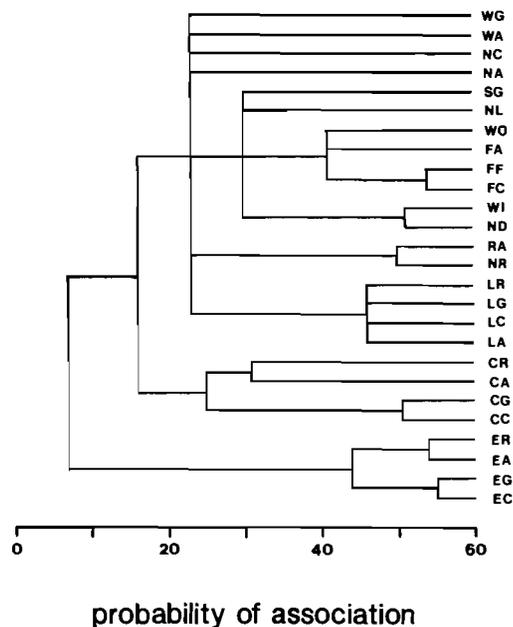


Figure 2 Dendrogram illustrating the probability of association between various behaviours of workers of *Platythyrea lamellosa*. Behavioural codes are explained in Table 1.

29% of acts (EA, EC, EG, CA, CC, CG, LA, LC, LG), while 25% were apportioned to nest maintenance (FC, NA, NC, ND, NL), 7% to social interactions (BG, WA, WG), and 29% to personal behaviours including resting (FF, SG, WX, CR, ER, LR, NR, RA). Resting alone forms 11% of the ethogram.

#### Organisation of workers

Five groups of workers were defined by arbitrarily selecting an inter-cluster distance of 0,7 as a cut-off level for group membership (Figure 3). A histogram analysis comparing the samples from each ant showed that ants of each group were characterized by a few behaviours that its members performed consistently more than was average for the colony (Figure 4). The groups were: two ants associated with cocoons; the single reproductive tending larvae; eleven nurses of larvae and eggs; nine ants tending cocoons and domestic tasks; and ten foragers that also tended and guarded the nest (Figure 4).

The levels of performance of these characteristic tasks also varied amongst the group members much less than levels of less characteristic behaviours (Table 2). Similarly, for such tasks, the group showing the least variation in its performance was the one that it characterized (Table 2). Variation in the behavioural profiles of workers belonging to the same group was smaller than variation between groups.

The two ants associated with cocoons (Group A) merely inspected them, and did not groom or move them. They were newly eclosed callow ants that were insufficiently sclerotized to begin working.

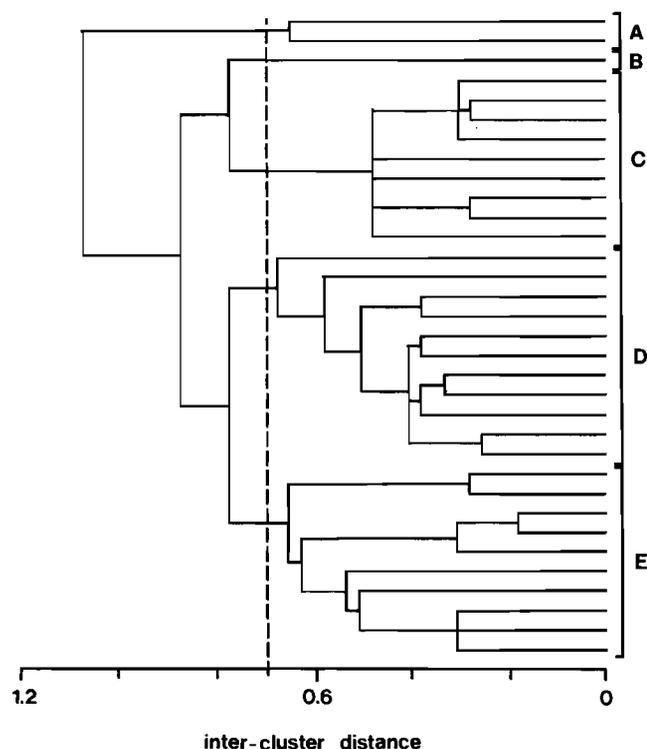
The ethogram of the single mated worker (Table 1) was dominated by personal behaviours (LR, RA, SG — 42%), inspecting larvae (LA — 34%) and care of larvae (CC, CG — 13%). No unusual postures or other behaviours were

Table 1 Behavioural catalogue and ethogram of *P. lamellosa*. M = males (13 behaviours); G = mated workers (20 behaviours, 62 acts); W = virgin workers (38 behaviours, 1635 acts). The occurrence or absence of behaviours in a particular group during the study is marked as follows: \* = not seen during quantification of ethogram; - = not seen at any time

Behavioural catalogue		Behavioural ethogram		
Code	Description	Males	Virgin workers	Mated workers
BC	Be carried	*	*	*
BG	Be groomed	*	0,0061	-
CA	Inspect cocoon(s)	-	0,0954	-
CC	Carry cocoon(s)	-	0,0116	-
CG	Groom cocoon(s)	-	0,0385	-
CR	Rest on cocoon(s)	-	0,0300	-
D	Drink	-	*	-
EA	Inspect egg(s)	-	0,0110	0,0161
EC	Carry egg/larva packet	-	0,0067	0,0161
EG	Groom egg(s)	-	0,0086	0,0323
EL	Lay egg	-	-	*
ER	Rest on eggs	-	0,0018	-
FA	Inspect live prey	*	0,0398	-
FC	Carry prey	-	0,0031	-
FF	Feed on prey	*	0,0318	-
FS	Sting prey	-	*	-
LA	Inspect larva(e)	-	0,0765	0,3387
LC	Carry larva(e)	-	0,0104	0,0484
LG	Groom larva(e)	-	0,0324	0,0806
LR	Rest with larva(e)	-	0,0312	0,2742
MA	Inspect male	-	*	-
MC	Carry male	-	*	-
MF	Fly	*	-	-
MG	Groom male	-	*	-
NA	Inspect nest	*	0,1939	0,0161
NC	Carry refuse	-	0,0098	-
ND	Dig	-	0,0318	-
NG	Guard nest entrance	-	*	-
NL	Look out of nest	*	0,0110	-
NR	Rest in nest	*	0,0294	-
NS	Lick nest floor	-	*	-
RA	Resting but alert	-	0,0159	0,0645
SG	Preen	*	0,1450	0,0806
WA	Inspect worker	*	0,0538	0,0161
WC	Carry worker	-	*	-
WG	Groom worker	-	0,0128	0,0161
WI	Walk in nest	*	0,0422	-
WO	Walk out of nest	*	0,0159	-
WS	Carry stone	-	*	-
WX	Excrete	*	0,0031	-

noted in mated ants in any of the colonies, and they were carried during migrations to new nests.

There was evidence of temporal polyethism in the virgin workers (Figure 4). Newly eclosed ants were dark chocolate brown and took four or five days to sclerotize to a uniform slate black colour, but remained soft for about two weeks.



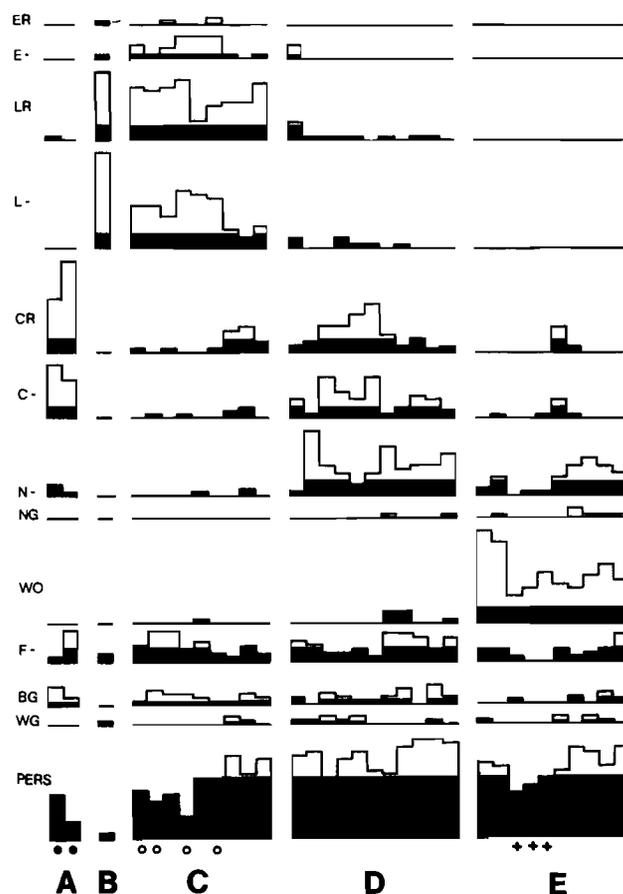
**Figure 3** Hierarchical cluster analysis of all workers in a colony of *Platythyrea lamellosa*, based on behaviour. A — callow workers; B — mated worker; C — nurses of eggs and larvae; D — workers tending nest and cocoons; E — foragers. The groups correspond to those in Figure 4.

**Table 2** Coefficients of variation (%) in frequency of performance of various categories of tasks by virgin workers in Groups C, D and E of Figures 3 and 4

Behavioural category	Group C	Group D	Group E
Tending eggs	75	316	—
Tend larvae	42	136	—
Tend cocoons	132	64	183
Tend nest	200	53	72
Guard nest	—	212	129
Walk out	283	181	40

Soon after eclosion they were found amongst the cocoons (Group A in Figure 4), and later moved to the larvae and eggs (Group C). All of the ants that died were foragers (Group E). Ants performing nest-related tasks (Group D) were sometimes seen foraging, but this behaviour formed a smaller proportion of their activities than it did in workers that died soon after observation.

Although the species is monomorphic, workers tending larvae and eggs were smaller, on average, than those performing nest-related tasks. However, the largest difference between mean size of workers performing different behaviours was 0,26 mm. Of the 1156 pairs of behaviours examined by ANOVA, the LSD criterion indicated that only four were statistically significant at the 1% level, and another 33 were significant at the 5% level. Many of the



**Figure 4** Sociogram of workers' behaviours, ordered and grouped as in Figure 3. Unshaded portions of each histogram are above the colony-wide average level of performance of that behaviour. A–E = groups defined in Figure 3; PERS = personal behaviours; other behavioural codes given in Table 1; ● = workers 1–5 days old; ○ = older callow workers; + = workers that died during the study.

pairs included personal behaviours, and no biologically meaningful pattern emerged.

### Nest architecture

Nests consisted of a single, vertical shaft dug into the ground, usually in an open, unvegetated area, and sometimes against a rock. The shaft descended 30–120 cm, and passed two to four lateral chambers in the deeper regions before ending in a final one about 80 mm square and 15 mm high. The single entrance was often surrounded by a low mound, 10–15 mm high and 150–300 mm in diameter, produced by the compaction of excavated soil by rain, which had also eroded some of them. If suitable stones were available in the vicinity of the nest site, they were piled on the mound around the entrance, raising it to heights of over 40 mm in the Esigodini area of Zimbabwe. In sandy soils there were several chambers within and immediately beneath the mound. In hard soils, especially if the mound was mainly of gravel, only one or two chambers were made. Two marked nests at Dunstable Farm, in the eastern Transvaal, were occupied for over 16 months.

When nests were dug up during the day, larvae, cocoons

and most of the workers and males were found in the surface chambers. Males were usually found clustered in one chamber, and larvae and cocoons were tended in separate chambers. Nests excavated when temperatures were low, either in the evening, or early in the day, had few or no brood or workers in the surface chambers, and most were found in the lowest chamber. The location of mated workers was not established.

## Discussion

The absence of a morphogenetically distinct reproductive caste in *Platythyrea lamellosa* is not related to an unusual division of labour, the general pattern of which resembles that of other ponerines (Corbara *et al.* 1989; Dantas de Araujo *et al.* 1988; Fresneau 1984; Fresneau *et al.* 1982; Fresneau & Dupuy 1988; Perez-Bautista *et al.* 1985; Rubin *et al.* 1989; Villet 1989, 1990, 1991). The mechanisms underlying individual behaviour include mating and age. The organization of labour could be related to the way individuals encounter tasks, both from moment to moment, and during the course of their lives. The relationship of nest structure to the spatial distribution of tasks may be important in this regard.

Whether a worker of *P. lamellosa* is mated or not also influences the tasks it attends. This is also true in other obligately queenless ponerines such as *Ophthalmopone berthoudi* (Peeters & Crewe 1985), *Streblognathus aethiopicus* (Ware *et al.* 1990), *Pachycondyla* (= *Bothroponera*) *krugeri*, *Platythyrea sp. A* (Villet 1989) and *P. schultzei* (Villet 1991). In *P. lamellosa* the only qualitative behavioural marker that distinguishes a mated worker is oviposition, but they can be identified quantitatively by other, more common, behaviours. This is useful for studies of regulation of reproduction in queenless ponerine societies.

As in other monomorphic ants (Brian 1979; Sudd 1982), factors related to age appear to shape the behaviour of virgin workers. Prime amongst these are expected to be each ant's accumulating experiences of tasks and stimuli (Deneubourg, Goss, Pasteels, Fresneau & Lachaud 1987), and physiological changes affecting their responses to these experiences (Feneron, Lachaud & Jaisson 1989). The variation between ants belonging to the same functional group could be due to such mechanisms. There is also evidence of a link between ovarian development and behaviour in *P. lamellosa* (Villet *et al.* 1990a).

How does variation in individual behaviour relate to the organization of work at the level of the colony? There is a fair measure of individual variation (Table 2) within the groups defined in Figure 3, including the occasional occurrence in some groups of behaviours more characteristic of other groups (Figure 4). Despite this, there is greater variation in behaviour between groups. Since four of the groups can be defined functionally, their members can be said to fill different roles in their colony. There must be some feature of the society that produces this pattern of relatively discrete roles.

Patterns of association among behaviours depend upon the way individual workers encounter opportunities for work within the nest. The association of several behaviours into one task occurs when they share a common focus. Other

behaviours may be excluded from a group because they have spatially isolated focuses. Similarly, localization of tasks and the readiness of workers to move about the nest (a physiological trait) are probably important in determining which (and how many) tasks are combined into a role. Both task localization and localized movement of workers occur in nests of the ponerine ant *Pachycondyla* (= *Neoponera*) *apicalis* (Fresneau, Corbara & Lachaud 1989). Cocoons and larvae are generally kept in separate chambers in the nest mound of *P. lamellosa* during the day, and ants tending them fill separate roles. Nests of *Megaponera foetens* also comprise two main chambers, one containing the queen, eggs and larvae, and the other the cocoons (Lepage 1981; Villet 1990b). Division of labour in this polyphenic species is more complicated than in *P. lamellosa*, but it also shows a separation of workers tending larvae and cocoons (Villet 1990). *M. foetens* is also known to sun its cocoons around the nest entrance, and remove them to the depths of the nest when ambient temperatures fall (Villet 1990). Task localization is thus not static in either of these species.

Little research has been done on the functional significance of nest structure in ponerine ants. The occurrence of at least two chambers in the mound can be related to the spatial localization of brood. The lateral chambers of nests of *P. lamellosa* probably represent old bottom chambers of nests that have subsequently been deepened. The stones piled on the mound might have a thermoregulatory function related to brood rearing in the hot, semi-arid habitats preferred by this species. Similar reasons may lie behind the sunning of cocoons by *M. foetens*.

The Amblyoponini and Cerapachyinae, primitive members of the poneroid complex (Bolton 1990), have opportunistically structured nests (e.g. Hölldobler & Wilson 1986; Traniello 1982). The development of highly structured, excavated nests in the more advanced Ponerini and Platythyreini may be a secondary evolutionary development in response to the need to localize tasks effectively in the nest. Why this need should arise is not entirely clear, but may be related to an evolutionary trend of increasing behavioural specialization and the advent of age polyethism in workers. Thus, while nest structure offers a proximate explanation for the maintenance of division of labour in some ants, it does not explain its ultimate origins (Sherman 1988). A deeper insight into division of labour is sure to emerge when phylogenetic studies of nest architecture are integrated with existing knowledge of division of labour.

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