

Caste specialization in food storage in the dimorphic ant *Colobopsis nipponicus* (Wheeler)

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Summary

Food-storage abilities of both minor and major workers of the dimorphic ant *Colobopsis nipponicus* were examined to prove the hypothesis that major workers of this species have a trophic role in addition to a defensive one. Both worker subcastes accumulated water, that was supplied with water-soluble food, as well as fat, that probably originated from food given. However, the major workers accumulated much larger amounts of water and fat than did the minor workers. Difference in water accumulation increased as food supply increased. In spite of their difference in body weight, the residual amount of fat after starvation did not differ between the two subcastes. Although the amount of stored fat increased with colony size in both subcastes, the stored fat per dry weight of the major worker was significantly larger than that of the minor worker regardless of the colony size. When workers of a colony were starved, minor workers with a single major worker survived significantly longer than those without a major worker. In addition, about half the behavioral acts of major workers were regurgitation for minor workers. These results demonstrate that major workers of *C. nipponicus* functioned as a trophic caste. On the basis of the results, quantitative relationships of storage abilities between the two worker subcastes are discussed.

Introduction

In many ant species, marked worker polymorphism is known (see Hölldobler and Wilson, 1990). In these species, dimorphism, in which two physical worker subcastes are shown, is regarded as the most advanced state (Wilson, 1953). Major workers in various dimorphic ant species have been shown to specialize in nest defense (Detrain and Pasteels, 1992; Wilson, 1976), food milling (Wilson, 1978), and food storage (Lachaud *et al.*, 1992; Tsuji, 1990).

In the genus *Colobopsis*, which is completely dimorphic, the major workers engage in nest defense by plugging the nest entrances with their heads (Szabo-Patay, 1928: cited in Wilson, 1971; Wilson, 1974; Walker, 1984; Walker and Stamps, 1986). Wilson (1974) demonstrated that the major workers of *C. fraxinicola* are specialized in liquid-food storage. However, Walker (1984) found no evidence of this function in

the major workers of *C. impressus*, which may be a synonym of *C. fraxinicola*. Thus, their possible functions have remained unclear.

Worker-subcaste systems are hypothesized to evolve when they optimize the ergonomic efficiency of the colony (Oster and Wilson, 1978). The ergonomic efficiency can be maximized by the optimal ratio of worker subcastes because the subcastes would be functionally differentiated. Therefore, to understand the worker-subcaste system of polymorphic species, the functions of each subcaste must be examined quantitatively.

The objectives of this study were 1) to demonstrate the specialization of the major workers in a nutritional role and 2) to determine the relative food storage ability of the major and minor worker subcastes in *C. nipponicus*.

Materials and methods

Colobopsis nipponicus is a completely dimorphic ant distributed in broad-leaf evergreen forests in Japan. This species possesses two worker subcastes that are distinct physically. The members of the major caste are larger than those of the minor caste and possess truncated heads. They engage in nest defense, using their heads to plug the nest entrances. The minor workers engage in daily tasks in the colonies, such as foraging and brood care. The colonies used in the experiments were collected in coastal forests located in Amatsukominato, Chiba, Japan. At this site, most of the *C. nipponicus* nests were found in hollows of dead twigs attached to live trunks of the tree *Lythocarpus edulis*.

To examine whether both subcastes are capable of storing food in their body, three experiments were conducted as described below. Experimental colonies were housed in a hollow bamboo culm (length: ca. 100 mm, diameter: ca. 10 mm). Then, the culm was put in a plastic box (195 × 105 × 25 mm) and the colonies were fed with the Bhatkar's artificial diet (Bhatkar and Whitcomb, 1970) without agar, i. e. in liquid form. Dissections of workers confirmed that both subcastes have large numbers of fat bodies and that the contents of crop is water-soluble. This means that workers can store nutrients as fats and liquids. Thus, both water- and fat-storage abilities were examined.

Relation of food intake to storage. Since callow workers of *C. nipponicus* have lesser fat bodies than older workers (Hasegawa, pers. obs.), the larger fat bodies in older workers must be formed by metabolizing food. To know whether workers accumulate food in their bodies, eight experimental colonies were established from each of eight large mature colonies collected in the field. Each colony consisted of one queen, 80 minor workers, and 20 major workers. All colonies were exposed to a photoperiod of 14L:10D at 26 °C, from 7 September to 19 October 1990, and fed 50 µl food every three days. Then, eight colonies were each given a trophic condition, either 0, 10, 25, 50, 75, 100, 200, or 700 µl food with 20 µl water per week for 58 days. After this period, 5–10 ants from each subcaste were randomly selected from each colony and weighed individually (LW) using an electric balance with a sensitivity of 0.1 µg. Ants were dried to constant weight in a desiccator, then weighed

again (DW). Fats were extracted from these samples by placing them in a 3:1 ethanol-ether mixture for 40 days. The dry weight of the residual bodies (BW) was measured for each sampled ant. The volume of the solvent was large enough to avoid its saturation with extracted fats. The water and fat contents from each individual were estimated by subtracting DW from LW and BW from DW, respectively.

Relation of fat storage to colony size. Since the body size of the workers is correlated with the colony size (see Fig. 3c), the relationship between colony size and fat-storage ability of the workers was examined. For this purpose, ten colonies were selected from the field so as to include the usual range of colony size (from 4 minors to ca. 800 minors and 200 majors; corresponding from 1 to 560 mg of total worker dry weight) in this species. Two nest fractions were established from each colony. Each fraction generally consisted of 10 minor and 10 major workers. When the original colony size was small, a minimum of three individuals of each subcaste was used. These nest fractions were cultured under the same conditions as in the previous experiment except for the nutritional one. One fraction of each colony was fed ad libitum, while the other was supplied with water only. All fractions were inspected twice daily, and when any individual had died, she was removed from the fraction and preserved in a desiccator. After all members of the starved group had died out, the fat weight of all individuals was estimated using the same procedure as in the previous experiment. The average fat content was also calculated for each subcaste in each treatment.

The effect of the presence of majors on group survival. If major workers cannot regurgitate the stored nutrients to other colony members, their group cannot be regarded as a trophic caste, even if they have a large amount of nutrients. In this experiment, a possible contribution by the major worker to colony survival was examined. A large colony collected in May 1990 was divided into two groups of nest fractions. One group contained four fractions consisting of 21 minor workers, while the other group had eight fractions, each with 20 minor workers and 1 major worker. Each nest fraction was housed in a glass vial (16.5 × 45 mm) with a wet cotton plug. They were starved under the same conditions as in the first experiment. The numbers of surviving minor workers were counted daily. Since each major worker in the group with majors was replaced with one minor worker in the group without majors, the number of surviving minor workers from the group without majors was reduced by one in each counting. Thus, the fractions without majors were regarded as died out when one minor survived in that fraction.

Behavioral profiles of both subcastes. An ethogram of *C. nipponicus* was made to learn whether the major workers of this species show the same high rate of regurgitations as in the other *Colobopsis* species (Cole, 1980). A colony containing 1 queen, 80 minors, 20 majors, and about 100 larvae was housed in an artificial nest (50 × 70 × 3 mm) covered with a clear-red plastic plate. The nest floor was meshed with black lines at 10-mm intervals, thus the nest was divided into 35 quadrates. The nest was settled in the same plastic box used in the other experiments and the colony was fed 100 µl food once in every week. The experimental colony was reared under a

constant conditions (14L:10D, 23°C, 60% RH). Observations were made each one hour for 10 days without food supply. In each observation, the 35 quadrates of the nest were inspected once every 5 minutes, and all of behavioral acts were recorded by physical caste.

Estimation of colony size. Because there are two distinct worker subcastes in *C. nipponicus*, worker number is not simply related to the biomass of the colony. Therefore, colony size was expressed as the total dry weight of adult workers. In addition, since the dry weight of adult workers in field colonies can vary to a great extent with their nutritional condition (Hasegawa unpublished), the estimated pupal dry weights of both subcastes were used rather than the actual adult dry weight in that colony. This also means that colony size was expressed as an estimation of "production cost" of the colony. To estimate the dry weight of majors and minors from 20 colonies collected in June 1991, ten pupae of each subcaste in each colony were dried, and the mean weight was calculated. The regression equations of the log transformed pupal dry weight of each subcaste on the log transformed number of the major workers were obtained (for minor, $DW = 0.09 \text{ No.} - 1.26$, $R^2 = 0.634$, $P < 0.001$; for major, $DW = 0.11 \text{ No.} - 0.23$, $R^2 = 0.764$, $P < 0.01$). The proportion of majors in the total worker population is roughly 20% and constant with colony development in *C. nipponicus* (Hasegawa unpublished), thus, the regression equations on the number of majors would give a plausible estimation for pupal weight. The mean dry weight of each subcaste in the experimental colonies was estimated from the regression equation, and total worker weight was calculated using these estimates.

Results

The mean water and fat content of individuals of both subcastes in the experimental colonies increased with their food quantity up to 100 $\mu\text{l}/\text{week}$, thereafter no further increase in weight was observed (Figs. 1 and 2). Ants were apparently overfed in these latter colonies, because food always remained uneaten. Therefore, for the colonies with food quantities of 0 through 100 $\mu\text{l}/\text{week}$, regression equations were obtained for log transformed weights of water or fat on the trophic conditions. All four slopes were statistically significant (ANOVA, for minor: water, slope = 0.0062, $F = 14.45$, $df = (1, 4)$, $P < 0.05$; fat, slope = 0.0058, $F = 12.13$, $df = (1, 4)$, $P < 0.05$; for major: water, slope = 0.0108, $F = 116.11$, $df = (1, 4)$, $P < 0.001$; fat, slope = 0.0075, $F = 38.08$, $df = (1, 4)$, $P < 0.01$). The difference in slopes between the two subcastes for each content was also significant (ANOVA, for water: $F = 58.87$, $df = (1, 81)$, $P < 0.001$; for fat: $F = 6.72$, $df = (1, 81)$, $P < 0.05$). These results indicate that an increase in food consumption results in an increase of water (and the nutrients dissolved in them) and fat in the worker's bodies. Since dependent variables were log transformed, the difference in slopes between the two subcastes means that when food was abundant, major workers accumulated a disproportionately larger amount of water and fat than minor workers did. Assuming the water content of workers with 0 μl food is the minimum requirement, the amount of stored water can be calculated by

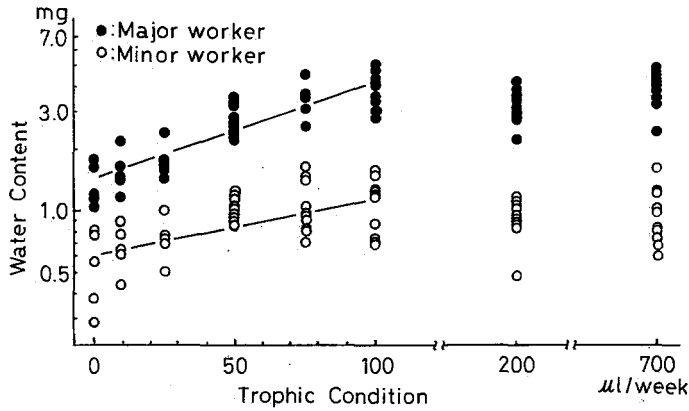


Figure 1. Relationship between trophic conditions of colonies and body water of the two worker subcastes of *C. nipponicus*. The regression equations are calculated for the trophic conditions of 0 to 100 μl/week

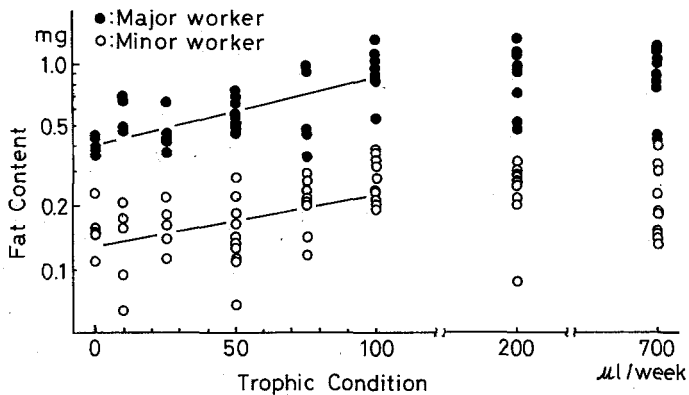


Figure 2. Relationship between trophic conditions of colonies and body fat of the two worker subcastes of *C. nipponicus*. The regression equations are calculated for the trophic conditions of 0 to 100 μl/week

subtracting this value from total water content. Storage ability of each subcaste can be calculated by dividing the stored water amount by the estimated dry weight (production cost) of each subcaste. The water-storage ability was 0.84 mg/unit dry weight for a minor and 1.81 mg/unit dry weight for a major. Thus, the ability ratio (storage efficiency) of a major to a minor was 2.14 for water storage.

The optimal body fat with unlimited food increased with colony size in both subcastes, and the difference between the two subcastes was strong (Figs. 3 b, c). Pupal weight of both subcastes also increased with colony size (Fig. 3 a). The average ratio of pupal weight of a major to a minor was 2.9; however, the residual body fat under no-food conditions did not significantly differ between the two subcastes (Wilcoxon signed-ranks test, $T = 15.5$, $P > 0.05$). The average amount of fat storage in a given individual in a given colony size was calculated by subtracting the average

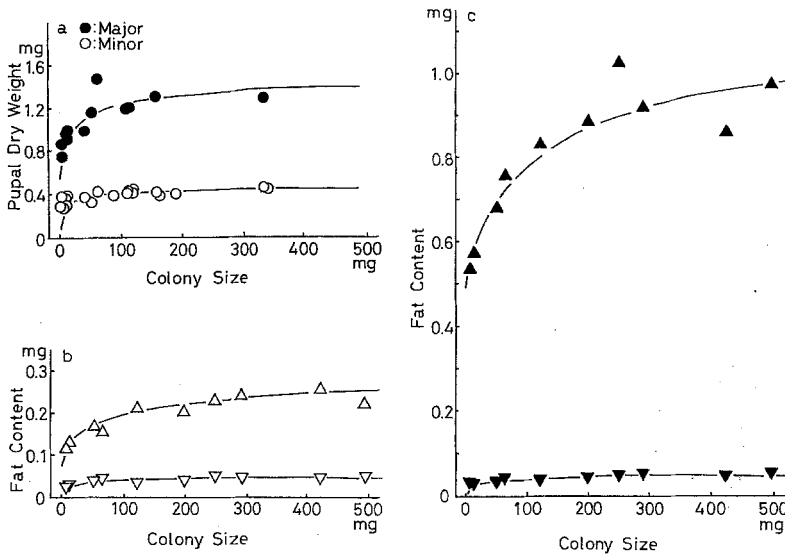


Figure 3. Relationships between colony size and pupal dry weight (a) or average fat content of minor workers (b) and major workers (c) of *C. nipponicus*. In Figs. 3b and 3c, \triangle or \blacktriangle show fat content during food-saturation conditions, whereas ∇ or \blacktriangledown show fat content when no food was supplied. Regression curves are fitted by the least-squares method for the log transformed variables

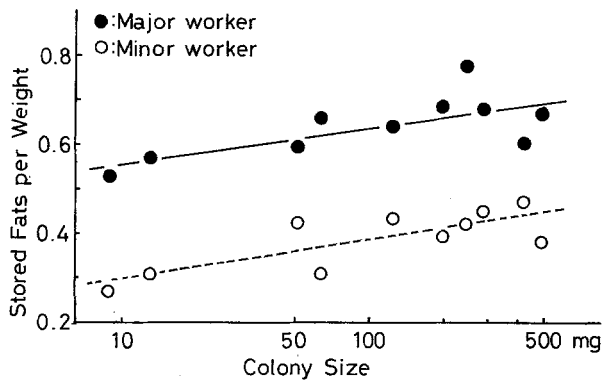


Figure 4. Fat-storage abilities of minor workers (open circle) and major workers (closed circle) of *C. nipponicus*. Storage ability is represented by the amount of stored fat per dry body weight of an individual

residual fat content from the average optimal fat content. A standardized index of storage ability was calculated by dividing the average fat storage by the estimated dry weight. For each subcaste, the relationship between colony size and this index is shown in Figure 4. The slope of the regression equation was significant in each subcaste (for minor, $t = 3.638$, $P < 0.01$; for major, $t = 2.893$, $P < 0.05$). There was no difference in the slope between the two subcastes (ANCOVA, $F = 0.007$, $df = (1, 8)$, $P > 0.25$). However, Y intercepts differed between subcastes to a great ex-

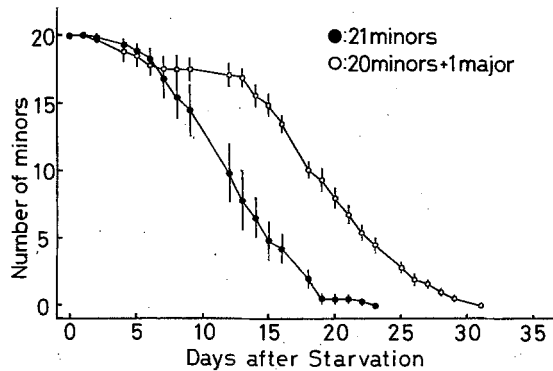


Figure 5. Survival curves of minor workers in the colony fraction with one major worker (open circle) and in the nest with no major worker (closed circle). Each circle and vertical bar indicates the mean \pm S.E

tent (ANCOVA, $F = 140.54$, $df = (1, 17)$, $P < 0.001$). Therefore, although the fat-storage ability of both castes similarly increases with colony size, the ability of the major workers is always higher than that of the minor workers regardless of colony size. Furthermore, the ratio of fat storage of the major caste to that of the minor caste was not correlated with colony size ($r = -0.45$, $N = 10$, $P > 0.05$). Thus, the overall ability ratio (storage efficiency) for fat storage was obtained by averaging the ratios for each colony size. The ability ratio of a major to a minor was 1.68 for fat storage.

In the last experiment, more minor workers survived in the fractions with majors than in those without majors, while the colony fractions persisted (Fig. 5). In seven of the eight fractions from the group with majors, the major workers survived throughout the experiment. The longevity of each fraction was determined by the number of days until twenty minor workers died in each group. The mean longevity (day \pm S.D.) of the group without majors was 19.8 ± 2.2 , whereas that of the group with majors was 29.3 ± 2.1 . The longevity was significantly longer in the group with majors than in the one without majors (Mann-Whitney U-test, $U = 0$, $P < 0.01$).

Table 1 shows behavioral profiles of both subcastes. Many of the minor's acts were devoted to foraging and brood care, while more than 50% of the acts of majors were regurgitation for other colony members. The majors were never observed conducting brood care, while minors were never seen plugging of the nest entrance.

Discussion

The present study demonstrated three important facts. First, both subcastes can store more water and fat in their body when trophic conditions are good. Second, major workers can store more fats per dry weight than minor workers. Third, the group fractions with majors survived longer than those without majors, indicating that the major workers probably provide the nutrients stored in their bodies to other colony members. These facts strongly support the hypothesis that major workers of *C. nipponicus* specialize not only in nest defense but also in food storage.

Table 1. Behavioral profiles of both minor and major workers in *C. nipponicus*. Observed numbers of acts and relative frequencies (in parentheses) are shown

Behavioral act	Minor	Major
Selfgrooming	172 (0.1322)	45 (0.2133)
Allogrooming		
with queen	11 (0.0085)	0 (0.0000)
minor	103 (0.0792)	21 (0.0995)
major	21 (0.0161)	0 (0.0000)
Regurgitation		
for queen	4 (0.0031)	0 (0.0000)
minor	79 (0.0607)	117 (0.5545)
major	117 (0.0899)	1 (0.0047)
Grooming		
pupa	21 (0.0161)	0 (0.0000)
larva	38 (0.0292)	0 (0.0000)
egg	7 (0.0054)	0 (0.0000)
Carrying		
pupa	10 (0.0077)	0 (0.0000)
larva	4 (0.0031)	0 (0.0000)
egg	1 (0.0008)	0 (0.0000)
Plugging the nest entrance	0 (0.0000)	4 (0.0190)
Licking the nest wall	24 (0.0184)	19 (0.0900)
Walking inside nest	18 (0.0138)	4 (0.0190)
Walking outside nest	671 (0.5158)	0 (0.0000)
Total number of acts	1301 (1.0000)	211 (1.0000)

The specialization in water (and the nutrients dissolved in them) storage is indicated by the significant difference in the two regression coefficients for the water content in the two subcastes. For example, a major worker contained 2.5 times more water than a minor worker when no food was supplied. This ratio increased up to 3.8 with the 100- μ l food supply. During food-saturation conditions, the water-storage ability of major workers was higher than that of minor workers. Thus, the major worker can be regarded as specializing in water storage, at least during resource-rich conditions. This result is consistent with that of *C. fraxinicola* in which major workers store larger amounts of liquids per body weight than do minor workers (Wilson, 1974). There have been other studies on liquid storage by ant workers. In the genus *Myrmecocystus*, known as honey pot ants, relatively large individuals served as a liquid-storage caste (Rissing 1984), and there were some differences in the stored substances among individuals (Burgett und Young, 1974; Conway, 1977, 1990). Snelling (1976) argued that the "replete" caste in *Myrmecocystus* is important for genus' adaptation to an arid habitat. Strong resistance to desiccation has also been shown in arboreal ant species by Hood and Tschinkel (1990). *C. nipponicus*, for example, inhabits the hollows of dead twigs and was observed drinking pure water in laboratory (Hasegawa, pers. obs.). Liquid storage and the majors' specialization in this role may be one way of resisting dessication in an arboreal habitat.

The specialization in fat storage is evident, since the fat-storage ability was always higher in major workers. Fat accumulation in the gaster (adipogastry) has been shown for several ant species. Kondoh (1968) reported fat accumulation in hibernating workers of *Formica japonica*. In *Prenolepis imparis*, a species active in winter, Tschinkel (1987) demonstrated that fat accumulation in workers rapidly decreases during the brood-production period. He postulated that fat bodies are used as the source of nutrients for the production of new generations, since colonies are inactive above ground during this period. In another case, Espadaler et al. (1990) found adipogastric major workers in the polymorphic species, *Camponotus foreli*, but they showed no quantitative details. Recently, Lachaud et al. (1992) showed that in another dimorphic ant, *Pheidole pallidura*, major workers with a distended abdomen functioned as nutritional tanks, and that more than 50% of the dry body weight in these individuals was fat, whereas only 20% was fat in soldiers and minors. Tsuji (1990), using *Pheidole ryukyensis*, also showed extended survivorship in starved colonies with majors having a distended abdomen. In *Colobopsis nipponicus*, the proportion of fat to total dry body weight in food abundant conditions was about 40% for majors and 33% for minors. This difference is less than in *Pheidole* species. However, since *C. nipponicus* also stored water (and the nutrients dissolved in them), fat proportion to total dry weight can change even among individuals that have the same amount of fat. Thus, in the case of *C. nipponicus*, the storage ability for both water and fat can be represented more correctly by the indices used in this study. The ability ratios of a major to a minor were 2.14 and 1.68 for water and fat, respectively. These values represent the extent of the major's specialization in each role in *C. nipponicus*.

Although Wilson (1974) suggested fat storage in *C. fraxinicola*, there has been no further information on fat accumulation in this genus. However, several studies have suggested that there are some relationships between the production of reproductive females and the existence of major workers with respect to fat storage. Glancey et al. (1973) reported that in *Solenopsis invicta*, the dye that was fed to colonies along with soybean oil was found in all the major workers and in few of the minor ones after six months. The dye was also found in all alate female pupae, but not in males. In *Colobopsis impressus*, Walker (1984) found that when the number of minor workers was controlled, the partial correlation coefficient between the number of reproductives produced and the number of major workers was significant. In contrast, when the number of the major workers was controlled, there was no correlation between the number of reproductives and the number of minor workers. In addition, Cole (1980) demonstrated an extremely high rate of regurgitation by the major workers of *Colobopsis* sp. About 50% of the behavioral acts of the major workers were regurgitation for other colony members. This is consistent with *C. nipponicus*. All of these indicates the importance of the nutritional roles of the major workers, especially in fat storage. Whether fat accumulation in the field colonies of *C. nipponicus* is correlated with reproduction needs to be examined.

The caste system is said to be tuned to maximize the ergonomic efficiency of the colony (Oster and Wilson, 1978). Therefore, knowing the quantitative relationships of partial functions is especially important because maximization of ergonomic efficiency should be achieved through regulation of the ratio of subcastes that

specialize in each roles to a different extent. Assessment of the ability of each subcaste in other roles, such as colony defense and brood care, incorporated with the food-storage abilities presented here, would give us further insight into the caste system of *C. nipponicus*.

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