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ARTICLE

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Variable investments in nests and worker production by the foundresses of *Polistes chinensis* (Hymenoptera: Vespidae)

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Abstract The allocation pattern of proteinaceous resources was estimated in preemergence colonies of *Polistes chinensis*. Foundresses that nested at exposed sites consumed a larger relative amount of proteinaceous resources to produce oral secretion, which is used for construction and maintenance of nests, than those at sheltered sites. Numbers of immatures reared by foundresses were smaller in exposed nests than those in sheltered ones, and further, workers that emerged from exposed nests were significantly smaller in size than those from sheltered ones. Foundresses had to partition available proteinaceous resources not only among the first batch of the brood but also, before that, between brood nourishment and secretion production in response to given environmental conditions.

Kew words *Polistes chinensis* · Foundresses · Preemergence nests · Oral secretion · Worker size · Resource allocation

Introduction

To understand the social life of insects, it is important to know the bioeconomic aspects, such as utilization patterns of resources, time, and energy. Heinrich (1979) developed the knowledge of social life of bumblebees along these lines. Suzuki (1981) traced the flow of nitrogen (proteinaceous resources) in colonies of *Polistes chinensis* throughout the colony cycle and estimated that approximately 51% of the total nitrogen was invested in workers and 49% was allocated to male and female reproductives.

Paper wasps utilize proteinaceous resources not only to nourish their brood but also to produce oral secretion, which is used for gluing nest materials, i.e., plant fibers or plant hairs, and maintaining the built nests (Maschwitz et al. 1990; Wenzel 1991). Kudô et al. (1998) and Yamane et al. (1998) recently clarified that a large proportion (50%–70%) of dry weight was composed of the oral secretion in solitary nests of *P. chinensis* and *Polistes riparius*. Kudô et al. (1998) estimated, in *P. chinensis*, that approximately 14% of the total nitrogen input into a colony was utilized in producing the oral secretion in nests built at sheltered sites during the founding phase. They further predicted that foundresses nesting at exposed sites must invest much more in secretion production to prevent the nest from being destroyed by rains. However, they did not analyze the pattern of nitrogen resource allocation by foundresses at exposed sites.

The primary aim of this study is to confirm this prediction by comparing amounts of nitrogen consumed by the foundresses for producing the secretion between exposed and sheltered nests of *P. chinensis* that receive different amounts of rain. Second, I discuss the importance of effective allocation of proteinaceous resources during the founding phase. Foundresses are required to partition the resources at two different steps: (1) between nourishing the brood and producing oral secretion (nest construction) and (2) among the first batch of the brood. The question of allocation of food resources has focused only on brood (O'Donell 1998; Miyano 1998), but it should also include relations between nourishing brood and nest construction, because nonnegligible amounts of nitrogen resources (~14%) were consumed by the foundresses to produce the oral secretion (Kudô et al. 1998).

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Materials and methods

Nest collection

Twenty-seven preemergence nests of *Polistes chinensis antennalis* Pérez were collected together with lone foundresses in Toki (35°21′ N, 137°11′ E), Gifu Prefecture, central Japan, on June 6 and 7, 1997. To estimate the foundresses total investment in brood nourishing and nest construction, these nests were collected immediately at or slightly before the first worker emergence.

Because it has been known that foundresses activities are influenced by rains (Kudô et al. 1998), the collected nests were divided into two categories, i.e., exposed and sheltered nests (henceforth abbreviated as EN and SN, respectively). Most ENs were built on bright-colored stone fences, where they were exposed to direct rain and sun, whereas SNs were built on the underside of the roofs of houses. Because 1 of 9 ENs and 4 of 18 SNs were parasitized by an *Anatrachyntis* moth, 8 ENs and 14 SNs were used for analyses. There was no significant difference in days from nest collection to the first worker emergence among those nest categories (*U*-test), indicating that foundresses nesting periods were regarded as nearly equal among those nest categories.

Measurements of nest and some other parameters

Size (mm)

Maximum length of cell (excluding petiole) and major and minor nest diameters of comb were measured with a vernier caliper to 0.1 mm.

Weight (mg)

After all the matter left inside cells, i.e., eggs, larvae, meconia, larval silk, and exuviae of postfeeding larvae, was removed under a binocular microscope, broken cell walls and the petiole were dried for 5 h in an electric oven and weighed by an electronic balance to 0.1 mg. In addition, all the protein-containing matter, i.e., workers that emerged after nest collection and all the matter left inside the cells, was dried for 48 h at about 70°C and then weighed to 0.1 mg.

Weight of plant material and oral secretion

To separate plant material from oral secretion, weighed nests were immersed in a 0.5 N KOH solution at about 70°C for 5–8 h to dissolve the oral secretion. The solution with nests was then filtered. The plant material remaining on the filter paper was washed with distilled water to remove elements of the secretion and then dried in an electric oven. Plant material was weighed together with the filter paper to 0.1 mg, and then the weight of filter paper was subtracted.

However, it is known that a part of the plant material, such as proteinaceous and other elements, is lost by KOH treatment (Kudô et al. 1998; Yamane et al. 1998). Because the loss of substances soluble in the KOH solution has been estimated at about 11%, the weight of remains on the filter paper was multiplied by 1.12 for a correction. The weight of the oral secretion was calculated by subtracting that of plant material from the total nest weight.

Table 1. Comparisons of the means (±SE) of foundress-reared immatures between exposed (EN) and sheltered (SN) nests

No. of immatures in each developmental stage	EN	SN	Significance
Eggs	8.3 ± 1.1	10.9 ± 0.8	Yes*
Larvae	11.3 ± 1.5	12.8 ± 0.8	No
Pupae	7.4 ± 0.8	9.9 ± 0.8	No
Total brood	26.9 ± 1.4	33.6 ± 1.7	Yes**

*, $P < 0.05$; **, $P < 0.005$ (Mann–Whitney *U*-test)

Table 2. Comparisons of the mean (±SE) of five nest parameters between exposed (EN) and sheltered (SN) nests

Parameter[a]	EN	SN	Significance
No. of cells	28.9 ± 1.2	35.9 ± 1.7	Yes*
Maximum cell length	21.3 ± 0.4	22.1 ± 0.4	No
Major diameter	26.8 ± 0.9	26.9 ± 0.9	No
Minor diameter	21.6 ± 0.4	25.1 ± 0.9	Yes*
Weight	90.0 ± 3.9	107.3 ± 8.9	No

[a] Length and diameter are shown in mm and weight in mg
*, $P < 0.05$ (Mann–Whitney *U*-test)

Weight of foundresses

Foundresses were dried for 48 h at about 70°C and weighed to 0.1 mg ($n = 22$).

Statistical analyses

All the obtained values are shown as mean ± SE, and all comparisons between EN and SN were made by Mann–Whitney *U*-test.

Results

Colony composition

Mean numbers of immatures at various developmental stages for SN were larger than those for EN (Table 1). The number of eggs and total brood for SN was significantly larger than those for EN ($P < 0.05$). These data indicate that foundresses at sheltered sites could rear many more immatures than those at exposed sites.

Nest size and weight

Nest size and weight for SN were also larger than those for EN (Table 2). Mean number of cells and minor diameter of comb in SN were significantly larger than those in EN ($P <$

0.05). This result means that foundresses' nest construction activities were more disturbed at exposed sites than at sheltered sites, and shifted to perform nest maintenance (see nest material composition).

Nest material composition

Weights of plant material significantly differed between nest sites (Fig. 1; $P < 0.05$), whereas the amount of oral secretion used was nearly comparable. Thus, percent oral secretion to dry nest weight for EN was greater than that for SN ($P < 0.05$).

Weights of foundresses and foundress-reared workers

Although there was no significant difference in weight between foundresses of EN (31.5 ± 1.4 mg; $n = 8$) and those of SN (33.8 ± 1.8 mg; $n = 14$), weight of adult workers in SN (19.3 ± 0.3 mg; $n = 104$) was greater than that in EN (18.0 ± 0.4 mg; $n = 48$) ($P < 0.05$).

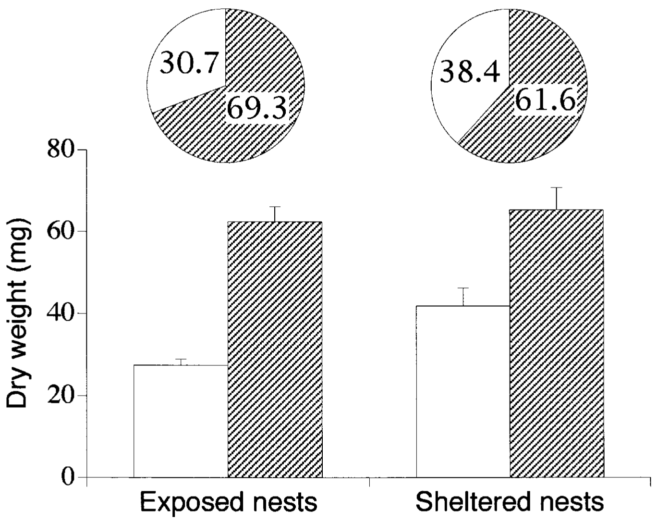

Fig. 1. Material composition of preemergence nests in Toki. Relative weights of the two components are indicated in *pie diagrams at top*. *Vertical bars*, mean SE; *Shading*, oral secretions; *White areas*, plant material

Estimation of patterns of nitrogen allocation

The patterns of nitrogen allocation for both exposed and sheltered nests were estimated by the method of Kudô et al. (1998). All adult workers, immatures, and wastes left inside cells were weighed, and then weight of nitrogen (N) contained in each item was estimated by multiplying the N content analyzed in an Itako population (Kudô et al. 1998) (Table 3) by dry weight. Use of the N content with those obtained for a different population may not be so problematic, because interpopulation differences, at least in central Japan, have been known to be slight in this species (see Table 2 in Suzuki 1980 and Table 3 in Kudô et al. 1998).

Mean amount of N contained in each item in SN was more than that in EN (Table 3) (significant in eggs, exuviae, workers, subtotal, and total, at $P < 0.05$). These facts clearly show that foundresses that nested at sheltered sites could bring more proteinaceous food into their nests than those at exposed sites.

Foundresses use proteinaceous (nitrogen) resources mainly for the following three purposes: (a) nourishing their brood, (b) producing oral secretions, and (c) their own metabolic requirements.

a. Nourishing brood: the amounts of N used for all items except oral secretion were summed up to obtain the total N for nourishing the brood during the founding phase. Mean values were 26.7 mg for EN and 41.8 mg for SN ($P < 0.05$).
b. Oral secretion: the amounts of N used for producing the oral secretion were 7.3 mg for EN and 7.7 mg for SN ($P > 0.05$).
c. Metabolic wastes of foundress: although the amount of N consumption in the metabolic wastes of foundresses could not be measured, it was expected to be considerably smaller than for other items.

Assuming amounts of N consumed for metabolic wastes of foundresses were zero, the mean total N input into a

Table 3. Mean dry weights (±SE) of adult workers, immatures, matter left inside cells, and oral secretion in exposed (EN) and sheltered (SN) nests and mean percent nitrogen content in these items

	Mean weights of dry matter (mg)		Mean percent nitrogen content[a]	Mean weight of nitrogen (mg)	
	EN	SN		EN	SN
Eggs*	0.6 ± 0.1	1.0 ± 0.1	10.5[b]	0.07 ± 0.01	0.11 ± 0.01
Larvae	63.0 ± 10.7	122.6 ± 18.7	8.19 ± 0.32	5.2 ± 0.9	10.0 ± 1.5
Workers*	130.5 ± 16.4	193.4 ± 16.5	13.37 ± 0.12	17.4 ± 2.2	25.9 ± 2.2
Silk	7.7 ± 1.4	11.5 ± 1.6	15.76 ± 0.20	1.2 ± 0.2	1.8 ± 0.2
Exuviae*	2.9 ± 0.3	4.5 ± 0.4	9.32 ± 0.12	0.27 ± 0.03	0.42 ± 0.04
Meconia	45.5 ± 5.3	61.7 ± 5.7	5.81 ± 0.27	2.6 ± 0.3	3.6 ± 0.3
Subtotal*				26.7 ± 3.5	41.8 ± 3.7
Oral secretion	62.8 ± 3.7	65.7 ± 5.5	11.68 ± 0.10	7.3 ± 0.4	7.7 ± 0.6
Total nitrogen*				34.0 ± 3.1	49.5 ± 4.1

[a] From Kudô et al. (1998)
[b] Sample size = 1
* Significant difference in the weight of nitrogen was detected between EN and SN (Mann–Whitney U-test; $P < 0.05$)

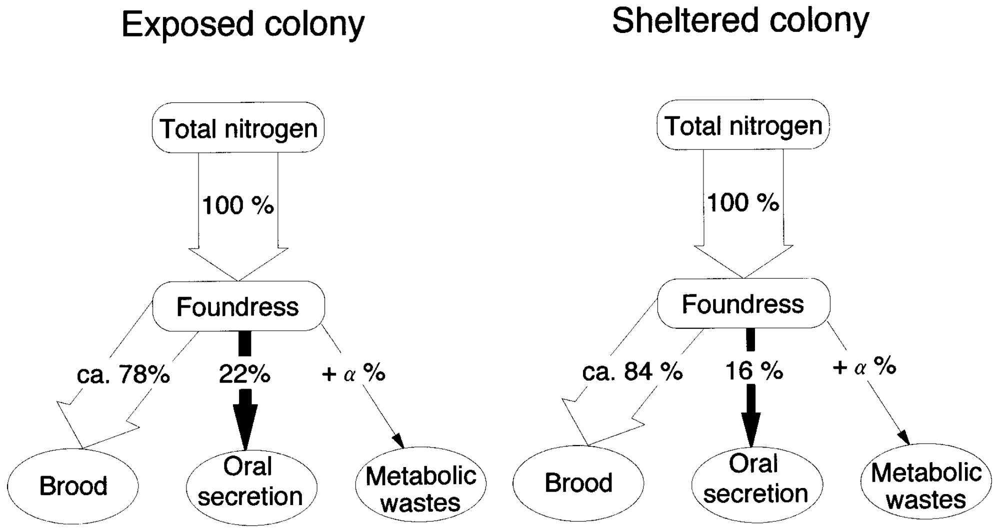

Fig. 2. Estimated amounts of nitrogen (proteinaceous element) for both exposed and sheltered colonies taken in Toki

colony from outside was estimated at 34.0 mg for EN (26.7 mg for nourishing brood + 7.3 mg for oral secretion) and 49.5 mg for SN (41.8 mg + 7.7 mg).

Based on these facts, patterns of nitrogen allocation by the foundresses at exposed and sheltered sites are shown in Fig. 2. Mean amounts of N consumed by the brood were about 78% in EN and 84% in SN, suggesting that foundresses nested at sheltered sites could invest more in larval growth. On the other hand, the mean relative amount of N for producing oral secretion for EN (22%) was greater than that for SN (16%) ($P < 0.01$). This result indicates that foundresses at exposed sites had to invest much more in secretion production.

Discussion

Foundresses that nested at sheltered sites brought more prey animals into their nests than those nested at exposed sites. Kudô et al. (1998) also noticed the same tendency in an Itako population of *P. chinensis* throughout three consecutive years. Foraging activities of foundresses that nested at exposed sites were apparently more reduced, because these foundresses had to do some extra tasks, such as nest maintenance and defense. They had to remove rain droplets on the nest and smear the oral secretion over their nest surfaces to repel rain. Another possible factor for decreased foraging activities of foundresses of EN is higher predation pressure or parasitism. If natural enemies could easily detect exposed nests, the foundresses had to stay on their nests to defend their brood. Analyzing foraging behaviors of the foundresses of *P. chinensis*, Kasuya (1983) concluded that it would not be easy for foundresses to obtain food because they were often exposed to strong conspecific attacks.

A comparison of dry weights of oral secretion produced at exposed and sheltered sites showed no significant differences between the two types of nests. The dry weights were also comparable to those of nests taken in Itako (Kudô et al. 1998). It seems that the dry weight of the secretion produced by a foundress of *P. chinensis* in central Japan is physiologically constant at about 60 mg. This study, however, confirmed, by comparing the N content, that there was a great difference in the relative investment in oral secretion production between two types of nest sites. Foundresses of ENs used larger relative amounts of proteinaceous resources to produce the secretion (22% for EN vs. 16% for SN). According to Kudô et al. (1998), mean the proportion of nitrogen allocated to produce the secretion during the founding phase was about 14% in sheltered nests in Itako. The mean value obtained for SNs in Toki (16%) is nearly comparable to that for SNs in Itako, showing that in *P. chinensis* about 15% of protein input is consumed in producing the secretion during the founding phase, in sheltered environments.

Rain seems to be a decisive factor in causing a difference of relative investment in secretion production between EN and SN, because foundresses at exposed sites had to increase the mechanical strength and water repellency of their nests. It is already known that wasp nesting activities, including extranidal tasks (Yamane 1971) and nest maintenance (Yamane and Itô 1994), are influenced by rains. Kudô et al. (1998) considered that such behavioral flexibility of *P. chinensis* foundresses may ultimately increase the colony survival rate.

The problem for allocation of proteinaceous food resources by *Polistes* foundresses has been discussed from a point of brood nourishing. For example, O'Donell (1998) stated that foundresses must partition available proteinaceous resources among their first offspring. Miyano (1998) clarified that foundresses of *P. chinensis* produced the first batch of workers with varying body sizes in response to food availability. Their discussion is, of course, indispensable for understanding the mechanism of caste determination in social Vespidae. However, it should be stressed that the allocation of proteinaceous resources between brood nourishing and production of oral secretion must be considered first. Amounts of oral secretion used were nearly comparable between two colony categories (Fig. 1), while the number of immatures reared in ENs was much smaller than that in SNs. This finding indicates that foundresses at exposed sites assigned larger relative amounts of proteinaceous resources to secretion production than did those at sheltered sites. It was recently suggested that foundresses of *P. chinensis* may adjust utilization patterns of the resources for these purposes in response to given environmental factors, such as precipitation (Kudô et al. 1998).

Next, foundresses allocate the remaining proteinaceous resources to immatures. In this step, they may produce a batch of first workers according to the following two alternative tactics: (1) to produce a relatively large number of small-sized individuals and (2) vice versa. In this study, body weights of workers in ENs were significantly smaller than those in SNs, but the difference in the number of pupae produced was not significant between two nest categories. This result supports tactic (1), suggesting that the number of workers produced is more important to colony success.

Miyano (1990) showed, in *P. chinensis*, that mean number and dry weight of workers reared by lone foundresses were 10.2 individuals and 24.0 mg, respectively. Thus, foundresses in Toki produced smaller and fewer workers (7.4 individuals and 18.0 mg for EN and 9.9 individuals and 19.3 mg for SN) than those from Miyano's results. Foundresses at sheltered sites produced as many workers as in Miyano's results, but their body weight was much smaller. Further, foundresses of ENs produced as many workers as those of SNs (also nearly comparable to Miyano's results), but their body weight was significantly smaller. Therefore, these facts also strongly suggest that number of workers is more important for colony success.

Because it seems to be important for colony survival how lone foundresses allocate proteinaceous resources efficiently to several purposes at different steps, relationships between foundresses' decision making and colony survival rates must be clarified in future work.

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