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**HEAT PRODUCTION BY THE FOUNDRESS OF VESPA  
SIMILLIMA, WITH DESCRIPTION OF ITS EMBRYO  
NEST (HYMENOPTERA: VESPIDAE)**

By SHUN'ICHI MAKINO and SEIKI YAMANE

*Abstract*

MAKINO, S. and YAMANE, Sk. 1980. Heat production by the foundress of *Vespa simillima*, with description of its embryo nest (Hymenoptera: Vespidae). *Ins. matsum. n.s.* 19: 89-101, 2 tabs., 9 figs.

An embryo nest of *Vespa simillima* was studied to test the hypothesis proposed by Brian and Brian (1948) and Ishay (1973) that the vespine foundress' curling around the pedicel when resting serves for incubating immatures. The temperature of cell wall was taken with an electrical thermometer on three occasions. Although there was no direct evidence of incubation, the present results proved a considerable temperature rise in the cell wall to which the immatures were attached. We suggest that the heat produced by the foundress during the curling can efficiently be conducted to the immatures via the cell wall. The embryo nest architecture is described as a supplement to the review of vespine embryo nests by Sk. Yamane and Makino (1977).

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## INTRODUCTION

It is well known that the temperature in vespine mature nests is maintained in a regular range by the inhabitants (e.g. Spradbery, 1973). However, except for the work of Gibo et al. (1977), little has been studied on the temperature regulation in embryo (queen) nests, namely during the solitary stage. In some vespine species, the foundress is known to perform a characteristic behaviour in the solitary nesting stage (Table 1). She frequently curls herself around the pedicel between the comb and the innermost envelope sheet (Fig. 6). This behaviour ("curling") occupies a fairly large proportion of intranidal activity time (cf. Sk. Yamane and Makino, 1977). Brian and Brian (1948) and Ishay (1973) observed the behaviour in *Dolichovespula sylvestris* and *Vespa orientalis*, respectively, and regarded the behaviour as having a function of egg incubation, although without any actual data. On the other hand Gibo et al. (1977) did not mention this behaviour at all in their study on the heat production in the embryo nest of *Dolichovespula arenaria* and *D. maculata*, and they concluded that in the solitary stage the foundresses themselves were rather powerless heat producers, compared with mature larvae. Our study was done to test the hypothesis proposed by Brian and Brian (1948) and Ishay (1973), using an embryo nest of *Vespa simillima* in Sapporo, northern Japan.

In this occasion, the architecture of embryo nest of this species will be described as a supplement to the review of vespine embryo nests by Sk. Yamane and Makino (1977).

Table 1. Vespine species in which the curling has been observed.

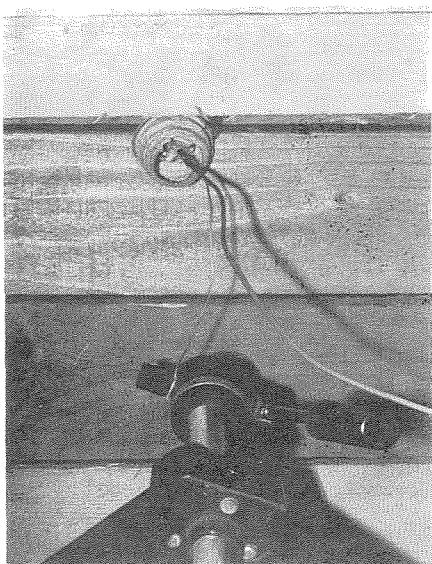
Species	Locality	Author (s)
<i>Vespa crabro</i>	France	Janet, 1895
<i>V. orientalis</i>	Israel	Ishay, 1973
<i>V. analis insularis</i>	Hokkaidō, Japan	Sk. Yamane and Makino, 1977
<i>V. simillima</i>	Hokkaidō, Japan	present study
<i>Dolichovespula sylvestris</i>	England	Brian and Brian, 1948
<i>D. saxonica nipponica</i>	Hokkaidō, Japan	Makino, unpub.
<i>D. media media</i>	Hokkaidō, Japan	Makino, unpub.

## HEAT PRODUCTION BY THE FOUNDRESS

*Materials and methods.* An embryo nest, made on the ceiling of a cabin, was studied (Nest Sm7844; see p. 95). Observations were made on May 27 (11:04–11:30; 16:44–19:00) and May 29 (12:00–14:05) to assess the ability of the foundress to regulate the nest temperature. The probe of an electrical thermometer was inserted in a cell located about the centre of the comb, and laid on the cell wall near the bottom, where an egg had been deposited (Fig. 1). The temperature and foundress activity were recorded nearly every minute. On May 27 the nest had one completed and one half-built envelope sheet, and about 15 cells, most of which had an egg (Fig. 2, A).

On June 18, the nest temperature was again taken with the same nest to study the role of mature larvae in heat production. The nest had four completed and one half-built envelope sheet and 36 cells of which six had pupae, eight mature

larvae and the rest younger immatures (Fig. 2, B). In this case the temperature was taken at the following points: 1) on the ceiling to which the nest was attached, 2) between a cell wall and the ventral surface of a mature larva, 3) near the head of the larva, 4) at the aperture of the second envelope sheet, and 5) at about 2 cm under the entrance hole (Fig. 4). It was taken four times at each point except for point 1.



← Fig. 1. Nest Sm7844 used in the study of heat production. The probe of an electrical thermometer was inserted into a cell to take the temperature of the cell wall. May 27, 1978.

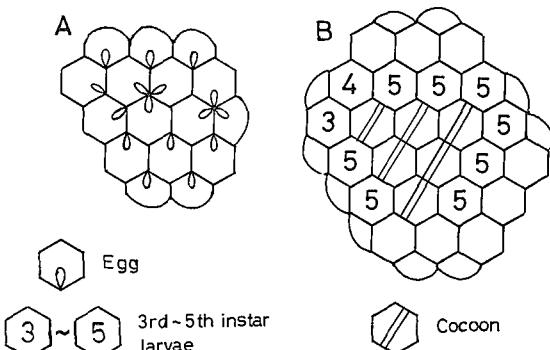


Fig. 2. Cell maps of Nest Sm7844 on May 29 (A) and June 19 (B), 1978. Marginal cells without symbols could not be confirmed for their contents.

*Results.* Figure 3 shows chronological changes in the foundress activity and corresponding changes in the temperature of the cell wall on May 29 (12:38–13:59). A 2.5–4.0°C rise in temperature was always associated with the curling and the risen temperature was usually kept during the act. After the cessation of curling the temperature declined rather gradually. However, as seen in Fig. 3, it began to rise shortly before the commencement of curling. This may be due to the foundress' turning around the pedicel, which almost always occurred prior to the curling, a stationary posture (cf. Sk. Yamane and Makino, 1977). Thus both the turning and curling seem to be responsible for the rise in temperature of the cell wall. In the morning of May 27 (11:04–11:30) we met the same result, that is, the curling by the foundress was always accompanied with the temperature rise.

On the contrary, in the afternoon (16:44–19:00) of the same day no significant rise in the temperature of cell wall was observed when the foundress rested in the curling posture. Although we can not give any decisive explanation to this, there is a strong possibility that in this case the probe was not precisely attached to the cell wall.

Curiously a foundress of *V. simillima* (Nest Sm7846; see p. 95) was observed to curl herself around the pedicel even in the absence of eggs in the nest (Fig. 6). In this case the curling had apparently no function other than resting.

Mature larvae also showed their ability to produce heat. Figure 4 shows the temperatures at five points of the nest taken at four different times. At point 2, the temperature was always higher by 6–7°C than at point 5.

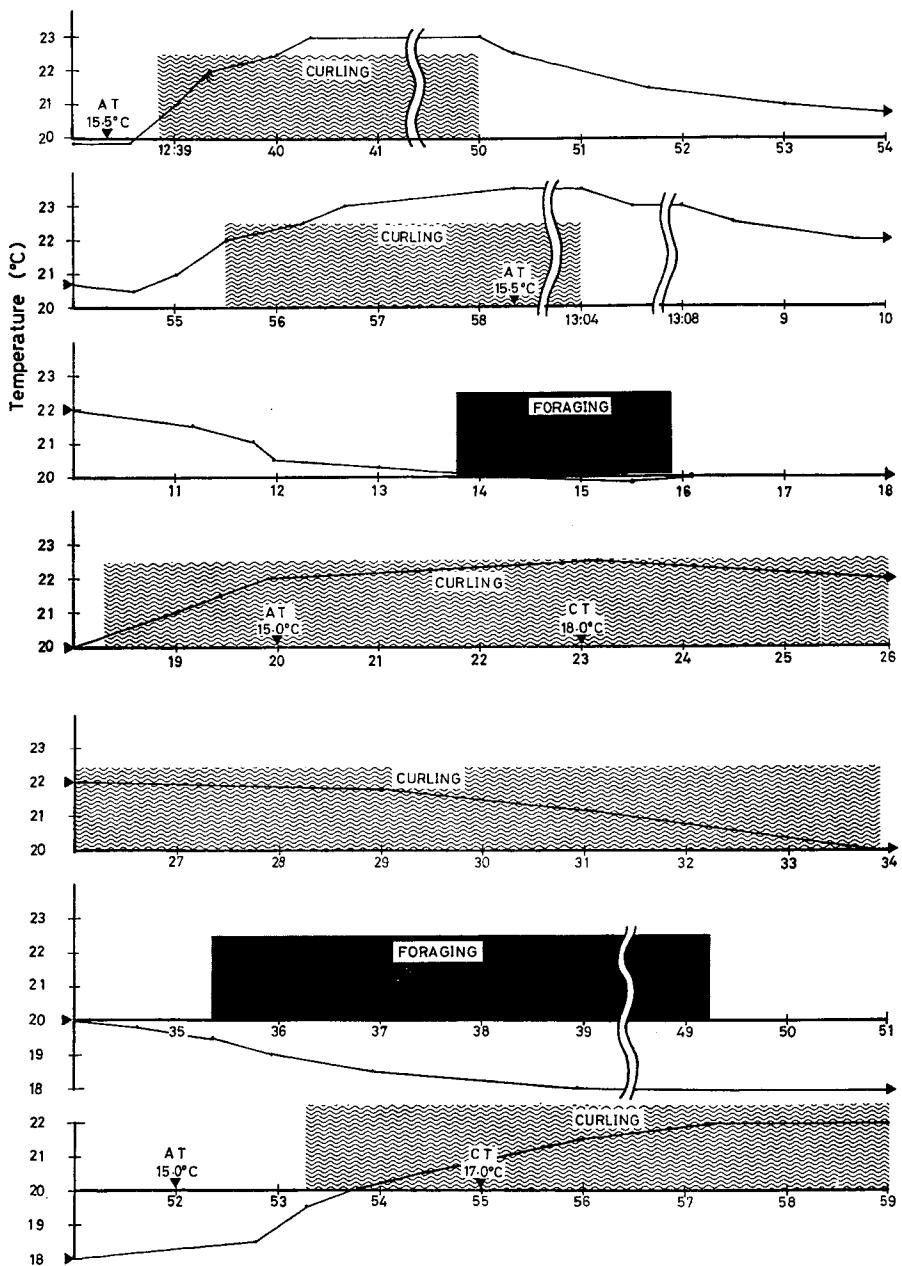


Fig. 3. A series of chronological changes in temperature on the cell wall in Nest Sm7844 (May 29, 1978). Corresponding activities of the foundress are indicated only for curling and foraging. Abscissa: time (12:38–13:59); Ordinate: temperature of the cell wall. AT: ambient temperature; CT: temperature of the ceiling to which the nest was attached.

*Discussion.* The monogynic vespines are, when at the solitary stage, at a critical time, because the foundresses are frequently lost by accident, or their nests happen to be damaged or ruined. Therefore, if the duration of this stage can be shortened through accelerating the development of worker immatures by incubating them, the foundresses who behave so will be favoured by natural selection.

Through this study it has become evident that the curling actually serves for raising the cell wall temperature. At present it is not certain that the rise in temperature actually accelerates the development of eggs or young larvae. However, the total heat produced through the curling should be large, unless this behaviour is only occasional. In this regard it may be useful to cite the proportion of time spent in the curling to the total time of intranidal activity. For example, in the *V. simillima* queen here studied, it amounted to 58.1% on June 2, and 45.4% on June 10, 1978, in a *Vespa analis insularis* queen 66.3% on June 2, and 71.0% on June 4, 1976 (Sk. Yamane and Makino, unpub.), and in a *Dolichovespula media media* queen 78.1% on June 11, 1977 (Makino, unpub.). These data clearly show that in the nest a fairly large proportion of time was spent in the curling, which, however, usually disappeared after the emergence of mature larvae or pupae, as far as our observations are concerned\*.

Brood incubating behaviour by a foundress is reported in *Bombus vosnesenskii* (Heinrich, 1972). The queen presses her abdomen onto the brood clump containing eggs and larvae, and the heat produced by the thoracic flight muscle is conducted to the clump via the abdomen. She devotes almost all of her time to this act except when foraging. This behaviour of the *Bombus* queen seems to bear a close resemblance to the curling of vespine species in their function.

At any rate, our results strongly support the hypothesis presented by Brian and Brian (1948) and Ishay (1973). On the contrary, Gibo et al. (1977) who studied the heat production in embryo nests of *Dolichovespula maculata* and *D. arenaria*

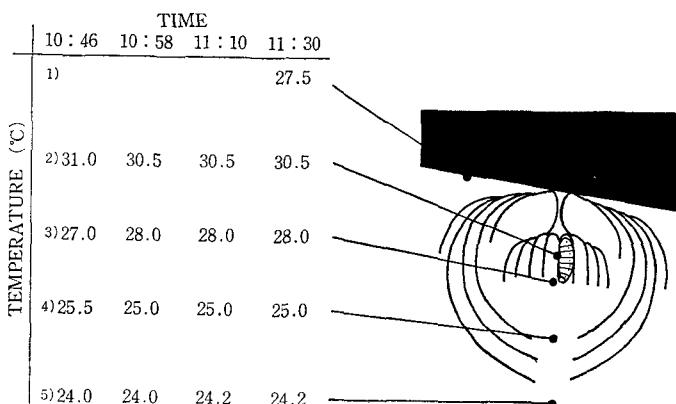


Fig. 4. Points at which the probe was placed to assess the heat production by mature larvae, and corresponding temperatures for each (Sm7844; June 18, 1978). 1)-5): see text.

\* For example, in a queen nest of *D. saxonica nipponica*, which was observed by one of us (S.M.) from May 25 to June 22, 1978, the curling disappeared on June 16 when the nest had five pupae as well as younger immatures.

concluded that the foundresses alone can produce little heat, and they put stress on the heat production by mature larvae. But, in their experiments, the probe of thermometer was placed adjacent to the comb so that they took the air temperature in the nest. Further they paid no attention to the curling or other equivalent acts. We suggest that the heat produced by the foundress can be more efficiently conducted to the immatures via the cell wall than via the air, because her capacity of producing heat is probably too small to raise the air temperature within the nest. The curling may be quite effective to incubate immatures in at least the initial stage of nesting. And after the appearance of mature larvae, with the foundress' retirement from the curling, they become major heat producers as Gibo et al. (1977) suggested.

#### EMBRYO NEST ARCHITECTURE

*Nests examined.* Six initial and embryo nests are examined.

Sm7623: This nest was collected after the foundress had died (Jun., 1976, Sapporo). It had 18 cells and three envelope sheets ( $E_1$ : 44 mm in diam., 50 mm long;  $E_2$ :  $51 \times 53$  mm in diam., 42 mm long;  $E_3$ : incipient). The pedicel (5 mm long ?, 1.7 mm thick) was coated and lustrous (see also Sk. Yamane and Makino, 1977, Fig. 24).

Sm7732: This nest was suspended from a twig of a young todo-fir tree, near the ground (Jun. 4, 1977, Maruyama Park, Sapporo). The diameter of the first envelope sheet was 42 mm.

Sm7843: This nest was found on May 21, 1978 at the foot of Mt. Hakken, Sapporo. It was suspended from the ceiling of an abandoned stove in a cabin (Fig. 9). The nest was composed of nine cells (of which eight had eggs) and two envelope sheets (one completed and the other one-third completed). The foundress was present, and the two sheets were being constructed simultaneously; the foundress curled when resting. The diameters of envelope sheets constructed by June 18 were as follows:  $E_2=46$  mm,  $E_3=58$  mm,  $E_4=63$  mm ( $E_1$  could not be measured).

Sm7844: This nest was suspended from the ceiling of the same cabin as for Sm7843, and observed from May 21 to June 22, 1978 as given in the preceding section. On May 21 it was composed of an incipient envelope sheet and nine cells containing eggs. The pedicel (13 mm long) was coated and lustrous. The diameters of envelope sheets constructed by June 22 were as follows:  $E_1=45$  mm,  $E_2=54$  mm,  $E_3=61 \times 65$  mm,  $E_4=70 \times 74$  mm.

Sm7846: This nest had just been initiated when found on June 8, 1978 in Kôshunai, Bibai. It was suspended from a twig of a willow tree at about 60 cm above the ground, and had two incipient cells without egg. The pedicel (10 mm long, 1.7–2.0 mm thick) was not coated, and the coating behaviour was not observed during the day. The foundress was observed to add pulp to the base of the pedicel (Fig. 5). By the evening, the envelope was started, and two cells were added, but still without egg. The foundress curled around the pedicel when resting (Fig. 6). The nest was destroyed by the next morning.

Sm7862: This nest was found in a building wall void after it had been abandoned by the foundress (Aug. 2, 1978, Otaru). It had 16 cells and two envelope sheets  $E_1=41 \times 43$  mm in diam., 50 mm long;  $E_2$ : not completed). The pedicel (8.5 mm long, 1.6 mm thick) was not coated.

Table 2. Size of embryo nest envelope sheets in *Vespa simillima*.

	E <sub>1</sub>	E <sub>2</sub>	E <sub>3</sub>	E <sub>4</sub>
Diameters of sheets (five nests)	41-45 mm	46-54	58-65	70-74
Time required for the comple- tion of each sheet in Sm7844	10 days	11 (17)*	12 (25)*	9 (32)*

\* Days from the initiation of the first sheet.

*Embryo nest architecture.* Nest material brittle, and buff to brown in colour as in other *Vespa* species. The completed embryo nest comprises a pedicel, more than 30 cells (estimation) and four to five envelope sheets. The pedicel is 5.0 (?)–13.0 mm long, 1.6–2.0 mm thick, and is coated probably with salivary secretion. However, in two of the four nests in which the condition of pedicel was examined it was not coated (one nest had 16 cells and one completed and one half-built envelope sheet when examined). The first envelope sheet is started from the substrate near the pedicel. The second and subsequent sheets are usually each started from on the preceding sheet near the top. The diameter of each sheet and the time required for its completion are summarized in Table 2. The length of the first sheet is about 50 mm. Two or three sheets are usually constructed simultaneously, that is, a sheet may be initiated before the completion of the preceding one.

The embryo nest of *Vespa analis insularis*, which is the most well-known species of the genus for embryo nest structure, differs from that of *V. simillima* in the following points: The envelope is single-sheeted, with a long vestibule. It is much larger than the first sheet built by *V. simillima* (61–73 mm vs. 41–45 mm in diam.; 64–80 mm excluding the vestibule vs. ca. 50 mm in length). The time required for the completion of the sheet may be longer than that for the first sheet in *V. simillima* (17 days vs. ca. 10 days; only one observed case for each species).

#### ACKNOWLEDGEMENTS

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**PLATE**

## Plate I

- Fig. 5. Incipient nest Sm7846 with the foundress adding pulp to the base of the pedicel.  
June 8, 1978.
- Fig. 6. The same nest with the foundress in curling posture. June 8, 1978.
- Fig. 7. Nest Sm7844 with the foundress building the cell wall. May 23, 1978.
- Fig. 8. The same nest, with an envelope sheet half-built. May 24, 1978.
- Fig. 9. Embryo nest Sm7843, constructed in an abandoned stove. May 24, 1978.

