Appl. Ent. Zool. **25** (2): 283–287 (1990)

Nutrient Storage in the Major Workers of *Pheidole ryukyuensis* (Hymenoptera: Formicidae)[1]

Kazuki TSUJI

Laboratory of Applied Entomology and Nematology, Faculty of Agriculture, Nagoya University, Chikusa-ku, Nagoya 464–01, Japan

(Received September 25, 1989; Accepted January 22, 1990)

There are functionally 2 types of major workers in the subtropical ant *Pheidole ryukyuensis*. One has a largely distended abdomen in which the crop is repleted with nutrient, and the other has a non-distended abdomen. In laboratory starvation experiments, minor workers kept with a major worker having a distended abdomen survived significantly (about 4 times) longer than minor workers kept alone or with a major worker who did not have such an abdomen. The major workers with distended abdomens were thus considered as 'repletes' (workers bearing the nutrient storage task). They were less pigmented and slightly larger than non-replete majors. This indicates that young and larger major workers tend to become the repletes.

INTRODUCTION

Pheidole ryukyuensis is a subtropical ant species distributed in Taiwan and the Yaeyama Archipelago in Okinawa, southern Japan. This species has dimorphic worker subcastes consisting of major and minor workers, as common in other *Pheidole* species (WILSON, 1971). Although the major workers in *Pheidole* are generally known or postulated to serve as soldiers and seed millers (WILSON, 1971, 1984), details of their ergonomic function have not been fully understood. Their function as 'repletes' (the nutrient storage caste) has also been suggested in some species because a portion of the major worker population has greatly distended (i.e. exposed intersegmental membranes) abdomens (WHEELER, 1910; WILSON, 1984). I had noticed a similar phenomenon in *P. ryukyuensis* (Fig. 1) and here examined the hypothesis that the major workers with distended abdomens in this ant function as 'repletes', like the larger classes of workers of some species of other genera, e.g., *Myrmecosystus*, *Camponotus* and *Melophorus* (WILSON, 1971). Finally, I discuss the adaptive aspects of repletism in the genus *Pheidole*.

MATERIALS AND METHODS

A colony of *P. ryukyuensis* was collected from Urauchi, Iriomote Island, Okinawa, on March 20th 1986. Before experiments, the colony had been reared for 7 months in a plastic container (20.5 × 14 × 3 cm, floored with 3 mm-thick plaster) in the laboratory

[1] This study was supported in part by a Grant-in-Aid (No. 62304002 to Y. Itô) from the Japan Ministry of Education, Science and Culture.

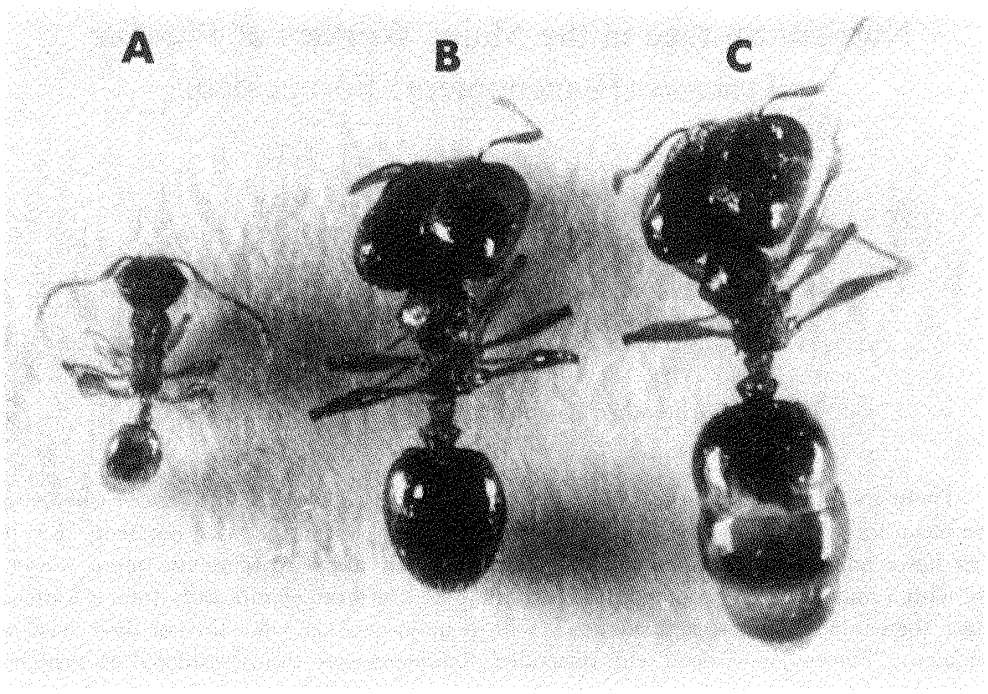

Fig. 1. Three types of workers of *Pheidole ryukyuensis*. A: a minor worker, B: a major worker with a ordinary-sized abdomen, C: a major worker with a distended abdomen. Dissection showed that major workers with distended abdomens had crops filled with transparent liquid (personal observation).

(24±2°C, 16L–8D). From this source colony, the following 3 types of experimental units were set up by transferring the ants to 30 ml glass vials on October 20th 1986: (A) units each containing 20 minor workers only, (B) units each containing 20 minor workers and a major worker having a fully distended abdomen, and (C) units each containing 20 minor workers and a major worker whose abdomen was not distended. Each type of unit consisted of 10 replications. The floor of each vial was covered with 3 mm of plaster to hold water. No food was supplied during experiments but water was given everyday to avoid desiccation. Number of surviving workers was recorded everyday until all workers died.

RESULTS

Figure 2 shows the survivorship curves of minor workers. In treatments A and C survival rates decreased immediately after the beginning of confinement in the vials. On the other hand, in B, almost all minor workers survived for at least 10 days, and thereafter the survivorship gradually declined. The average survival period in days was significantly different between A (8.0±2.6 SD, $N=10$) and B (31.3±2.3 SD, $N=9$), and B and C (7.4±1.8 SD, $N=10$; both $p<0.01$, two-tailed MANN-WHITNEY U test). However, there was no significant difference between A and C ($p>0.05$).

For major workers the average survival period in days was significantly different between B (46.1±15.0 SD, $N=10$) and C (13.9±2.3 SD, $N=10$) ($p<0.01$). In the B vials it was often observed that the minor workers gathered around the mouthparts

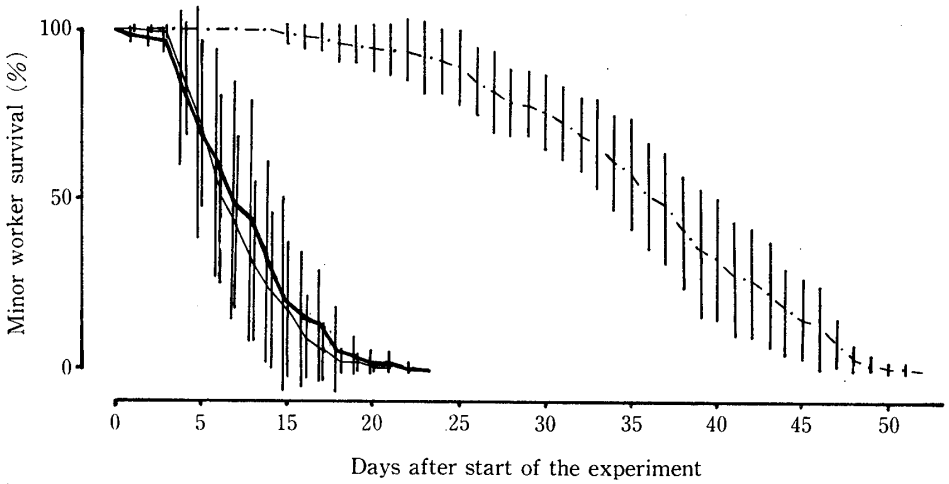

Fig. 2. Survivorship curves (mean±SD) of minor workers reared under varying conditions: (A: thick line) only 20 minor workers present, (B: chain line) 20 minors and a major worker with a distended abdomen present (C: thin line) 20 minors and a major worker with a normal abdomen present. Data from one vial in treatment B was omitted because of the death of the major worker on the 4th day after vial establishment.

Table 1. Relationship between the degree of abdominal enlargement and the degree of pigmentation of head and alitrunk in major workers[a]

Pigmentation of head and alitrunk	Repletes	Non-repletes
Pale	14	6
Intermediate	15	13
Dark	2	13

[a] Numerals represent numbers of observed major workers sampled from the laboratory colony used in this study. Repletes are the major worker whose abdominal intersegmental membranes were exposed, and non-repletes are the major workers whose intersegmental membranes were not exposed. Frequencies were significantly different from each other ($\chi^2=11.4$, $DF=2$, $p<0.005$).

of the major workers, locating their heads between the major worker's mandibles. Nutrient transfer from the major worker to the minor workers by regurgitation was not observed directly, but there was no means by which the minor workers could have survived except utilization of the nutrient stored in the major worker's crop. Therefore it can be concluded that in *P. ryukyuensis* the major workers with distended abdomens function as 'repletes'.

Relationship between the degrees of the body color and of the abdominal enlargement in repletes and non-repletes is shown in Table 1. Degree of the pigmentation was arbitrarily divided into 3 categories (pale, intermediate and dark), and had a significant negative correlation with the enlargement of abdomen, i.e., the repletes tended to be less pigmented than were the non-repletes. Furthermore, measurements of the head and alitrunk width indicated that the repletes were slightly but significantly larger than the non-repletes (Table 2).

Table 2. Comparison of head width and alitrunk width between repletes and non-repletes measured under dissecting microscope[a]

		Head width	Alitrunk width
	N	Mean±SD (mm)	Mean±SD (mm)
Repletes	10	1.23±0.02	0.56±0.01
		$0.05<p<0.01$	$0.05<p<0.01$
Non-repletes	10	1.19±0.04	0.54±0.02

[a] Probabilities were from two-tailed Mann-Whitney *U* test.

DISCUSSION

Besides *P. ryukyuensis*, replete individuals, though their function remains to be experimentally shown, have been observed in *P. hortensis* and *P. medicala* in the New World (Wilson, 1984) and *P. pieli* and *P. nudus* in Japan (Tsuji personal observation). However, repletes may not be so common in *Pheidole*, since some species, e.g. *P. megacephala*, apparently lack repletes (Tsuji personal observation). To infer the adaptive significance of repletism in *Pheidole*, comparison of environmental conditions should be made between the habitats where *Pheidole* species have produced repletes and where *Pheidole* species lack this specialization. Repletes found in *P. ryukyuensis* may be classified as an intermediate stage of repletism, that is represented by species of *Plenolepis*, *Proformica* and *Oligomyrmex* (Wilson, 1971). Extreme repletism as seen in 'honeypot' workers of *Myrmecosystus* (Wheeler, 1910; Wilson, 1971), is inferred as an adaptation for highly fluctuating temperature in arid environments (Creighton, 1950; Wilson, 1971). By contrast, *P. ryukyuensis* lives in relatively humid subtropical forests, or their surrounding grassland, where the fluctuation of temperature is not so large.

The worker size distribution in ants were often discussed in relation to ergonomic efficiency (Oster and Wilson, 1978; Wilson, 1971, 1984, 1985). For *Pheidole*, Oster and Wilson (1978) examined the optimal major/minor ratio from a theoretical viewpoint, postulating the major's function to be colony defense and seed-milling. However, repletism may be an additional important evolutionary and ontogenetic event affecting the major/minor ratio in ant colonies (even though this ratio may have been originally determined soley by the majors' function as soldiers, seed millers or foragers). The present study reveals that the repletes in *P. ryukyuensis* are the larger and younger class of the major workers, though further study is needed to evaluate the relative importance of age and size, i.e., whether all major workers can be repletes or not. Larger individuals would have an advantage for food storage because of their larger internal volume per surface area. And if age-polyethism operates in the major workers of this species, as commonly known in ants (Wilson, 1976a, b; Oster and Wilson, 1978; Calabi et al., 1983), their younger members are most suitable for repletes. Since young members do not defend the nest or forage outside, heavy abdomens do not pose any disadvantage.

ACKNOWLEDGEMENTS

I would like to thank M. Terayama for identification of the specimens, and Y. Itô and Y. Tsubaki for discussions.

REFERENCES

CALABI, P., J. F. A. TRANIELLO and H. MICHAEL (1983) Age polyethism: its occurrence in the ant *Pheidole hortensis*, and some general considerations. *Psyche* **85**: 395–412.

CREIGHTON, W. S. (1950) The ant of North America. *Bulletin of the Museum of Comparative Zoology, Harvard.* **104**: 1–585.

OSTER, G. F. and E. O. WILSON (1978) *Caste and Ecology in the Social Insects.* Princeton Univ. Press, Princeton.

WHEELER, W. M. (1910) *Ants: Their Structure, Development and Behavior.* Columbia University Press, New York.

WILSON, E. O. (1971) *The Insect Societies.* Harvard University Press, Cambridge.

WILSON, E. O. (1976a) The organization of colony defense in the ant *Pheidole dentata* MAYR (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **1**: 63–81.

WILSON, E. O. (1976b) Behavioral discretization and number of castes in ant *Pheidole dentata* MAYR (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **1**: 141–154.

WILSON, E. O. (1984) The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **16**: 89–98.

WILSON, E. O. (1985) The sociogenesis of insect colonies. *Science* **228**: 1489–1495.