

Adaptive Nesting Tactics in a Paper Wasp, *Polistes riparius*, Inhabiting Cold Climatic Regions

by

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ABSTRACT

Thermal effects on the nest sizes constructed by *Polistes riparius* foundresses, their nesting activities, and colony compositions were determined in laboratory conditions during the pre-emergence period. In this study, foundresses were placed in cold (20°C) and warm conditions (27°C), and ample food and nest materials were supplied. Nest sizes were larger in the cold condition; particularly, the elongation of cells was remarkable. The number of cells between the 2 conditions was not significantly different. Inter-condition colony composition was similar, while more honey drops were observed in the cold condition nests. A positive relation was observed when the relationships between body weight and developmental days were investigated, i.e., small offspring required shorter developmental days in both thermal conditions. In the cold condition, the first offspring were very small, whereas offspring size increased steeply after the second order, and was comparable to that of the foundresses; the size increase in the warm group was slight. This result indicates that the cold condition foundresses manipulated the sizes of their offspring. When inter-condition foundresses activities were compared, cold condition foundresses spent more time and energy on flight activities. These results support the view that foundresses change nesting activities in relation to environmental temperatures, i.e., they can improve the thermal condition of nests by adding extra cells and manipulate the sizes of adult offspring.

Keywords: Nesting tactics, *Polistis*, nest building, body weight, cold climate, Hymenoptera, Vespidae.

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INTRODUCTION

It has been revealed that social wasps vary their nesting habits flexibly in order to maximize their fitness in relation to their environments (Wheeler 1986). Among the activities of social wasps, the nest building is one of the most important and interesting aspects because the nest is where social activities take place, and it is used for nursing the brood, i.e., it is directly connected with reproduction (Jeanne 1991).

Many studies have shown that wasps build nests in response to the environments they inhabit (Matsuura 1990; Yamane 1996), since the development of the immature stages depends on the ambient temperature. In tropical and cold climatic ecozones, and nest thermoregulation is carried out by constructing nests with unique structures (Hozumi *et al.* 2007, 2008ab, 2009). In tropical regions, wasps insulate nests to maintain a constant temperature against daily temperature fluctuations (15–40°C) (Hozumi *et al.* 2010); in these regions, nests must be prevented from overheating. On the other hand, in cold climatic regions such as the Arctic and high mountainous areas, the most pressing environmental problem is the low temperature, which shortens the development of the immature stages and activities of adult individuals (Henrich 1993). Due to the short nesting period, the strategy in cold regions is that wasps should increase colony production by accelerating the development of the immature stages and produce gynes as early as possible.

In paper wasps belonging to the genus *Polistes*, the colony cycle is divided into 3 periods: pre-emergence, worker, and reproduction. The foundresses (independent founding) build exposed nests and manage all tasks before the worker individuals emerge (pre-emergence period). After the workers eclose (worker period), the adult individuals steeply develop colony production, and finally produce as many reproductive gynes as possible; therefore, the wasps make an effort to shorten the colony cycle (Yamane 1969; Yamane & Kawamichi 1975; Miyano 1980).

Among these periods, shortening of the pre-emergence period is more important in the colony cycle, since this period is the longest of the 3 periods (1.8 months/3 months) and is when most colony failure occurs (Kudô 1997). A major cause of colony failure is the loss of foundresses during extranidal activities such as foraging for prey and nest materials. In order to reduce the

risks during the pre-emergence period, foundresses hasten development of the immature stages by 2 methods, i.e., nest thermoregulation and control of larval feeding: incubation of brood (Miyano 1981; Jeanne & Morgan 1992), feeding intensely on ample food (Kudô *et al.* 1998), and manipulating worker sizes to be as small as possible (Miyano, 1980).

Polistes wasps often improve the thermal conditions of their nests. For example, the foundresses of *Polistes riparius*, which inhabit cold areas in northern Japan, not only choose warm sites, but also construct extra cells around the brood cells (Yamane & Kawamichi 1975). Such long and numerous cells further increase nest temperatures when the nest receives sunlight (Hozumi *et al.* 2008b). Generally, nest construction requires a very high cost in the form of extranidal activities and resources for nest material; foundresses have to collect nest materials and forage for prey to produce an oral secretion that is used for construction and maintenance of the nest (Yamane *et al.* 1998). In nests built by lone *P. riparius* foundresses, both the amount of nest materials and oral secretion are twice of that in nests with no extra cells (Kudô *et al.* 1998), i.e., *P. riparius* foundresses have to carry out more extranidal work despite the high cost and high risk of colony failure. However, whether the nest building activities of foundresses are influenced by cold ambient temperature has not been studied.

Regarding the control of larval feeding, it has been emphasized that very small first adults are produced to end the pre-emergence period as early as possible, even in temperate regions (“small worker” hypothesis; Miyano 1981). Recently, further manipulation by foundresses has been reported. Fucini *et al.* (2009) reported that *P. biglumis* inhabit severely cold areas; the very short nesting period changes the nesting behavior in that foundresses produce gyne-like females instead of worker-like individuals, whereas worker-like individuals are produced in warm areas. This means that paper wasp foundresses can change nesting tactics in response to ambient temperature and shorten the colony cycle by omitting the worker period in order to produce gynes immediately (“omission” hypothesis). However, it is still unknown whether *P. riparius* foundresses plastically change the caste of offsprings in cold conditions.

This study aimed to determine whether the nesting activities of *P. riparius* foundresses are influenced by the environmental temperature. I hypothesized that foundress responses against a cold environment would be revealed in

activities improving the thermal conditions of the nest, i.e., construction of extra cells and manipulation of the sizes of foundress-reared adult individuals to end the pre-emergence period immediately. To achieve this objective, foundresses work more, build a larger nest, and produce small first adult individuals ("small worker"); otherwise, they produce foundress-sized adults or gynes ("omission"). I defined 2 goals for this study. The first goal was to confirm that larger nests are built in colder, rather than warmer conditions. The second goal was to compare the size of foundress-reared adult individuals reared in 2 different thermal conditions. I expected the first adults in the cold condition to be very small; in addition, foundress-sized adults or gynes would be produced instead of workers. In order to examine this, the foundresses were placed in different thermal conditions, and the behaviors and the nest size constructed by lone foundresses were compared. Furthermore, the dry weights of foundress-reared offspring were compared to determine whether foundress manipulation of body size occurred.

MATERIALS AND METHODS

Colonies used and experimental conditions

Ten *P. riparius* foundresses were captured together with their nests on 20 May 2000 in Sapporo (43°03'N, 141°20'E), Hokkaido, Japan. At collection, all nests were virtually at the same development stage with only a few short cells. All of the eggs previously laid in the nests were removed prior to the experiment in order to equalize the initial conditions of the immature development.

Foundresses and their nests were divided into 2 groups: 5 colonies were kept at $20 \pm 1.0^\circ\text{C}$ (hereafter, cold group); the other 85 colonies were kept at $27 \pm 1.5^\circ\text{C}$ (hereafter, warm group). The dry weight of foundresses ranged 35.5–45.9 mg, and the mean weights (\pm SD) of foundresses in the cold and warm groups were 39.9 ± 1.4 mg ($N = 5$) and 41.1 ± 1.4 mg ($N = 5$), respectively, and there was no significant difference (Mann–Whitney U-test, $N = 10$, $U = 7.0$, $P = 0.2506$). Hence, I regarded the influence of the mother's body size on nesting activities as small or negligible in this study. The initial size of the nests did not differ between the conditions: cell lengths in the cold and warm groups were 8.2 ± 0.2 mm ($N = 5$) and 8.4 ± 0.3 mm ($N = 5$), respectively, with no significant difference determined (Mann–Whitney

U-test, $N = 10$, $U = 9.5$, $P = 0.5309$); numbers of cells in the cold and warm groups were 12.2 ± 3.0 ($N = 5$) and 12.6 ± 4.0 ($N = 5$), respectively, and there was no significant difference (Mann–Whitney U-test, $N = 10$, $U = 12.0$, $P = 0.9161$). Each foundress and her nest was placed in a wire-screened cage measuring 30·30·40 cm (L·W·H), and was provided with ample water, and diluted honey and silkworms (*Bombyx mori*) for food. In addition, filter paper was provided as nest material. The photoperiod for both groups was defined as follows: light, 16 h; dark, 8 h. All colonies were maintained under constant conditions until the first workers emerged, and the activities of the foundresses were observed throughout the experiment.

On the day the first adult offspring emerged, the foundresses were removed and the experiment was stopped; eggs and larvae were carefully removed from the nests with tweezers. To determine the body size of adult offspring reared only by foundresses, the pupae were kept intact in the nests, and further incubated under each temperature condition to allow the remaining pupae emerge. Foundresses and foundress-reared adult wasps were dried in an electric oven for more than 48 h at approximately 70°C, and the dry body weights were measured to the nearest 0.1 mg by an electronic scale.

The pattern of cell arrangement and each cell occupant (egg, larva, pupa, honey, or empty) in each colony were recorded. The following nest parameters were measured just after emergence of the first adults: (1) maximum cell length (mm), (2) number of cells, and (3) nest volume (mL). Cell lengths were measured by inserting a scaled stick ($\phi < 1$ mm) into each cell, and the length of the stick was measured with a vernier caliper to the nearest 0.1 mm; the longest value for each cell was recorded. The number of cells was counted right after the emergence of the first adults, and the value was standardized as follows; total number of cells minus initial number of cells. Nest volume was measured as follows: cells were filled with minute and granular glass beads ($\phi < 0.1$ mm), and the volume of the beads was measured with a graduated cylinder to the nearest 0.1 mL.

Behaviors of foundresses

Observations of foundress behaviors in each colony began when the first larvae hatched. One observation episode spanned 3 h between 10:00 and 13:00 or 14:00 and 17:00. Total observation time was 75 h (25 observation episodes)

for 7 colonies in the cold group and 63 h (21 episodes) for 8 colonies in the warm group. Foundress behaviors were categorized as follows: nest building, including elongation of cells, initiation of a new cell, reinforcement of petiole and licking of nest surfaces; collection of nest material; feeding the brood; hunting prey; collection of water or honey; seeking (seeking something or extranidal activities involving no visible tasks); oviposition; body cleaning; resting; and shivering. Shivering activity often occurred just before flight in order to warm the body up by shivering the flight muscle of the thorax, and it required intense respiration, as it involved a sequence of rapid pumping motions with the abdomen. Since most wasps and bees raise their body temperature up to 35°C, the duration of the pumping motion can be an index of pre-flight warm-up in hymenopteran insects (Heinrich, 1993). In this study, direct measurements of body temperature by thermocouples was unfavorable, and the duration of pumping just before flight was measured as an index of environmental influence on the foundresses' activities.

Statistics

The Mann–Whitney U-test was employed to analyze the following features between the cold and warm groups: nest parameters, body weights of adult individuals, colony composition, and foundress activities. Fisher's exact test was used to determine the production rates for large females (see below). All analyses were made with StatView ver. 5.0 (SAS Institute Inc.) on a Macintosh personal computer.

RESULTS

Nest sizes and colony compositions

In both groups, pupae were reared in center area of the nests, and larvae and eggs were located concentrically around the pupae. The elongation of the cells around the pupae was remarkable. Honey dew and empty cells were found in the lower portions of the nests. More cells in the cold group were used to store honey than in the warm group (Table 1) (Mann–Whitney U-test, $N = 10$, $U = 2.0$, $P < 0.05$), whereas the numbers of immature stages and empty cells between groups were similar and no significant difference was detected.

Table 1. Mean (\pm SD) number of contents in the cells in cold ($N=5$) and warm ($N=5$) condition observed at the end of pre-emergence period.

	Eggs	Larvae	Pupae	Honey	Empty
Cool group	19.0 \pm 15.6	15.1 \pm 2.6	7.2 \pm 2.8	15.7 \pm 6.9	4.1 \pm 3.1
Warm group	22.1 \pm 16.9	17.4 \pm 5.5	7.0 \pm 2.4	5.0 \pm 4.0	6.8 \pm 4.7

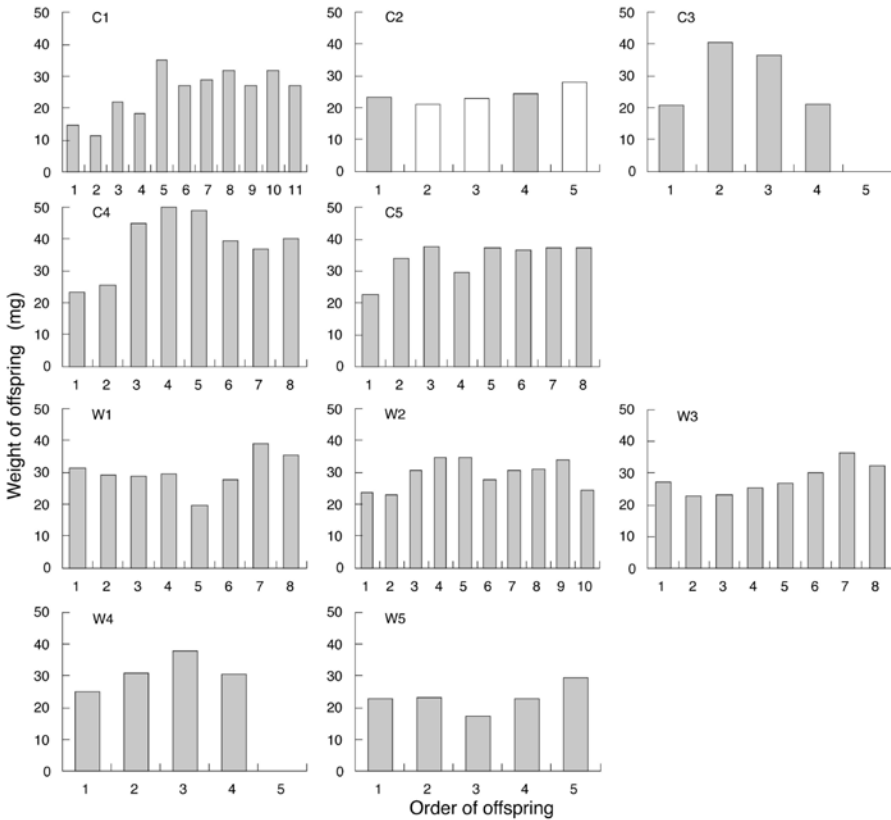


Fig.1 Body weights of foundress-reared adult wasps produced in cold and warm conditions; C1–C5, cold group colonies; W1–W5, warm group colonies. White bars indicate male offsprings.

The nests in the cold group contained longer cells (37.7 ± 2.6 mm) than those in the warm group did (33.2 ± 2.5 mm) (Mann–Whitney U-test, $N = 10$, $U = 2.0$, $P < 0.05$). Cell numbers in the cold group (56.3 ± 13.9) were slightly smaller than in the warm group (56.4 ± 25.8), whereas no significant difference was found between the groups. The volume of nests in the cold group (19.1 ± 4.7 mL) was larger than that in the warm group (13.5 ± 2.1 mL) (Mann–Whitney U-test, $N = 10$, $U = 3.0$, $P < 0.05$).

Figure 1 illustrates the sequent changes of body weights of foundress-reared adult wasps produced in cold and warm conditions. The mean weight of first offspring in the cold group (21.0 ± 3.8 mg) was significantly lower than that of the warm group (26.0 ± 3.5 mg) (Mann–Whitney U-test, $N = 10$, $U = 3.0$, $P < 0.05$). The weight in the cool group steeply increased after the second offspring emerged, and the weight of some individuals was comparable to that of the foundresses (>35 mg; the minimum weight observed in this study): 14 large female individuals were produced from 4 colonies, and 3 males were produced from 1 colony (Fig. 1, from C1 to C5). However, the body weight of offspring in the warm group was relatively similar between individuals (about 30 mg), and 4 large females (>35 mg) were produced from 3 colonies (Fig. 1, from W1 to W5); males were not produced. The number of large adults in the cold group was significantly greater than that in the warm group (Fisher's exact test, $N = 10$, $P < 0.05$).

Foundress activities

The mean times spent on each behavior during the observation period are listed in Table 2. Brood feeding activities were most frequently observed in both thermal conditions, followed by resting and nest building in the cold group or nest building and hunting prey in the warm group. Comparison of activities between the groups determined that shivering in the cold group was significantly longer than in the warm group (Mann–Whitney U-test, $N = 10$, $U = 3.0$, $P < 0.05$). The time distribution patterns for other activities were similar between both groups, and there was no significant difference.

DISCUSSION

It was confirmed that the foundresses in the cold group built larger nests, namely, by virtue of the length of the cells (“extra-cells”). Cell elongation in

Table 2. Mean time (min) of relative activities in an hour of observation. Behavioral repertoire of the foundresses under cool ($N=5$) and warm ($N=5$) conditions was given.

Activity	Cool	Warm
Nest building	9.2 ± 1.3	9.6 ± 2.6
Collection of nest material	2.5 ± 0.6	3.0 ± 1.0
Feeding the brood	20.3 ± 1.8	18.4 ± 1.2
Hunting a prey	7.5 ± 0.4	8.8 ± 1.7
Collection of honey-water and water	0.7 ± 0.3	1.0 ± 0.3
Seeking	3.0 ± 1.5	4.8 ± 1.5
Resting	11.8 ± 1.5	8.7 ± 2.0
Cleaning	5.1 ± 0.5	5.5 ± 0.4
Oviposition	0.2 ± 0.1	0.2 ± 0.1
Shivering	1.7 ± 0.5	1.0 ± 0.4

*: Including elongation of cells, initiation of a new cell and reinforcement of petiole and licking of nest surfaces

cells containing pupae was remarkable. The numbers of cells between groups were not different; hence, the volume of nests in the cold group was larger due to the elongation of cells containing pupae. The cell length, rather than the total number of cells, greatly affects cell temperature (Hozumi *et al.* 2008b), and it is possible that the thermal effect of the cells accelerates development of the immature stages. In this study, the difference of cell length between the cold and warm groups was only 5 mm. However, even a 5-mm elongation may increase cell temperatures by 1–2°C when the nest receives solar radiation (Hozumi *et al.* 2001, 2008b).

In this study, environmental temperatures did not influence entire activity patterns of foundress. This means that the foundresses of cold group actually worked longer time because of the delay of the development of immature stages. Therefore, it cannot be denied that the larger nests built in the cold group were the result of prolongation of the pre-emergence period. However, such a building manner, i.e., building extra-cells throughout the pre-emergence period, has not seen in other wasps inhabiting temperate ecozone. For example, *P. chinensis antennalis* Pérez, a consubgeneric species of *P. riparius* dwelling in warm areas, the time for the construction behavior is short (less 2 min per hour) during the pre-emergence period, and the foundresses rarely leave nests at the end of founding phase, perhaps, in order to reduce the risks of predation and accident during the extranidal activities (Kasuya 1981).

Commonly, the construction of a new cell and elongation of cells is related to oviposition and development of larvae, respectively (Delacourance 1957), and it has been considered that there would appear to be no advantage to be gained by constructing cells at a fast rate at a faster rate than the colonial development (Jeanne & Bouwma 2004). The foundress' overall effort probably represents an optimization of the trade-off between the benefit of increased colony reproduction and the risk of colony failure (Wenzel 1996).

According to Yamane et al. (1998), *P. riparius* foundresses cost resources for nest building as much as rearing broods in terms of resource and time; i.e., foundresses enable to rear more immature stages during the pre-emergence period in spite of high risks during the extranidal activities. If so, foundresses should cost more for rearing immatures in order to produce more gynes, otherwise should stay on the nest until the emergence of first worker in order to reduce the risks of colony failure. However, *P. riparius* foundresses worked throughout the observation hours, and the number of immature stages between the 2 groups was almost similar. It is suggested that with nest construction requiring more resources, instead of rearing more immature stages, the foundresses had attempted to improve the thermal condition of the cells in order to produce offspring immediately during the limited nesting period.

Among the nesting activities of foundresses, whereas the duration of shivering in cold group foundresses was remarkably longer than that of warm group foundresses. This means that cold group foundresses spent more time shivering just before extranidal activities, indicating that activities required a high cost in terms of time spent warming up and energy consumption in cold conditions. Many honey drops stored in the cold group may be used both as food for the colony and as an energy source for warming up. This also supports the premise that extranidal activities require more resources under cold conditions.

I confirmed that foundresses in the cold group manipulated the body sizes of the offspring they reared. As expected, the body size of the first adults in the cold group was very small, suggesting that the foundresses had tried to produce first workers as early as possible. In some colonies of cold condition, however, the body size of offspring subsequent to the second order increased steeply, and the body size of approximately half the newly emerged adults was comparable to that of the foundress. Two hypotheses can be considered for the

altered body sizes: (1) foundresses produce large workers in cold conditions to increase working performance, or (2) produce gynes instead of workers; i.e., omission of worker period. The performance hypothesis is well known in bumblebees inhabiting cold climates (Heinrich & Heinrich 1981). It is expected that large *P. riparius* workers perform nesting activities efficiently, and such large individuals will warm up easily before extranidal flight. Regarding the omission hypothesis, a similar phenomenon has been reported in *P. biglumis* inhabiting high mountain regions (Lorenzi and Turrilazzi 1986); half of *P. biglumis* foundress-reared offspring were gynes. Despite the small number of samples, some male gynes were also produced in this study, and 4 colonies produced very large females whose sizes were comparable to that of the foundresses. These results may support the hypothesis on worker period omission, and it is possible that *P. riparius* foundresses alternate nesting tactics in relation to environmental temperatures.

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