

Social organization in some primitive Australian ants. I. *Nothomyrmecia macrops* Clark

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Summary

Results of laboratory-based ethological studies on two *Nothomyrmecia macrops* colonies with individually marked workers are reported. Interactive behavioural acts constituted less than 1% of all those recorded, revealing a strong tendency by the ants not to engage in social contact. Very few workers performed queen-directed acts. They stayed near the queen, though seldom in direct contact. Division of labour was otherwise barely apparent, except that some individuals showed a propensity to guard the nest entrance. No exchange of food was observed between workers, workers and queen, or adults and larvae (apart from worker placement of prey items with larvae). A queen fed from a *Drosophila* carcass retrieved from the nest floor, without assistance from workers. Systematic scanned observations confirmed levels of inactivity higher than previously observed in ants (comprising almost 2/3 of recorded behavioural acts). The time budget for activities directed toward the immature stages was the same in both colonies, and fluctuated during the circadian period. Non-nestmate larvae added to worker groups were more frequently licked than nestmate larvae, but this might not involve the particular recognition of nestmate *versus* non-nestmate brood. These observations support the hypothesis that *Nothomyrmecia* is primitively eusocial, and of special significance in myrmecology.

Introduction

Nothomyrmecia macrops Clark, 1934, was originally described from southeastern Western Australia, but has never again been collected there. It was rediscovered by Taylor and colleagues in 1977 in South Australia, where it is now known only from a limited area near Poochera (32°43'S, 134°50'W). It is considered to be one of the most primitive extant species of family Formicidae (Taylor, 1978; Hölldobler and Wilson, 1990). The evolutionary importance and rarity of *N. macrops* has motivated several field and laboratory studies on aspects of its biology (e.g. Taylor, 1978; Hölldobler and Taylor, 1983).

Anatomical considerations (especially the single waist node and non-tubulate abdominal segment IV, with stridulatory organ located ventrally) have supported taxonomic separation of *Nothomyrmecia* from the significantly primitive Australian subfamily Myrmeciinae (currently with the single extant genus *Myrmecia*). This led to reinstatement in 1978 of Clark's originally proposed, but subsequently subsumed, subfamily Nothomyrmeciinae, despite the recognition of substantial affinity between *Myrmecia* and *Nothomyrmecia* (Taylor, 1978; Bolton, 1990; Hölldobler and Wilson, 1990).

The cuticular hydrocarbons of *Nothomyrmecia* contain internally branched, internal alkenes, a remarkable feature unique not only among ants (including *Myrmecia*), but insects in general (Brown et al., 1990). The sting apparatus of *Nothomyrmecia* appears to possess more derived characters than in *Myrmecia* (Kugler, 1980).

Conversely, the structures and secretions of several pheromonal glands in *Myrmecia* are similar to those of *Nothomyrmecia*, and have been held to support the classification of both genera in subfamily Myrmeciinae (with the synonymy of subfamily Nothomyrmeciinae) as in W. L. Brown's (1954) classification (Billen, 1988, 1990; Billen et al., 1988). A further similarity between these ants is the presence of a true spermatheca in all workers of both genera (Hölldobler and Taylor, 1983; Crosland et al., 1988).

Nothomyrmecia has the highest chromosome number known for the Hymenoptera ($2n = 94$), and one of the highest of phylum Arthropoda. *Myrmecia* has species with numbers almost as high (known maximum $2n = 84$ in *M. brevinoda* Forel). It also has the greatest interspecific range of chromosome numbers known for any relevantly studied animal genus, including the exceptional $2n = 2$ of *M. croslandi* Taylor, the lowest number possible in a eucaryote (Imaï et al., 1991; Taylor, 1991). The significance of chromosome numbers in assessing the relationship between *Myrmecia* and *Nothomyrmecia* is thus not clear.

N. macrops has been referred to as a 'living fossil' (Taylor, 1978), and called 'the dinosaur ant' (Bartell, 1985). The implications of these epithets are supported by its cryptic habits, for example a preference to forage individually after dusk and in relatively low temperature conditions (Taylor, 1978; Hölldobler and Taylor, 1983), or the long periods (sometimes exceeding half an hour) spent in a cataleptic position by foraging workers when released in the field after being held with forceps for only a few minutes (Jaisson, *pers. obs.*).

Inter-nest tolerance in *N. macrops* seems much more pronounced than in other ant species, whether 'primitive' or 'advanced'. In the field, workers from different colonies may forage on the same small tree trunk without antagonism, and individuals from distant nests quickly settle when artificially mixed, even when the queen of one group is present (Taylor, 1978; Hölldobler and Taylor, 1983). Enzymatic electrophoresis has demonstrated that intra-colony relatedness is rather low (Ward and Taylor, 1981), perhaps supporting the possibility that workers might at times join nests other than their own, as implied by the experiments of Hölldobler and Taylor (1983). The blends of cuticular hydrocarbons analysed for three *Nothomyrmecia* colonies were very similar (W. V. Brown et al., 1990), and this might be a factor related to between-nest toleration.

The parameters of division of labour among ants are generally considered to reflect reliably their level of social evolution, with workers of advanced species being the more specialized ergonomically (Wilson, 1971; Hölldobler and Wilson, 1990). For example, Traniello's (1978) observations that worker age-based polyethism was absent in *Amblyopone pallipes* Haldeman (Ponerinae: Amblyoponini), at least under his experimental conditions, is held to reflect the primitive status traditionally accorded to *Amblyopone* by taxonomists.

We have investigated division of labour in *Nothomyrmecia* and in several *Myrmecia* species by observing colonies containing workers artificially marked to facilitate individual recognition. The first of these studies, covering *N. macrops*, is presented here. In addition we report an experiment exploring aspects of putative colony-brood recognition in *Nothomyrmecia*.

Materials and methods

Social organization

Two colony series from nests about 17 m apart were excavated at Poochera on November 29th and December 2nd, 1988. Colony 1 included a queen, 42 workers, 2 small larvae, 20 large larvae and 5 cocoon-enclosed pupae. Colony 2 comprised a queen, a male, 35 workers, an egg, 9 small larvae, 31 large larvae and 15 pupae. The colonies were installed several days later in artificial plaster nests, maintained at a constant 20 °C, at the CSIRO Division of Entomology, Canberra. All workers were marked with minute, photographically prepared identification labels (as used by Fresneau and Charpin, 1977). The nests, covered with a sheet of red perspex, were built using the same mould, and comprised an entrance tunnel 3 cm long, two small chambers (diameter = 5,5 cm) and one large terminal chamber (diameter = 11,5 cm) placed linearly and linked by two 3,5 cm-long tunnels. The entrance opened to a plastic box (26 × 19 cm), which provided a foraging arena. Living *Drosophila* flies were deposited daily in the foraging arena, and honey was permanently available in the second nest chamber. Systematic scanned observations (see Jaisson et al., 1988 for details) were carried out from December 7th to 15th on colony 1 (53 observations), and from December 13th to December 20th on colony 2 (68 observations), at times scattered throughout the 24-hour day. Each scan record noted the behavioural act and location of identified individuals ants. A total of 1692 such individual observations were obtained for colony 1 and 2310 for colony 2. *Immobility* was recorded as a specific behavioural act.

The data were analysed by summing the behavioural items recorded for individual ants, as noted in a matrix where the frequency of each elementary act was recorded for each individual. The frequencies were then totalled to obtain a social ethogram for the whole colony. The resulting ethograms are comparable to those previously presented by other authors (e.g. Wilson, 1976) using different data collection methods. Individual behavioural profiles were then determined using multivariate correspondence analysis. This permitted the regrouping of elementary acts in nine main categories corresponding to social functions.

Finally, numerical taxonomic methods, particularly including cluster analysis (algorithm CAH2CO, ADDAD library), enabled us to classify the ants according to the levels of affinity between their individual behavioural profiles. This provided a sociogram for each colony, summarizing the distribution of tasks within each. Graphical representation utilized the methods of Bertin (1977). The distribution of main behavioural categories in each colony was analyzed for each of six recognized groups of ants, and related to circadian period to investigate rhythms in activity.

Colony-brood recognition

The experiment on brood recognition was performed after completion of the scanning observations.

Sets of workers from each colony were removed and established separately in glass test-tube artificial nests (diameter 16 mm), each with a water reservoir retained by cotton wool at its closed end. Two hours later, 10 large larvae from each colony were mixed and placed together near the open end of each tube. Each larva had been previously marked with a small piece of coloured plastic glued ventrally, to denote its source colony. The order was recorded in which larvae in each series were gathered by workers and carried deep into the nest (close to the water reservoir). Twenty-four hours later, four 10-minute observation sessions at 30-minute intervals were conducted (under red illumination) with each series. Larval-oriented behavioural acts by workers were scored, and later analysed to investigate differences in the relationships between the workers and nestmate *versus* non-nestmate larvae. Data were compared using Chi-square tests.

Results

Ethograms

The ethograms for both colonies constitute Table 1. Behavioural acts (including those directed towards the queen) are classified there in nine higher categories. Similar frequency scores for recorded acts are indicated for both colonies, and the behavioural profiles of the two are not significantly different (Kolmogorov-Smirnov test). The three behavioural acts of the category *Self* comprise about 80% of the totals recorded for both colonies, with *Immobility inside nest* alone covering 65% of the relevant records. The frequencies of social interactions between workers, or between workers and queen, were remarkably low. Recordings of all interactive behavioural acts between adults in fact represent less than 1% of the total in both colonies.

A queen was observed once to feed directly on haemolymph exuding from a masticated *Drosophila* corpse retrieved by her from the nest floor (Fig. 1). The fly had been previously captured and stung in the foraging arena, and transported into the nest chamber by a worker. No other form of feeding by queens was noted during this study, and none has been observed by other investigators during many accumulated hours of systematic and casual observations of *N. macrops* colonies in artificial nests

Table 1. Social ethograms for colonies 1 and 2. Subtotals corresponding to each main behavioural category are indicated in italics

Behavioural act	Frequency of behavioural acts	
	Colony 1 (<i>N</i> = 1692)	Colony 2 (<i>N</i> = 2310)
Self		
Self-grooming	0.0681	0.0416
Immobility inside nest	0.6572	0.6558
Patrolling inside nest	0.0869	0.1316
<i>subtotal</i>	<i>0.8122</i>	<i>0.829</i>
Interactive (with worker)		
Allogrooming adult worker	0.0071	0.0039
Palping worker		0.0017
Licking teneral worker		0.0004
<i>subtotal</i>	<i>0.0071</i>	<i>0.006</i>
Interactive (with queen)		
Palping queen	0.0006	0.0013
Licking queen	0.0012	0.0004
<i>subtotal</i>	<i>0.0018</i>	<i>0.0017</i>
Guarding (nest entrance)	0.0343	0.0286
Outside acts		
Patrolling outside nest	0.0048	
Foraging	0.0148	0.0017
<i>subtotal</i>	<i>0.0196</i>	<i>0.0017</i>
Brood caring (except pupae)		
Palping larva	0.025	0.0459
Licking larva	0.0231	0.0117
Feeding larva		0.0009
Carrying larva	0.0083	0.0056
Standing upon spining larva	0.0284	
Banking spining larva with soil particles	0.0083	0.0004
Standing upon larvae		0.0004
Nibbling larva	0.0077	0.0013
<i>subtotal</i>	<i>0.1008</i>	<i>0.0662</i>
Brood caring (pupae)		
Palping pupa	0.0142	0.0346
Licking pupa	0.0006	0.0104
Carrying pupa		0.0009
Removing soil particles from pupa	0.0012	0.0005
Biting pupa		0.0039
<i>subtotal</i>	<i>0.016</i>	<i>0.0503</i>
Domestic		
Manipulating soil particles near nest entrance	0.0006	0.0004
Handling nest material		0.0009
Carrying empty pupa's envelope		0.0017
<i>subtotal</i>	<i>0.0006</i>	<i>0.003</i>

Table 1 (continued)

Behavioural act	Frequency of behavioural acts	
	Colony 1 (<i>N</i> = 1692)	Colony 2 (<i>N</i> = 2310)
Feeding		
Feeding on honey in the nest		0.0009
Licking the plaster	0.0035	0.0031
Carrying prey inside nest		0.0026
Chewing prey inside nest	0.0041	0.0069
<i>subtotal</i>	<i>0.0076</i>	<i>0.0135</i>
TOTAL	1	1

(notably by Taylor, *pers. com.*). Trophic egg production or the exchange of ingluvial food within nests have likewise never been observed in this species (Taylor, *pers. com.*). Feeding by *Nothomyrmecia* queens has not otherwise been observed. These and other observations imply (1) that queens in *Nothomyrmecia* are not fed directly by workers, that (2) the workers do not exchange food among themselves, and that (3) larvae are nourished entirely by feeding directly on worker-foraged preys.

Very few observed behavioural acts were directed by workers towards the queen, and their frequency was almost the same in both colonies (0.18 and 0.17% respectively). They included only palpation and licking. Overall, *Immobility inside nest* was the behavioural act most frequently observed, followed by *Self-grooming* and *Guarding* of the nest entrance.

Differences between the colonies were evident in two regards:

- 1) Foraging and feeding. Although foraging individuals were somewhat infrequently observed, the frequency of feeding acts recorded for colony 2 was twice that of

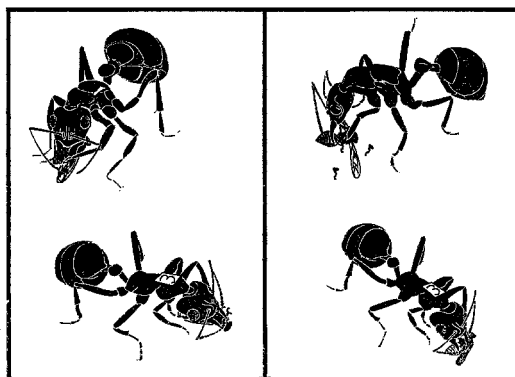


Figure 1. A *Nothomyrmecia* queen (up) is masticating a captured *Drosophila* while a nearby worker facing another direction does the same (drawings taken from two photographs separated by a seven-minute delay)

colony 1. This was possibly related to the fact that *Drosophila* flies released in the foraging arena sometimes penetrated the nest entrance, where guard workers caught them and carried them deeper into the nest (such behaviour would have been recorded as *Carrying prey inside nest*, not as *Foraging*).

- 2) Concerning brood-tending behaviours. *Standing upon spinning larva* was almost exclusively present in colony 1. This, we consider, relates to the greater crowding, and high worker: pupa ratio in colony 1. Behavioural acts involving the tending of pupae were almost three times as frequent in colony 2 than in colony 1, but this corresponds to the ratios of pupal numbers between the two colonies.

Finally, it is remarkable that, despite different global numbers of brood (much higher in colony 2) the time budget dedicated to brood-tending acts was nearly the same in both colonies (11,68% and 11,65% respectively). This implies that the nursing behaviour of workers in colony 2 was biased towards pupal brood.

Sociograms

The sociograms for both colonies (Fig. 2, 3) confirm a high level (approximately 75%) of self-oriented behavioural acts, expressed there in whole-colony settings. Differences between the six recognized worker-groups are evidenced. Behavioural acts involving the care of larvae and guarding of the nest entrance were substantially more prominent than elsewhere in groups 1 and 4 of colony 1, and groups 1, 2 and 3 of colony 2.

The queens were assigned to group 5, which was the largest and most behaviourally inactive set in both colonies. A co-presence index was developed, based on the probability of individual workers being recorded in the same chamber as the queen. Its values range from 0 (never in the queen's chamber) to 1 (always there). This index was generally lower than 0.5 for individuals of most behavioural groups. The exceptions were members of those groups which provided all records of allogrooming directed toward the queen. Their high co-presence indices clearly proceed from their regular close proximity to the queen, and indicate that they constitute a functional 'royal retinue'. All queen allogrooming in colony 1 was provided by the 3 workers of group 6. They had a mean co-presence index of 0.71, *versus* 0.22 to 0.53 for workers of other groups. In colony 2, queen allogrooming was performed by some brood nurses of group 2 (co-presence index = 0.69). Members of other groups had a lower intra-group co-presence index (0.10 to 0.44), as in colony 1.

The nine main behavioural categories were not equally distributed among the 6 defined worker groups. Only one, *Guarding the nest entrance*, evidenced a high degree of specialization among its executors (see the colony 1 sociogram, Fig. 2). This provides evidence of a limited, weak tendency towards division of labour among *Nothomyrmecia* workers. Tending behaviours and foraging (in colony 1) were generally distributed across almost all behavioural groups. The few more-or-less specialist nest-entrance guards identified above (group 4 in colony 1 and groups 3 and 4 in colony 2) were, however, clearly exceptional, since they participated only marginally in the tending of larval or pupal brood.

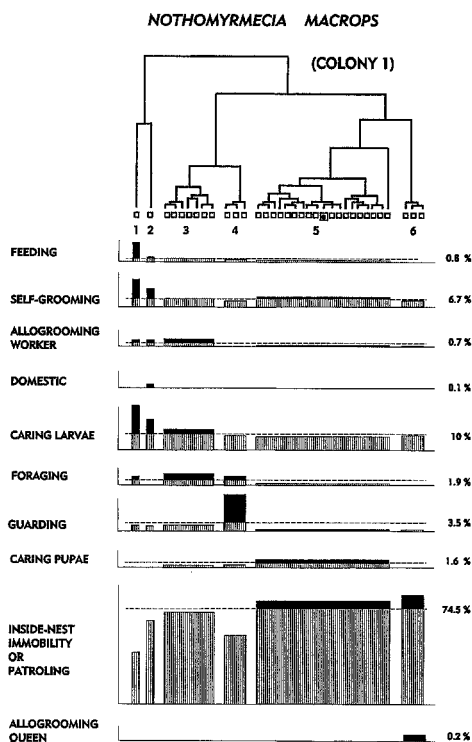


Figure 2. Sociogram of colony 1. Graphic representation summarizing the behavioural profiles of the groups obtained by clustering. The groups numbered 1 to 6 are placed in columns whose widths are proportional to the size (number of individuals) of the group. The 10 behaviours are placed in rows in which frequency histograms are located according to a standard scale. The horizontal dotted lines indicate the mean frequency corresponding to the percentage of each activity out of the total observed behaviours (shown on the right). The parts of the histogram below the dotted lines are shaded grey, while the above parts are black. This representation makes easier the visualization of the results, and allows one to describe the dominant or characteristic behaviours in each group.

Activity rhythms

The frequencies of most behavioural acts did not differ noticeably across the circadian period. Tending and foraging activities, however, varied importantly. Caring for larvae by workers predominated during the period 0000–0900 h and attention to cocoons tended to increase as larval care diminished (Fig. 4). Foraging behaviour, which occurs nocturnally in the field, peaked during the 1500–1800 h period, somewhat earlier than in nature. This probably related to laboratory conditions.

Brood recognition experiment

The order in which the 20 marked nestmate (*N*) and non-nestmate ('alien'-*A*) larvae were carried into the experimental nest tubes was random:

Colony 1: ANANNAANNANANAANANNA
Colony 2: ANANANNANANANAANNANA

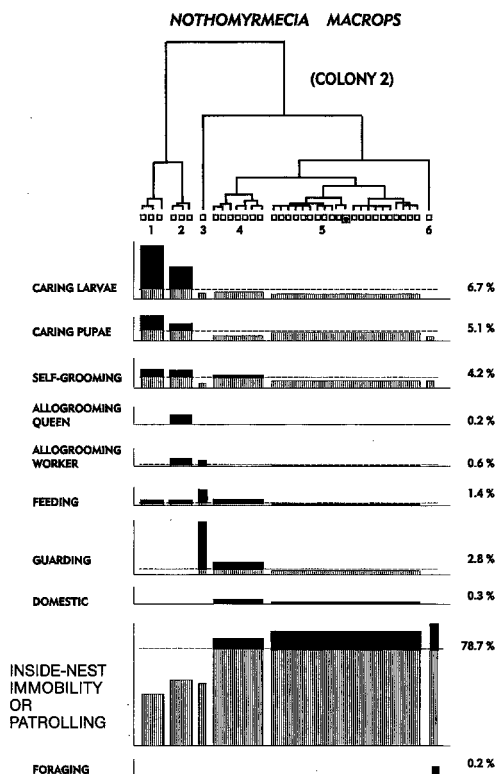


Figure 3. Sociogram of colony 2 (see Figure 2 for captions).

The tallies of subsequent brood-tending behavioural acts directed by workers towards the larvae are indicated in Table 2 (where results from the four observation sessions are pooled). Colony 1 workers delivered more tending acts to non-nestmate larvae than to nestmates (Chi square = 4.41; $P < 0.05$), but these activities were deployed almost equally in colony 2. The apparent colony 1 bias reduces to insignificance when data are pooled with those from colony 2. However, if licking alone among the relevant behavioural acts is considered, a preference for non-nestmate larvae appears significant for colony 1 (Chi square = 6.43; $P < 0.02$) and for both colonies when the results are pooled (Chi square = 6.45; $P < 0.02$). Such preference is no significant for colony 2 considered separately. The other tending behaviours (*Antennation*, *Transport*, *Nibbling* and *Feeding*) show no such putatively significant patterns, neither alone nor collectively.

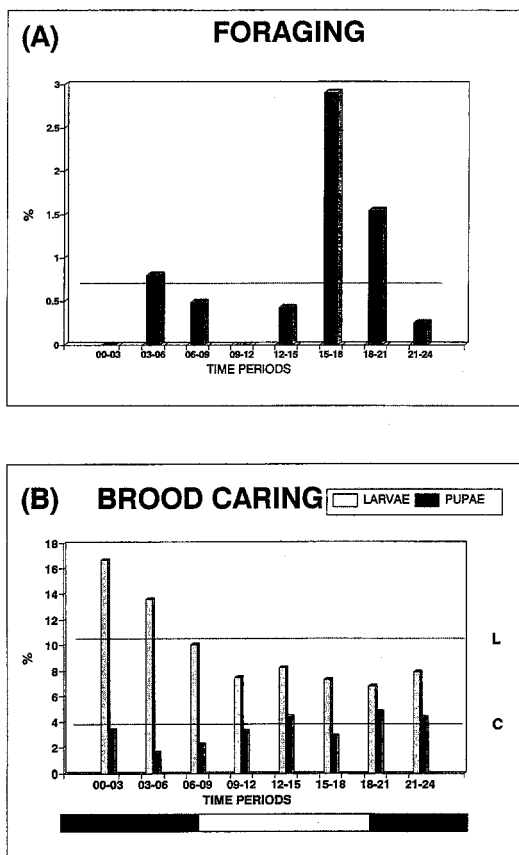


Figure 4. Evolution along the circadian period of the frequency of foraging (A) and brood-caring (B) activities for two colonies of *Nothomyrmecia macrops*.

Table 2. Colony-brood recognition experiment: number of tending behavioural acts delivered to nestmate larvae and non-nestmate larvae during the four observation sessions by workers from colonies 1 and 2

Workers from	Tending acts	toward:	
		nestmate larvae	non-nestmate larvae
Colony 1	licking:	10	25
	others:	11	12
	total:	21	37
Colony 2	licking:	11	16
	others:	17	11
	total:	28	27

Discussion

The very high level of inactivity (termed *Immobility* in Tab. 1) in both of our *Nothomyrmecia* colonies is striking. It provided 2/3 of all our recorded behavioural acts. Table 3 compares with those of other studies involving ponerine and myrmecine ants (of the genera *Amblyopone*, *Diacamma*, *Dinoponera*, *Ectatomma*, *Pachycondyla*, *Neoponera* and *Myrmecia*) in which techniques identical to ours were used. Interestingly, *Amblyopone pallipes*, which may be considered the most socially primitive of this set, is also closest to *N. macrops* in its level of observed inactivity.

The extremely low level of social interactions in *Nothomyrmecia*, when compared to *Pachycondyla* and *Ectatomma* (Tab. 3), is also of special interest. We believe that it relates partly to the large distances of separation reported elsewhere between individual ants stationed in *N. macrops* nests (Jaisson et al., 1991). *Nothomyrmecia* adults stand separated to a degree remarkable when compared with other ants, including those of several observed *Myrmecia* species (Fresneau et al., unpublished data). This lack of sociability might be a correlate of the generally hypothecated primitive eusocial status of *N. macrops*.

The apparent absence of any systematic mechanism for transfer of food from workers to queens further exemplifies the general tendency towards individuality in *Nothomyrmecia*. It can also be considered a significantly primitive attribute of this remarkable ant. In effect, evolution of eusociality to the level represented by *Nothomyrmecia* seems not to have incorporated special measures for sustenance of the permanently nest-enclosed queen, a matter which might otherwise have been considered a major adaptive problem for the earliest eusocial formicids. Queen sustenance could hardly be more simply effected than in the manner observed here, and no special adaptations seem to have been involved in its evolution to this stage.

This contrasts with observations on several *Myrmecia* species, where the consumption by queens of worker-laid trophic eggs is well documented, along with the transfer of trophic eggs between workers, and from workers to larvae (Freeland, 1958). Trophallaxis has been reported in *Myrmecia regularis* Crawley, *M. vindex*

Table 3. Review of available data on immobility, recorded by similar techniques on various ant species belonging to three primitive subfamilies

Species	Immobility level	Reference
<i>Amblyopone pallipes</i>	0.418	Lachaud et al. (1988)
<i>Diacamma</i> sp.	0.279	Dhabi and Jaisson (unpub.)
<i>Dinoponera quadriceps</i>	0.152	Dantas et al. (1988)
<i>Ectatomma quadridens</i>	0.299	Rubin et al. (1989)
<i>E. ruidum</i>	0.206	Corbara et al. (1986)
<i>Pachycondyla apicalis</i>	0.325	Fresneau and Dupuy (1988)
<i>P. obscuricornis</i>	0.288	Fresneau (1984)
<i>P. villosa</i>	0.287	Perez et al. (1985)
<i>Myrmecia croslandi</i>	0.277	Fresneau et al. (unpub.)
<i>M. fuscipes</i>	0.283	Fresneau et al. (unpub.)
<i>Nothomyrmecia macrops</i>	0.656	this paper

Smith (Haskins and Whelden, 1954) and *M. brevinoda* (Crosland et al., 1988), but it appears not to occur in some *Myrmecia* species otherwise known to lay trophic eggs (Taylor, pers. obs.).

Guarding at the nest entrance appears to be the most specialized activity practiced by *Nothomyrmecia* workers. This is consistent with observations on primitively eusocial bees, where nest-guarding appears to be the first behavioral act to appear in the development and evolution of division of labour among workers. In fact, an important general step in any evolution towards hymenopterous eusociality could be *communal nesting with nest-guarding*, the latter serving to reduce access to brood by predators and parasites (Andersson, 1984; and see, for example, Sakagami and Maeta, 1977, for *Ceratina* bees).

We see no evidence of a dichotomy in *Nothomyrmecia* between in-nest specialist workers (*Innendienst*) and others (*Aussendienst*) dedicated to out-of-nest activities. The most important group of foragers in colony 1 (group 3, Fig. 2), for example, was also significantly involved with the care of larvae. Such specialization appears to provide the organizing structure on which division of labour is based in the ponerine ant species discussed above (Fresneau, 1984; Fresneau and Dupuy, 1988; Corbara et al., 1989) and in others belonging to the same subfamily (*Megaponera foetens* Fabr.: Villet, 1990 a; *Platythyrea lamellosa* Roger: Villet, 1990 b). This matter, again, could relate to the hypothesized basal position of the *Nothomyrmecia* lineage in formicid phylogeny.

Foraging activity was low in our laboratory cultures, and this might relate partly to the fact that foraging occurs preferentially at lower temperatures in the field (Hölldobler and Taylor, 1983). *Nothomyrmecia* foragers in nature are now known to return promptly to nests once prey has been secured (but otherwise to forage until near dawn). Colonies have been observed to forgo foraging on some nights (when other nests were active, confirming that microclimatic conditions were suitable), possibly when fresh food supplies are not a priority (Taylor, pers. obs.). The abundance of easily-secured *Drosophila* prey at short range in our foraging arenas could well have depressed the levels of foraging activity observed in our subject colonies.

Nothomyrmecia appears to be significantly more primitive than *Myrmecia* (see our second paper on social organization in primitive Australian ants, Fresneau et al., in preparation), in that the division of worker labour is much more evident in the *Myrmecia*, and social interactions between individuals much more frequent. *Nothomyrmecia* is here confirmed in our opinion to be a 'living fossil' ant of genuinely primitive eusocial status.

The experiment on brood recognition evidenced a tendency by workers to preferentially lick non-nestmate larvae. Such licking might facilitate transfer of the colony odour 'visa' to larvae. This could explain our observations, assuming that adult workers are able to sense visa deficiency in individual larvae, and to respond by actively licking them in order to redress the deficiency. The non-nestmate larvae might thus have been preferentially licked *simply because they evidenced visa deficiency relative to nestmate larvae* – their particular recognition as aliens by the workers might therefore never have occurred. In this case our data would not support a hypothesis that nestmate and non-nestmate brood are specifically recognised as

such. The 'visa factor' effect we have hypothesized needs to be accounted for in all claims that colony-brood recognition in ants has been demonstrated.

This is of interest because of the previously noted similarity between *Nothomyrmecia* colonies in the composition of their epicuticular waxes, which could furnish the appropriate chemical visa cues (Brown et al., 1990). Despite the rarity of *Nothomyrmecia*, this matter, like so many others, would be worthy of further research.

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References

- Andersson, M., 1984. The evolution of eusociality. *Ann. Rev. Ecol. Syst.* 15:165–189.
- Bartell, R., 1985. The Dinosaur ant. *Bogong, March–April 1985* 10–12.
- Bertin, J., 1977. *La graphique et le traitement graphique de l'information*. Flammarion, Paris.
- Billen, J.P.J., 1988. Comparaison entre les fourmis Australiennes des genres *Myrmecia* et *Nothomyrmecia*. *Actes Coll. Ins. Soc.* 4:27–33.
- Billen, J.P.J., 1990. The sting bulb gland in *Myrmecia* and *Nothomyrmecia* (Hymenoptera: Formicidae): a new exocrine gland in ants. *Int. J. Insect Morphol. & Embryol.* 19:133–139.
- Billen, J.P.J., B.D. Jackson and E.D. Morgan, 1988. Secretion of the Dufour gland of the ant *Nothomyrmecia macrops* (Hymenoptera: Formicidae). *Experientia* 44:715–719.
- Bolton, B., 1990. Army ants reassessed: the phylogeny of the doryline section (Hymenoptera, Formicidae). *J. Nat. Hist.* 24:1339–1364.
- Brown, W.L., 1954. Remarks on the internal phylogeny and subfamily classification of the family Formicidae. *Ins. Soc.*, 1:21–31.
- Brown, W.V., P. Jaisson, R.W. Taylor and M.J. Lacey, 1990. Novel internally branched, internal alkenes as major components of the cuticular hydrocarbons of the primitive Australian ant *Nothomyrmecia macrops* Clark (Hymenoptera: Formicidae). *J. Chem. Ecol.* 16:2623–2635.
- Corbara, B., D. Fresneau and J.-P. Lachaud, 1986. An automated technique for behavioural investigations of social insects. *Behav. Process.* 13:237–249.
- Corbara, B., J.-P. Lachaud and D. Fresneau, 1989. Individual variability, social structure and division of labour in the ponerine ant *Ectatomma ruidum* Roger (Hymenoptera: Formicidae). *Ethology* 82:89–100.
- Crosland, M.W.J., R.H. Crozier and E. Jefferson, 1988. Aspects of the biology of the primitive ant genus *Myrmecia* F. (Hymenoptera: Formicidae). *J. Aust. ent. Soc.* 27:305–309.
- Dantas de Araujo, C., D. Fresneau and J.P. Lachaud, 1988. Premiers résultats sur l'éthologie d'une fourmi sans reine: *Dinoponera quadriceps*. *Actes Coll. Ins. Soc.* 4:149–155.
- Freeland, J., 1958. Biological and social patterns in the Australian bulldog ants of the genus *Myrmecia*. *Aust. J. Zool.* 6:1–18.
- Fresneau, D., 1984. Développement ovarien et statut social chez une fourmi primitive: *Neoponera obscuricornis* (Hym., Formicidae, Ponerinae). *Ins. Soc.* 31:387–402.
- Fresneau, D. and A. Charpin, 1977. Une solution photographique au problème du marquage individuel des petits insectes. *Ann. Soc. Entomol. Fr. (N.S.)* 13:1–5.
- Fresneau, D. and P. Dupuy, 1988. A study of polyethism in a ponerine ant: *Neoponera apicalis* (Hymenoptera: Formicidae). *Anim. Behav.* 36:1389–1399.
- Haskins, C.P. and R.M. Whelden, 1954. Note on the exchange of ingluvial food in the genus *Myrmecia*. *Ins. Soc.* 1:33–37.

- Hölldobler, B. and R. W. Taylor, 1983. A behavioral study of the primitive ant *Nothomyrmecia macrops* Clark. *Ins. Soc.* 30:384–401.
- Hölldobler, B. and E. O. Wilson, 1990. *The Ants*. Springer-Verlag, Berlin.
- Imai, H. T., R. W. Taylor, M. Kubota, K. Ogata and M. Y. Wada, 1991. Notes on the remarkable karyology of the primitive ant *Nothomyrmecia macrops* Clark, and of the related genus *Myrmecia Fabricius* (Hymenoptera: Formicidae). *Psyche, Camb.* 97:133–140.
- Jaisson, P., D. Fresneau and J. P. Lachaud, 1988. Individual traits of social behavior in ants. In: *Interindividual Behavioral Variability in Social Insects* (R. L. Jeanne, Ed.), Westview Press, Boulder, pp. 1–51.
- Jaisson, P. F. Nicolosi, R. W. Taylor, D. Fresneau and A. Lenoir, 1991. Distance to the nearest neighbour and workers' specialization along the evolution of primitive ants. *Proc. JSPS-CNRS Seminar 'Evolution of Animal Social Behaviour'*, Inuyama, Japan, pp. 5–7.
- Kugler, C., 1980. The sting apparatus in the primitive ants *Nothomyrmecia* and *Myrmecia*. *J. Aust. ent. Soc.* 19:263–267.
- Lachaud, J. P., D. Fresneau and B. Corbara, 1988. Mise en évidence de sous-castes comportementales chez *Amblyopone pallipes*. *Actes Coll. Ins. Soc.* 4:141–147.
- Pérez Bautista, M., J. P. Lachaud and D. Fresneau, 1985. La división del trabajo en la hormiga primitiva *Neoponera villosa* (Hymenoptera: Formicidae). *Fol. Entomol. Mex.* 65:119–130.
- Rubin, M., J. P. Lachaud and D. Fresneau, 1989. La structure sociale chez *Ectatomma quadridens*: comparaison au sein du genre *Ectatomma*. *Actes Coll. Ins. Soc.* 5:265–273.
- Sakagami, S. F. and Y. Maeta, 1977. Some presumably presocial habits of Japanese *Ceratina* bees, with notes on various social types in Hymenoptera. *Ins. Soc.* 24:319–343.
- Taylor, R. W., 1978. *Nothomyrmecia macrops*: A living-fossil ant rediscovered. *Science* 201:979–985.
- Taylor, R. W., 1991. *Myrmecia croslandi* sp.n., a karyologically remarkable new Australian bulldog ant (Hymenoptera: Formicidae: Myrmeciinae). *J. Aust. ent. Soc.* 30:288.
- Traniello, J. F. A., 1970. Caste in a primitive ant: absence of age polyethism in *Amblyopone*. *Science* 202:770–772.
- Villet, M. H., 1990a. Division of labour in the Matabele ant *Megaponera foetens* (Fabr.) (Hymenoptera: Formicidae). *Ecol. Ethol. Evol.* 2:397–417.
- Villet, M. H., 1990b. Social organization of *Platythyrea lamellosa* (Roger) (Hymenoptera: Formicidae): II. Division of labour. *S.-Afr. Tydskr. Dierk.* 25:254–259.
- Ward, P. and R. W. Taylor, 1981. Allozyme variation, colony structure and genetic relatedness in the primitive ant *Nothomyrmecia macrops* Clark (Hymenoptera: Formicidae). *J. Aust. ent. Soc.* 20:177–183.
- Wilson, E. O., 1971. *The Insect Societies*. Belknap/Harvard University Press, Cambridge, MA.
- Wilson, E. O., 1976. A social ethogram of the neotropical arboreal ant *Zacryptocerus varians* (F. Smith). *Anim. Behav.* 24:354–363.

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