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Proteinaceous Resource Distribution by Single Foundresses of the Paper Wasp *Polistes* (*Gyrostoma*) *jokahamae* (Hymenoptera, Vespidae)

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Abstract

Nests are structures built by animals to protect their own offspring from predation, parasitism, and harsh climatic conditions. However, these structures are generally costly to build and maintain. *Polistes* wasps build paper nests using plant fibers. They also use oral secretion, mainly composed of proteinaceous elements to construct and maintain their nests. Due to the high production cost of oral secretion, wasps must efficiently allocate proteinaceous resources between rearing their brood and producing the secretion. We evaluated the investment made by foundresses of *P. (Gyrostoma) jokahamae* in their nests based on the amount of oral secretions. It has been estimated that 7-9% of the nitrogen (proteinaceous) resources were used to produce oral secretions. The results suggested that a single *P. (Gyrostoma) jokahamae* foundress partitions available proteinaceous resources not only among the first batch of the brood but also produces the oral secretions. There is an intense pressure related to the limited allocation of resources during the single foundress period of *Polistes* wasps.

Introduction

Nests are structures built by animals to protect their own offspring, i.e., eggs and young immature animals, from predation, parasitism, and harsh climatic conditions (e.g., Deméré et al., 2002). Nest builders provide various degrees of parental care to the offspring, from the embryo to the adults. Parents, who are standard nest builders, construct elaborate and safe nests for their offspring. However, these nest structures are generally expensive to build and maintain. Mainwaring & Hartley (2013) reviewed the costs of nest construction for birds and concluded that nest construction is energetically expensive and considerably related to their life history.

Paper wasps (Polistinae, Vespidae) build elaborate nests using two types of materials for brood rearing. One is plant tissue, commonly composed of wood fibers (see a review by Wenzel, 1991). Adult wasps leave their nests, visit routine woods, and collect fibers from them. The time required for a series of material collections is short and is generally within a few minutes. The other is oral secretion, which is produced by the labial glands of the wasps themselves (see a review by Jeanne, 1996). Paper wasps use oral secretion, mostly comprising proteinaceous elements, to glue the plant fibres and maintain the nests (McGovern et al., 1988; Maschwitz et al., 1990; Espelie & Himmelsbach, 1990; Singer et al., 1992; Kudô et al., 1998). Adult wasps chew plant fibers collected from the environment, mixing them with oral secretions to use in nest construction. Additionally, they often smear their oral secretions on the surfaces of their nests to enhance their mechanical strength. As a result, the surfaces at the petiole and dorsal parts of the nest comb are thickly coated with the secretion, and plant fibers are hardly seen (Kudô et al., 1998).

While information on the types of plant materials used for nest construction in paper wasps has been reported by many researchers (see a review by Wenzel, 1991), little

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research has been conducted on oral secretions, particularly on their production costs. Because a major proportion of the secretion is proteinaceous elements, associated with foraging for insects by wasps themselves, the cost of producing the secretion is suggested to be high (Kudô et al., 1998).

Polistes is one of the genera in the subfamily Polistinae and is the most primitive group (Carpenter, 1991). Colonies of *Polistes* species are initiated by one or several inseminated queens (foundresses), independent of any worker. In temperate regions, the first-bathes of workers are produced in early summer, and the colonies proliferate during the summer. Gynes and males emerge from the colonies in late summer and mate until autumn. Gynes hibernate in shelters such as tree trunks until the following spring. The founding phase during the life cycle of temperate *Polistes* species has received special attention from many researchers (Reeve, 1991). For example, there is accumulating evidence of usurpation, a strategy used by foundresses that have lost their colonies (see a review by Reeve, 1991). Behavioral studies have been conducted on foraging for food using a lone foundress. She forages for various materials to rear broods and nests. Foraging for prey is the most time-consuming task (Suzuki, 1978; Kasuya, 1980; Kudô, 1998), and causes a high risk of predation on herself as well as her brood by ants (Jeanne, 1975) and conspecific attacks during her absence from the nest (Kasuya, 1983). Thus, a foundress must overcome the dilemma between the separate needs of nest defense and foraging for prey (Kasuya, 1983; Furuichi & Kasuya, 2013). Furthermore, it is necessary to produce the first batches of workers as early as possible by providing a large number of prey for ensuring the colony's success (Miyano, 1998; Karsai & Hunt, 2002; Kudô & Shirai, 2012).

Another dilemma relates to prey foraging during the founding phase. Foundresses allocate a limited amount of proteinaceous resources to larvae and to produce oral secretions. Kudô et al. (1998) estimated the amount of oral secretion used for constructing and maintaining nests by foundresses of *P. chinensis antennalis* (Pérez). The amounts consistently exceeded 50% of the mean percentage of secretion relative to the total dry nest weight, suggesting that the foundresses used a large portion of proteinaceous resources (prey) to produce oral secretions. In fact, it has been shown that 10-20% of total protein resources brought by a foundress is devoted to producing the secretion (Kudô et al., 1998). It is probable that foundresses reduce the production costs of secretions and raise their surplus resources for larval growth. One solution to this dilemma is known as "efficient cell use", in which foundresses lay eggs on silk caps and rear two immature individuals in a single cell (Wenzel, 1996).

A dominant female of *Polistes* wasps laid eggs in the empty cells. Thus, larvae were reared one per cell, spinning a completely closed cocoon upon pupation. The cells may be reused after an adult emerges from the cocoon. In contrast, the same cell is often, though not exclusively, occupied simultaneously by two successive broods. After cocoon spinning by the post-feeding larvae in a given cell, the dominant female laid one additional egg on the silk cap inside the cell (Fig 1). The egg grows and attains second - to third-instar larvae during the emergence of older occupants. Upon emergence, the adult crawls through the distal opening of the cell and presses a second larva onto the cell wall. The second larva moves back to the cell bottom at the fifth instar, that is, the final instar, when its distal end is liberated from the cell wall. The latter has been reported since the 1970s in the subgenus *Gyrostoma* of *Polistes* (Yamane, 1972; Yamane & Okazawa, 1977; Miyano, 1991). Yamane & Okazawa (1977) described a sequence of simultaneous use of the same cell by two successive immature individuals with several pictures of *P. tepidus malayanus* (Cameron) in New Guinea. The authors mentioned that the same cell use was observed in other consubgeneric species, such as *P. tenebricosus*, *P. jokahamae,* and *P. rothneyi* (Cameron). Wenzel (1996) labelled this "efficient cell use", because adult wasps do not construct cells for each immature individual and thus maintain a limited number of cells.

The efficient cell use hypothesis explains the rearing of two immatures in a single cell but has never been tested. In this respect, the proteinaceous resource allocation by foundresses provides an opportunity. If a foundress of *Gyrostoma* species rears two immatures in a single cell, it can reduce the proteinaceous resources for oral secretion production. This may be a good solution for a single foundress to solve the dilemma of limited resource allocation between brood rearing and the secretion production.

In this study, we estimated the investment made by the foundresses of *P.* (*Gyrostoma*) *jokahamae* in their nests based on the amount of oral secretion used for nest construction and maintenance. This species exhibits a typical colony cycle in the temperate regions mentioned above and rears two immature pupal cells (Yamane & Okazawa, 1977). Because a single post-hibernation foundress initiates each colony, it is possible to estimate the relative amount of proteinaceous resources (nitrogen) distributed to brood rearing and oral secretion production by foundresses until the emergence of the first worker. The relative nitrogen distribution obtained for secretion production in *P. jokahamae* was compared with that in a previous study on *P. chinensis antennalis*, in which each immature individual was reared separately in a single cell. The efficient cell use hypothesis is supported if the relative amount of nitrogen is smaller in *P. jokahamae* than in *P. chinensis antennalis*.

Additionally, we compared the frequencies of pupal cells containing the two immature strains between the different colony phases. If such cell use is strongly preferred during the founding phase, we hypothesize that the cell use will rarely be observed in the later phase, with many worker forces.

Fig 1. Eggs or young larvae were reared on silk caps of pupae in a nest of *P. jokahamae*. Photographs show the nest from an aerial view (left) and a cross-sectional perspective (right).

Materials and Methods

1. The founding phase

Nest collection

Newly initiated colonies were found on the Campus of Niigata University (37°49’ N, 138°52 ‘E), Niigata, Japan, during the daytime of May in 2012 and 2013. All the colonies were initiated by a single female that emerged post-hibernation. When a new nest was found, a unique enamel mark (Teranishi Chemical Industry) was placed on the thorax of the foundresses. A total of 198 and 190 colonies were identified in 2012 and 2013, respectively. We monitored the development and survival of each colony at 3-day intervals until the emergence of the first worker.

We collected nests a few days before the first worker emerged to estimate the foundresses’ total investments in brood-rearing and nest construction from late June to early July. 24 and 17 nests were collected in 2012 and 2013, respectively. However, we noted characteristics of the collected nests as foundresses’ investments in their brood rearing and nests differ between two environments, i.e., exposed nests (ENs) and sheltered nests (SNs), in *P. chinensis antennalis* (Kudô et al., 1998, 2000). They were built either at exposed sites, such as branches of bushes, where nests were exposed to rain and the sun, or at semi-sheltered sites, such as under the roofs of buildings. The number of ENs and SNs was 27 and 14, respectively (10 and 14 in 2012, and 17 and 0 in 2013, respectively).

Weights of nests and some other parameters

The collected nests were brought to the laboratory, and cell maps were recorded before all eggs and larvae were carefully removed using forceps. Nests containing pupae in several cells were placed in plastic cases under laboratory conditions until all workers emerged. Eggs, larvae, and newly emerging workers were dried for 48 hours in an electric oven (Toyo Engineering Works, FS-620) and weighed to the nearest 0.1mg using an electronic balance (Mettler, AE200). Other matter left inside cells, i.e., meconia, larval silk, and exuviae of post-feeding larvae, were removed under a binocular microscope (Olympus, SZ-61) and weighed to the nearest 0.1 mg after drying for 48 hours. Finally, broken cell walls and petioles were weighed to the nearest 0.1 mg after drying for 5 hours.

Weights of plant material and oral secretion

Polistes wasp nests consist of two kinds of material: plant fibers and oral secretions. Weighed nests were immersed in a 0.5 N KOH solution and incubated at 70 °C for 7-12 hours to dissolve the oral secretion to separate these materials. Previous studies showed that the oral secretion used in *Polistes* nests is completely soluble in a 0.5 M KOH solution (Kudô et al., 1998; Yamane et al., 1999). The dissolved constituents in the solution were filtered. The plant fibers remaining on the filter paper were washed with distilled water to remove secretory elements and then dried in an electric oven for 5 hours. Plant fibres were weighed together with filter paper to the nearest 0.1 mg, and the weight of the filter paper was subtracted.

However, the obtained value was underestimated because some plant fibres, such as proteinaceous fibres and other elements, are soluble in basic solutions. According to pre-emergence nests in *P. chinensis antennalis*, weight loss of plant fibers due to the KOH solution was approximately 11% (Kudô et al., 1998). Therefore, the loss of soluble substances to KOH was assumed to be 11% in this study, and the weight of the remains on the filter paper was corrected by multiplying it by 1.11. The weight of the oral section was estimated by subtracting the weight of the plant fibres from the total nest weight.

CN analysis

The nitrogen content of workers, larvae, matter left inside cells, and pure membranes of oral secretion on petiole surfaces was analysed for each specimen from five colonies collected in 2012 using the combustion method (CN Corder MT-700; Yanaco, Kyoto, Japan). There was not enough nitrogen content in an egg for the analyses; thus, a total of 91 eggs from nests in 2012 were analyzed as a single specimen.

2. The reproductive phases

Nest collection

In total, 3 and 10 nests were collected on the Campus of Niigata University and Sakata Park (37°49' N, 138°52 'E), Niigata, respectively, during the daytime of late August 2013. The colony cycle of these colonies was assumed to be in the reproductive phase because males co-existed with workers and possibly gynes in these nests (Reeve, 1991). Many immature individuals were still reared in the nests. The 13 nests were brought to the laboratory, and cell maps were recorded.

Data analysis

The data were analyzed using the nonparametric Mann-Whitney U-test, at a 5% significance level.

Results

1. Brood rearing and nest construction during the founding phase

1.1. Colony composition and nest size

The number of immatures was compared between ENs and SNs in 2012 and between the two years for ENs only (Table 1). Most comparisons showed non-significant differences, whereas the number of eggs was significantly greater in ENs than in SNs, and greater in 2013 than in 2012.

The number of cells and nest weight did not significantly differ between ENs and SNs in 2012, but were significantly greater in 2013 than in 2012.

Foundresses built larger nests in 2013 than in 2012 and laid a greater number of eggs.

Table 1. Foundresses-reared immatures and ENs and SNs (mean ± SE).

	2012		2013
	ENs	SNs	ENs
Number of immatures			
Eggs	6.90 ± 1.02[a]	3.14 ± 0.67[b]	12.29 ± 0.66[c]
Larvae	13.50 ± 1.15[a]	17.36 ± 4.43[a]	13.18 ± 0.68[a]
Pupae	9.00 ± 0.76[a]	8.36 ± 0.63[a]	9.18 ± 0.47[a]
Total brood	29.40 ± 2.07[a]	28.86 ± 1.66[a]	34.65 ± 1.17[a]
Number of cells	22.00 ± 1.43[a]	23.36 ± 1.36[a]	26.65 ± 0.08[b]
Nest weight (mg)	151.28 ± 7.27[a]	171.61 ± 7.23[a]	182.26 ± 5.60[b]

Significant differences were detected in Mann-Whitney U-tests among different letters at the $P < 0.05$ level.

1.2. Nest material composition

The weight of plant fibres did not differ significantly between nest sites or years (Mann-Whitney U-test, nest sites: $z = 0.11$, $P = 0.92$, years: $z = 0.44$, $P = 0.74$), although the weight of oral secretions was significantly higher in 2013 than in 2012 (Mann-Whitney U-test, $z = 3.31$, $P < 0.01$) (Fig 2). As a result, percent oral section did not differ significantly between nest sites in 2012 (EN: 37.59 ± 4.47%, SN: 43.14 ± 4.39%, Mann-Whitney U-test, $z = 0.99$, $P = 0.31$), but that in 2012 was significantly larger than in 2013 in EN (50.49 ± 2.26%) (Mann-Whitney U-test, $z = 2.66$, $P < 0.01$).

Foundresses built larger and heavier nests in 2013 than in 2012, producing more oral secretions.

1.3. Nitrogen content and estimate of proteinaceous resource distribution

The mean dry weights of all proteinaceous matter, such as eggs, larvae, adult workers, silk, exuviae, meconium, and pure membranes of oral secretions are shown in Table 2. No significant differences in matter, excluding oral secretion, were detected between ENs and SNs in 2012. In contrast, a significant difference in the total weight of larvae was detected between 2012 and 2013 in ENs.

We attempted to estimate the distribution of proteinaceous (nitrogen) resources used by the foundresses of *P.* (*Gyrostoma*) *jokahamae* to nourish broods and build their nests. The estimation follows that of Kudô et al. (1998) who estimated the distribution in pre-emergence nests of *P. chinensis antennalis*.

Brood: The amount of nitrogen (N) used for each item was estimated by multiplying the N content (%) of each item by its dry weight. The amount of N for all items was summed to obtain the total N input per colony into the brood during the founding phase. The mean total N varied between 97 and 123 mg between the years (Table 2). The mean N for egg production was considered quite small.

Oral secretion: since this secretion has 12.42 ± 0.23% N (Table 2), we obtain mean N contents between 7-11 mg.

Based on these assumptions, the patterns of nitrogen distribution in *P.* (*Gyrostoma*) *jokahamae* foundresses nourish broods and their nests. Most N was consumed for larvae, while a small proportion of N was used for producing the oral secretion (6.91 ± 0.61% for ENs and 8.08 ± 0.92% for SNs in 2012 and 8.59 ± 0.41% for ENs in 2013).

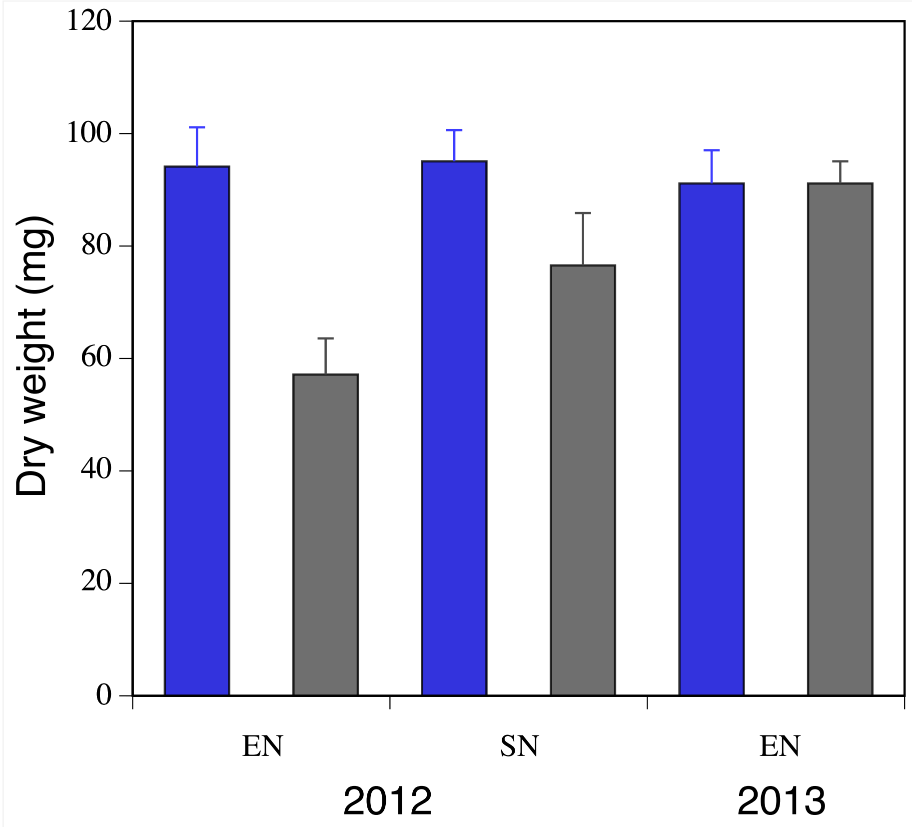

Fig 2. Material composition of pre-emergence nests of *P. jokahamae* at different nesting sites and years. Blue and grey lines mean plant material and oral secretion, respectively. Vertical bars indicate mean ± SE (ENs: exposed nests, SNs: sheltered nests).

2. Two immatures in pupal cells in different colony phases

The number of pupal cells in which the two immatures were reared did not significantly differ between nest sites in 2012 (Mann-Whitney U-test, $z = 1.02$, $P = 0.31$) or between years in EN ($z = 1.07$, $P = 0.28$) (Fig 3A) during the founding phase. We also compared the proportion of pupal cells in which two immature individuals were reared (number of pupal cells in which two immatures/total number of pupal cells). The mean proportions varied between 0.78 and 0.96 between different nest sites and years; however, this was not significant (between nest sites: $z = 1.83$, $P = 0.07$; between years: $z = 2.11$, $P = 0.04$, non-significant when a sequential Bonferroni test was applied after the Mann-Whitney U-test) (Fig 3B).

Table 2. Mean dry weights (± SE) of adult workers, immatures, and matters left inside cells, and mean percentage of nitrogen contents in these items + pure membranes of oral coatings on the petiole surfaces.

	Mean weights of each dry matter (mg)			Mean percent nitrogen	Mean dry weight of nitrogen (mg)		
	2012		2013		2012		2013
	ENs	SNs	ENs		ENs	SNs	ENs
Eggs	2.74 ± 0.74[a]	1.23 ± 0.17[a]	3.23 ± 0.15[a]	8.62	0.24 ± 0.06	0.11 ± 0.01	0.28 ± 0.01
Larvae	265.12 ± 0.38[a]	362.29 ± 48.02[a]	469.85 ± 48.02[b]	8.83 ± 0.38	23.34 ± 3.78	32.82 ± 4.30	41.35 ± 3.70
Workers	430.35 ± 37.06[a]	420.64 ± 29.84[a]	475.98 ± 25.92[a]	12.64 ± 0.42	55.60 ± 4.81	54.47 ± 3.86	61.69 ± 3.32
Silk	41.90 ± 3.72[a]	48.43 ± 2.90[a]	44.88 ± 2.35[a]	13.45 ± 0.70	5.64 ± 0.50	6.51 ± 0.39	6.04 ± 0.32
Exuviae	8.78 ± 0.60[a]	9.73 ± 0.91[a]	9.59 ± 0.58[a]	8.50 ± 0.13	0.75 ± 0.05	0.83 ± 0.08	0.82 ± 0.05
Meconia	170.23 ± 22.25[a]	161.06 ± 12.09[a]	178.67 ± 10.23[a]	7.05 ± 0.70	12.00 ± 1.57	11.35 ± 0.85	12.60 ± 0.72
Oral secretion	57.14 ± 6.43[a]	76.55 ± 9.32[a]	91.13 ± 3.94[b]	12.42 ± 0.23	7.10 ± 0.80	9.51 ± 1.16	11.32 ± 0.49
Total					104.66 ± 8.65	115.60 ± 6.39	134.09 ± 5.26

Significant differences were detected in Mann-Whitney U-tests among different letters at the $P < 0.05$ level.

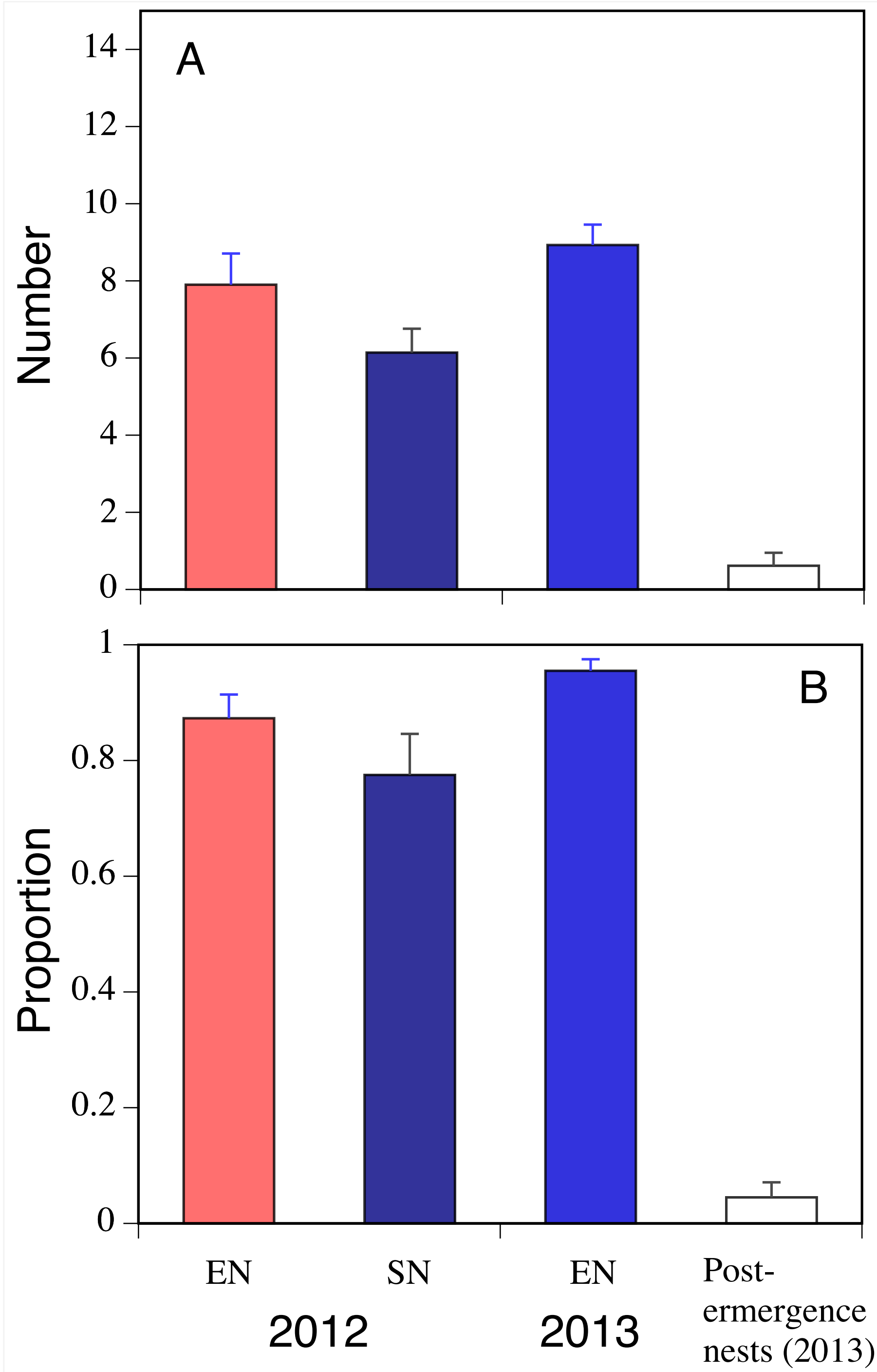

Fig 3. (A) Number and (B) proportion of pupal cells in which two immatures were reared in pre-emergence and post-emergence colonies at different nesting sites and years. The proportion of pupal cells in which two immatures were reared was defined as the number of pupal cells with two immatures/total number of pupal cells. Vertical bars indicate mean ± SE (ENs: exposed nests, SNs: sheltered nests).

In contrast, the number of pupal cells in which the two immature strains were reared decreased during the reproductive phase (Fig 3A). In fact, only 0.62 ± 0.34 pupal cells were used to rear two broods in a colony. Thus, there was a significant difference in the number between the founding and reproductive phases (Mann-Whitney U-test, z = 4.67, $P < 0.001$). Similarly, the proportion of pupal cells in which the two immature strains were reared was significantly lower during the reproductive phase than during the founding phase (Fig 3B).

Discussion

We evaluated the investment made by foundresses of *P.* (*Gyrostoma*) *jokahamae* in their nests based on the amount of oral secretions used for nest construction and maintenance. It was estimated that 7-9% of nitrogen (proteinaceous) resources were used to produce oral secretions. Two immature individuals were reared in 80-90% of pupal cells during the founding phase but were rarely observed in later and developed colonies.

This study estimated that only a small percentage of nitrogen was used to produce oral secretions in the pre-emergence nests of *P.* (*Gyrostoma*) *jokahamae*. We compared these values with those of previous studies conducted on another independent-founding polistine wasp, *P. chinensis antennalis*. Foundresses of *P. chinensis antennalis* allocated 14-25% of nitrogen into secretion production (Kudô et al., 1998; Kudô, 2000). The differences between the two species were significant in all comparisons across years (Mann-Whitney U-test, P<0.001), indicating that *P.* (*Gyrostoma*) *jokahamae* foundresses distributed proteinaceous resources, which originated from hunted prey to the nests than those of *P. chinensis antennalis*. Because structural and material differences in nests between the two species are unknown (Wenzel, 1991), it is highly likely that the difference detected in nitrogen distribution to oral secretions between the two species is whether these wasps rear two immature individuals in pupal cells. In fact, the relative amount of oral secretion in pre-emergence *P.* (*Gyrostoma*) *jokahamae* nests ranged from 35 to 50%, which was much lower than that of *P. chinensis antennalis* (53-68%, Kudô et al., 1998). Our study showed that two immature individuals were reared within 6-9 pupal cells/nest in *P.* (*Gyrostoma*) *jokahamae* during the founding phase, indicating that the foundresses did not require the same number of cells. Additionally, they did not use an additional amount of oral secretion to maintain their nests, particularly on the bottom surface of the cells. *Polistes* wasps frequently smear with oral secretion on the surface of the petiole and bottom of cells to increase the mechanical strength of the comb (see SEM photographs in Kudô et al., 1998). All of this evidence strongly supports the "efficient cell use" hypothesis, which has been proposed by Wenzel (1996).

The reduction of proteinaceous resources to produce oral secretions by *P.* (*Gyrostoma*) *jokahamae* foundresses indicated that they were able to allocate resources to brood rearing. This is advantageous for the success of the colony. Since the duration of larval development in *Polistes* wasps varies based on the number of prey provided (Strassmann & Orgren, 1983; Rossi & Hunt, 1988; Kudô & Shirai, 2012), it is favourable for the foundresses to shorten the founding phase by providing sufficient proteinaceous resources to their larvae. Foraging by a lone foundress of *Polistes* wasps is the most time- and energy-consuming and risky task (Suzuki, 1978; Kasuya, 1980), and causes a high risk of predation not only on herself but also on her brood by ants (Jeanne, 1975) and intraspecific species (Kasuya, 1983) during her absence from the nests. Efficient regulation of limited resources between brood rearing and oral secretion production is required for a single foundation.

In contrast, two immature pupal cells were rarely observed during the reproductive phase. The workforce of many workers in the nests peaks throughout the colony cycle (Reeve, 1991). Their labor provides sufficient amounts of proteinaceous food, causing great merit for colony development to construct new cells and rear broods in cells independently. Therefore, the temporal changes in the cell-use patterns between the two phases are reasonable. However, it is not known whether brood rearing in independent cells observed during the reproductive phase is caste-specific (foundresses or workers) or whether there is a difference in colony development. Yamane & Okazawa (1977) collected 37 colonies of *P. tepidus* in New Guinea and described their nest and brood development. This species rears two immature individuals in the pupal cells, even after worker emergence. However, cell use differences were not compared between the colony developmental stages of *P. tepidus*. Future studies should investigate whether rearing two immature individuals in pupal cells ceases suddenly or gradually after worker emergence.

This study addressed an interesting behaviour in which adult *Polistes* wasps rear two broods in their pupal cells for the first time. Such behaviour has been described in the last few decades in some species belonging to the subgenus *Gyrostoma* (Yamane, 1972; Yamane & Okazawa, 1977; Miyano, 1991) but has never been examined. Our results suggest that a single *P.* (*Gyrostoma*) *jokahamae* foundress efficiently reduced the limited proteinaceous resources for oral secretion production. These conditions strongly support "efficient cell use hypothesis" proposed by Wenzel (1996), which explains the simultaneous use of one and the same cell by two immatures. However, this type of cell use has been observed in the initial colonies of *P. tepidus* in New Guinea, which were managed by multiple foundresses (Yamane & Okazawa, 1977). Because multiple foundresses generally gain more proteinaceous resources than a single foundress, further studies are needed to examine whether such cell use is associated with the costs of nest construction in polygynous societies.

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Authors' Contribution

All authors participate in all stages of this paper.

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