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WORKER POLYMORPHISM AND NEST STRUCTURE IN *MYRMECIA BREVINODA* FOREL (HYMENOPTERA: FORMICIDAE)

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Abstract

A large nest of *Myrmecia brevinoda* (with a soil mound 70 cm tall) contained 2576 workers and 1 queen. Other small ants, termites and various insect larvae were also found in uninhabited parts of the mound. Although workers exhibit considerable size variation (length: 13-36 mm), relative growth (head length versus head width) among workers is not allometric. Thus workers are monomorphic although they fall into 2 obvious size classes which overlap broadly. Small workers were abundant in the lower parts of the nest while larger workers prevailed in the upper parts. Field observations confirmed the occurrence of size polyethism, i.e. larger workers were engaged in hunting, defence and extranidal building, while smaller workers excavated soil from inside the nest.

Introduction

Myrmecia F., found only in Australia and New Caledonia, are the most primitive living ants together with *Nothomyrmecia* Clark and perhaps *Amblyopone* Erichson (Wilson 1971). *Myrmecia* spp. are generally distinguished by simple social traits, although various species exhibit relatively advanced features. Thus, while many species have small colonies and nest simply in the ground, others have large colonies consisting of more than 1000 workers and construct imposing nest mounds (e.g. Gray 1974). Furthermore, in some species there is considerable intracolonial variation in the size of workers, and these are sometimes thought of as polymorphic. Social polymorphism has been defined (Wilson 1953) as "allometry occurring over a sufficient range of size variation within a normal mature colony to produce individuals of detectably different form at the extremes of the size range".

M. brevinoda Forel, which was previously referred to as *M. eudoxia* Forel (Wheeler 1933) as well as *M. gigas* Forel (Clark 1951) (see Taylor 1987), is a species with workers which range in size from 13-36 mm. We report on a morphometric analysis of worker variation, as well as observations on size polyethism and nest architecture.

Methods

In November 1987, several mounds of *M. brevinoda* were surveyed along a transect in *Eucalyptus-Casuarina* woodland located 8 km w of Paluma, north Queensland. These mounds were measured, and one nest ("A") was completely excavated in order to study its architecture, population size, presence of inquilines, and worker polymorphism. In another nest ("B"), workers engaged in various activities were collected: hunters retrieving prey, guard ants who responded to our partial destruction of their mound, extranidal builders repairing the surface of the mound, and intranidal builders bringing up soil from inside the nest.

In the laboratory, various head measurements were taken: nest A — outerorbital distance of all workers, and also head length in a sample of 60 workers; nest B — outerorbital distance (also body colour and mandibular wear) of 176 workers.

Vouchers specimens have been placed in the Australian National Insect Collection, CSIRO, Canberra.

Results

Nest structure

Eight mounds were found along a 1 km-long transect. They were conical (Fig. 1a) with volumes varying from 0.011 to 0.142 m^3 (Table 1). Following partial destruction of the entrances, the builders first plaited *Casuarina* needles and then covered them with soil. Each mound had 1 (occasionally 2 or 3) entrances near the top of the mound (Fig. 1b).

The mound of nest A was 70 cm tall and had 2 openings, but 1 of them was little used. Shafts descending from the active opening frequently ramified and fused again in the lower half of the mound, forming a complicated network of many tunnels. At the base of the mound, these tunnels were sporadically enlarged to form brood chambers. Below ground, 3 shafts continued downward and chambers occurred at 5-20 cm intervals. The deepest shaft reached 120 cm. Pupae were found in the upper parts of the nest while larvae occurred lower. Eggs were found in several chambers, while the queen was collected at a depth of 108 cm. Nest A yielded 1 queen, 2576 workers, 218 cocoons, 9 incompletely-spun cocoons, and 972 larvae. The eggs of *Myrmecia* do not adhere in packets and therefore all could not be collected and counted.

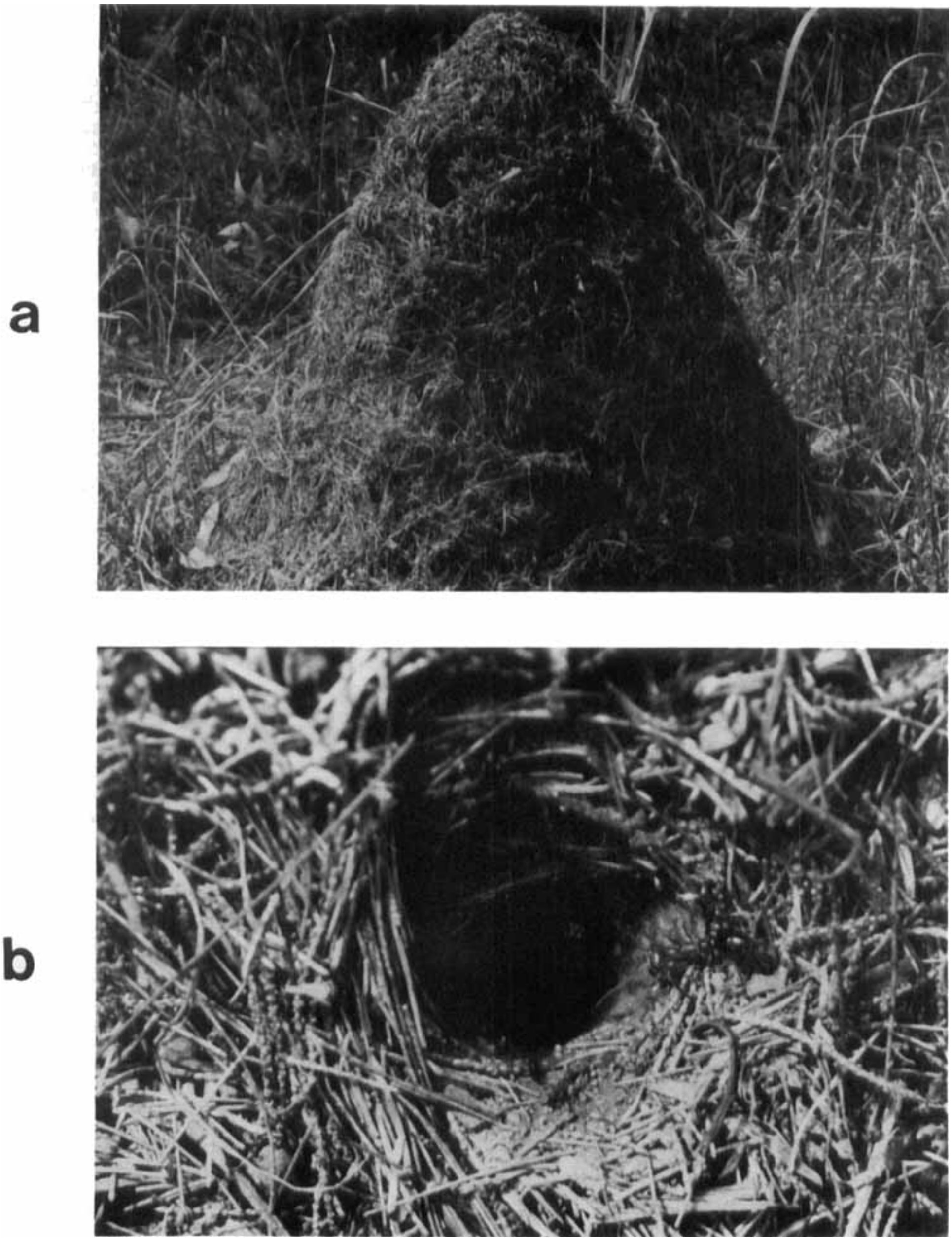

FIG. 1—Nest A: (a) soil mound covered with a layer of *Casuarina* pine needles, (b) nest entrance.

Various species of small ants were collected from the mound of nest A: *Oligomyrmex* sp., *Mayriella abstinens* Forel, *Monomorium* sp., *Sphinctomyrmex* sp. and *Pheidole* sp. (1 dealate queen). Only *Oligomyrmex* sp. cohabited nest chambers with *M. brevinoda*, while the other species nested in cavities away from the tunnels of the host. We also found 12 dipteran larvae, 7 coleopteran larvae, 2 cicada larvae and 4 small termite chambers. Prey that were brought back to the nests by *M. brevinoda* foragers included cicadas, ants (*Camponotus* sp., *Rhytidoponera* "*metallica*" (Fr. Smith), *Polyrhachis* sp.), termite alates, caterpillars and locusts.

Table 1. Size measurements of various *Myrmecia brevinoda* mounds near Paluma, north Queensland.

Nest code	Diam. (cm) Max.	Min.	Height (cm)	Estimated volume (m^3)	Number of entrances
A	70	82	70	0.142	2
B	30	44	21	0.013	1
C	70	82	58	0.118	3
D	44	56	37	0.034	1
E	48	82	47	0.061	1
F	57	62	38	0.049	1
G	41	50	32	0.027	1
H	33	41	20	0.011	1

Size variation and polyethism

Measurements of outerorbital distance (X) and head length (Y) of 60 workers from nest A produced the regression equation $Y = 1.02X^{0.94}$ (Fig. 2), where 0.94 is the rate of divergence of the 2 body parts. This is close to unity, which means that almost no divergence takes place with an overall increase in size, and thus growth is non-allometric. When outer-orbital distance was measured in all the workers from nest A, 2 size classes were obvious, although there was considerable overlap (Fig. 2).

Larger workers appeared to be more abundant in the mound while smaller workers prevailed below ground (Fig. 2), reflecting the occurrence of size polyethism among workers. This was supported by the observation of workers from nest B (Fig. 3). Hunting, defence and extranidal building were done mainly by large workers but intranidal building by smaller workers. The proportion of old workers (i.e. having well-worn mandibles and darker cuticle) was not significantly different ($p > 0.05$; t-test) between these functional groups.

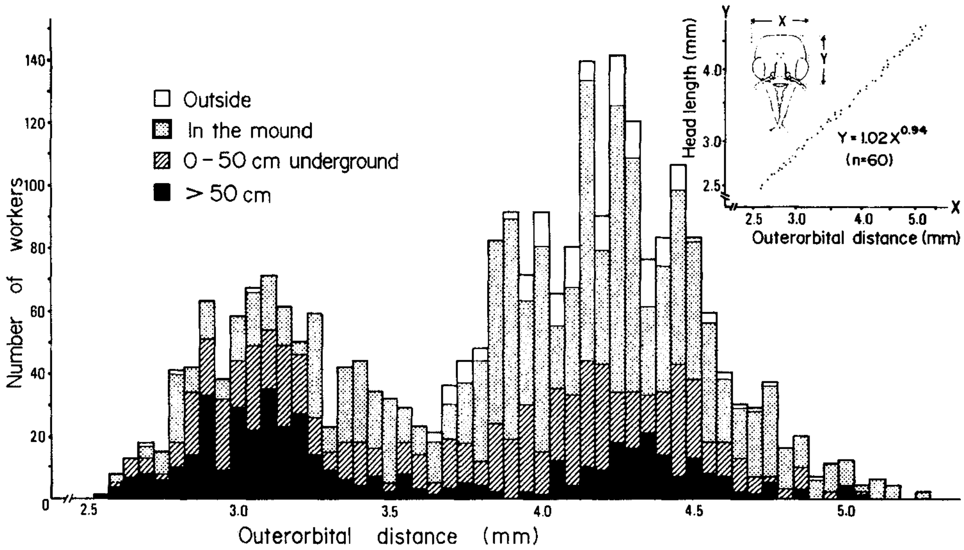

FIG. 2—Plot of outerorbital distance vs. head length (with the regression equation), and size-frequency histogram using outerorbital distance (also indicating the depth at which workers were collected), for workers from nest A.

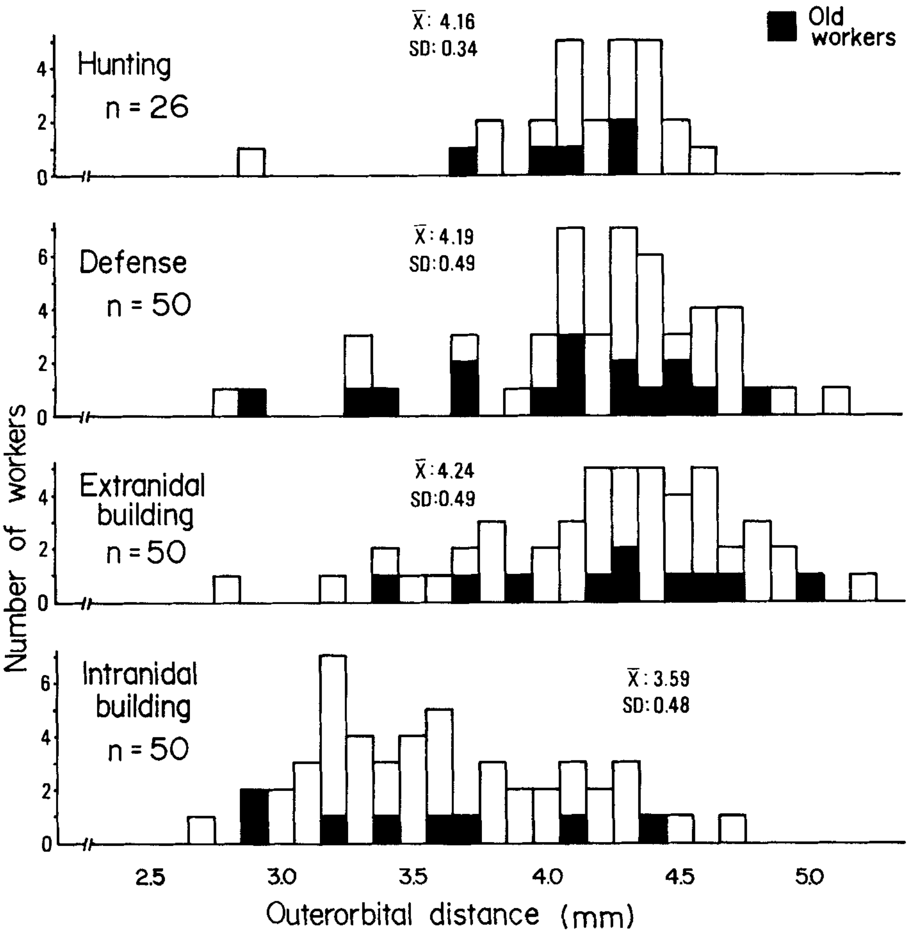

FIG. 3—Size-frequency histograms of different functional groups of workers from nest B, showing the relationship between size and behaviour. "Old workers" were classified on the basis of mandible wear and darker body colour.

Discussion

Some reports (Clark 1925; Wheeler 1933; Brian 1965) have given the general impression that *Myrmecia* colonies are small, e.g. rarely exceeding 200 adults. However, as more data accumulate, it has become clear that there is significant variation in colony size within the genus. Gray (1974) excavated 56 nests of 20 *Myrmecia* spp. and found that, while a few hundred workers is the average, more than 1000 workers can occur in *M. nigrocincta* Fr. Smith, *M. pyriformis* Fr. Smith and *M. tarsata* Fr. Smith, and 2284 workers were collected in a *M. gulosa* (F.) colony. The present colony of *M. brevinoda* is the largest hitherto reported in the genus.

Wilson (1971) stressed that allometry and multimodality in the size-frequency curve constitute 2 separate phenomena in the evolution of polymorphism. Indeed, in some species exhibiting strong allometry, workers remain unimodally-distributed. Our measurements of *M. brevinoda* indicate that workers of different sizes are almost isometric, while their size-frequency approaches bimodality. However, size-frequency data for additional *M. brevinoda* colonies are necessary. A similar pattern was also found in *M. gulosa* (Haskins and Haskins 1950). Thus according to Wilson (1971), *M. brevinoda* is monomorphic. However, workers at the extremes of the size spectrum behave differently in a colony, which has also been reported in other *Myrmecia* species (Haskins and Haskins 1950; Freeland 1958; Gray 1974). Gray (1971) suggested that most of the larger *Myrmecia* spp. with 2 size-groups of workers and few intermediates are polymorphic *sensu* Wilson, but the present data indicate that this is not general.

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