

## Comparison of Nest Architecture of *Megachile (Chelostomoda) spissula*, Occurring in Subtropical and Temperate Zones in Japan (Hymenoptera, Megachilidae)

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**Abstract** *Megachile spissula* is univoltine and distributed throughout Japan from subtropical to temperate zones. Nest architecture was compared between nests trapped in subtropical Iriomote Island and temperate Nagano Pref. (MAETA, unpubl.). The following differences were recognized. 1) The number of brood cells per completed nest was larger in Iriomote ( $5.1 \pm 1.7$ ) than that of Nagano ( $3.4 \pm 1.5$ ). 2) Only 7.7% of total nests (20/219) had a single intercalary cell, but others had none in Iriomote, while 44.5% of total nests (113/254) had one to 4 intercalary cells in Nagano. Extra space unnecessary to make brood cells was principally regulated by an empty space in both areas. 3) The entrance structure was constructed regularly, according to the increase of the vestibular cells in Nagano, but such regular patterns were not recognized in Iriomote. The nest entrance of Iriomote was multi-layered, composed of up to 8 partitions. Closing plug(s) were often skipped. Only 14.9% (37/249) of total nests were closed with a single layered closing plug. On the other hand, most entrances were closed by a single closing plug in Nagano (96.7%, 326/337). These differences seem to be derived from the innate nesting behaviors not from the geographical variations, depending on the climatic circumstances.

Key words: Types of nest entrance structure, empty space, brood cells, intercalary cells, vestibular cells, closing plug, number of brood cells/completed nest, natural enemies.

### Introduction

Closely related 2 sibling species of megachilid bees, *Megachile (Chelostomoda) spissula* COCKERELL and *M. (C.) esakii* YASUMATSU are known to occur in Japan. The former is distributed in temperate zone (ca. N 30°30'–41°55'), while the latter in subtropical zone (ca. N 24°15'–28°30') (HIRASHIMA, 1989; YAMANE *et al.*, 1999). However, NAGASE (2014) proposed *M. esakii* could be *M. spissula*, except for *M. esakii* that inhabits in subtropical Amami Islands. *Megachile spissula* is also recorded from Taiwan, China and Korean Peninsula (WU, 2006; NAGASE, 2014; NIU *et al.*, 2012). In this paper, we found some remarkable differences in nest architecture between 2 populations examined in Iriomote Island (N 24°20') (henceforth Iriomote) and Oshoji, Nagano, Nagano Pref. (N 36°40') (henceforth Nagano), as described below.

### Materials and Methods

Reed tubes as trap nests were set at 2 places, Ohhara and Mimikirihama in Iriomote Island, southernmost archipelago of Japan for 3 years (2004–2006). The setting of trap nests were conducted before and during the nesting activities of bees in Iriomote. Twenty to 30 bundles,

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each contained ca. 20–30 reed tubes were set in each nesting box that was attached under the sun shades of huts. The length of reed tubes was 15 cm with having diameters ca. 3 to 10 mm. Nests were categorized into completed and uncompleted. Nests in which entrances were closed by either with plugs or multi-layered partitions in front of the last brood cells, even if the closing plugs were skipped, were regarded as completed nests. Schedules of setting, withdrawing and examining of nests were summarized in Table 1.

The nest architecture was compared with that obtained from nests trapped in Nagano for 6 years (1967–1972) (MAETA, unpubl.). Terminology of nest structures followed KROMBEIN (1967) and MAETA (unpubl.).

The results of Iriomote are mentioned by combining the data examined at 2 places and for 3 years.

## Results

### 1. General life history in subtropical zone

*Megachile spissula* is univoltine, and overwinter at prepupal stage both in subtropical and temperate zones. In Iriomote the flying period was little over 2 months from late April to early July. It commenced later in temperate zones, for instance in Matsue, southwestern Honshu (N 35°30′) from mid June and in Morioka, northern Honshu (N 39°70′) from mid July (MAETA *et al.*, 2009; MAETA, unpubl.). The phenological sequence of flying period is determined according to the descendant latitude. This species was uncommon in Iriomote, and only 22 individuals (0.2% of the total 13852 individuals of 30 bee species collected during 6 years in this island) were collected on the following floral plants: *Pemphis acidula* (Lythraceae) 2 ♀ 1 ♂, *Premna serratifolia* (Verbenaceae) 2 ♂, *Verbena litralis* (ditto) 1 ♀ 1 ♂, *Vitex bicolor* (ditto) 15 ♂ (MAETA *et al.*, 2010).

The low temperature and subjecting periods to break prepupal diapause differed between the 2 climatic zones. The low temperature of 14–18°C for 3 months was effective subjecting prepupae to break diapause in temperate individuals, while that of 15–18°C and also a little higher temperature (21°C) were effective, but very shorter duration (about a month or less) in subtropical individuals (MAETA *et al.*, 2009).

Table 1. Dates of setting, withdrawing and dissecting trap nests, which were set at two different places in Iriomote Island (2004–2006).

Year	Place	Setting	Withdrawing	Dissecting	No. of nests
					Completed/Uncompleted
2004	Ohara	V/23, 2004	IX/5, 2004	X/16, 2004	112/73
2005	Ohara	IX/5, 2004	X/13, 2005	X/23, 2005	78/28
	Mimikirihamana	in VI, 2005	X/13, 2005	X/23, 2005	48/3
2006	Ohara	X/13, 2005	VII/15, 2006	VII/21, 2006	13/0
	Mimikirihamana	V/19, 2006	VII/15, 2006	VII/21, 2006	8/0
Total					259/104

## 2. Preference of nest diameter

Bees in Iriomote preferred the reed tubes with ranges of 3.1–6.5 mm, and mostly selected 4.1–5.5 mm in diameter (Fig. 1). Selection ranges were similar with those in Nagano (MAETA, unpubl.).

## 3. Nest architecture

*Megachile spissula* use various tubes and deserted beetles' hollows in natural timbers as nests materials. They make empty space, brood cells, intercalary cells, vestibular cells in nests by partitioning with sticking several leaf pieces, which are partially masticated with mandibles. The outer surfaces of every partition is coated with soil powder and down collected from the field and the inner wall of reed tubes, respectively (MAETA, unpubl.).

### 3.1. Number of brood cells per completed nest

The number of brood cells/completed nest was 1 to 9 (mean±SD:  $5.1 \pm 1.7$ ,  $N=259$ ) in Iriomote. On the other hand, that was 1 to 8 ( $3.4 \pm 1.5$ ,  $N=254$ ) nested in similar length of reed tubes (14.5–17.4 cm) in Nagano (MAETA, unpubl.). Oviposition numbers might change, depending on the nesting circumstances, especially floral resources. In the population reared in a greenhouse where abundant flowers of *Melilotus officinalis* were supplied, the number of brood cells per completed nest was  $4.3 \pm 1.3$  even in the first nested tubes in which the highest numbers were involved (MAETA, unpubl.). The difference between Iriomote and Nagano nests were significant ( $p < 0.001$ , t-test).

### 3.2. Basal plug and empty space in completed nests

In most reed tube nests the basal plug was absent and empty space was constructed as in temperate *M. spissula*. Around the knots of the reed tubes were always rough. Bees left this part and made empty space. Moreover, the length 15 cm that was used in the study was longer than that they needed to make brood cells.

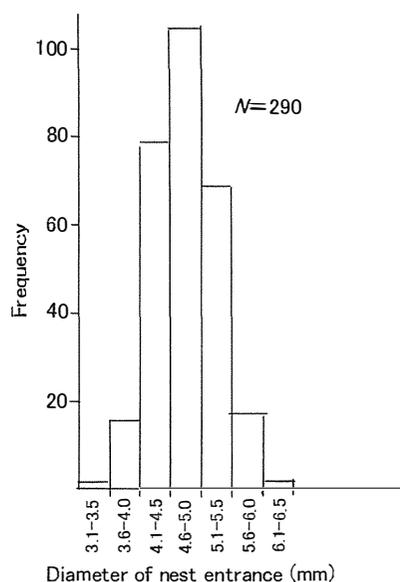


Fig. 1. Frequency distribution of the diameters of nests selected by *Megachile spissula* in Iriomote Island.

In Iriomote majority of the nests (85.9%, 220/256) had usually one (208 of 220) or rarely 2 (11) and 3 (1) empty space at the innermost part of the tubes. The length of empty space(s) was 5.0–125.0 mm (mean±SD: 36.4±23.0 mm). In Nagano, 67.7% ( $N=254$ ) of the similar length of reed tubes (14.5–17.4 cm) had empty space(s) (MAETA, unpubl.). This value is a little lower than that of Iriomote nests. The economical length of nest tubes, where the mean number of brood cells are accommodated ( $5.1\pm 1.7$ ), could be regarded around 12 cm in *M. spissula* (MAETA, unpubl.).

### 3.3. Intercalary cells in completed nests

All of the nests in Iriomote had only one intercalary cell, and these nests were 20 (7.7%) out of 259 nests, showing that it was scarcely constructed in Iriomote. On the other hand, in Nagano, 113 (44.5%) out of 254 nests, which were nidicated in similar length of reed tubes (14.5–17.4 cm), had one to 4 intercalary cells. Apparently, the rate of existence of intercalary cells in Nagano nests was significantly higher than that of Iriomote nests ( $p<0.001$ ,  $\chi^2$  test).

### 3.4. Vestibular cells and type of nest entrance structure in completed nests

Types of nest entrance structures are exhibited by the number of vestibular cells (I–III), a combination of partitions, each is named a–h from the last brood cell partition toward the closing plug. The closing plug(s) are shown in the parentheses. Usually, a combination of 2 or more vestibular partitions and multi-layered closing plugs occurred in the nests. The combined partitions are indicated with an underline. When the entrance was left without closing, it is shown with an empty parenthesis.

Those nests in Iriomote had zero to 3 vestibular cells, no clear relationship between the length of vestibular space and the number of vestibular cells were found, as shown in Table 2. Zero vestibular cell (0) means that the last brood cell was closed directly with closing plug(s) or skipped to close the entrance. Enormous types of entrance structures were recognized in Iriomote, which were up to 49 types. If more nests were examined more different types would be added. No prominent types were found, however, the following 7 types, 0ab( ), 0abc( ), 0abcd( ), Ia(bc), Ia(bcd), Iabc( ) and IIabc(de), exceeded 10 in numbers among total examined 249 nests. Some nests in Table 2, entrance of which was closed with multi-layered composed of up to 8 partitions. Conversely, those nests trapped in Nagano had as many as 7 vestibular cells/completed nest, and typical types were Ia(b) for one vestibular cell, IIab(c) for 2, IIIabc(d) for 3, IVacd(e) for 4, Vabcde(f) for 5 and VIIabcde(fg(h) for 7. Among the aforementioned types Ia(b)(105/337) and IIab(c)(135/337) were common. Most nests had a single layered closing plug, and double layered vestibular cell partitions and double layered closing plugs were scarce (MAETA, unpubl.).

Table 3 shows the typical types of nest entrance structure in tube-renting *Osmia* bees, which also separates the vestibular space by arranging the partitions as in *M. spissula*. No clear trait was obtained from the number of vestibular cells increases, according to the increase of the length of vestibular space in *Osmia* as well as in *M. spissula*, where the most common and dominant types of nest entrance structure was recognized (Table 3). However, in *O. imaii* and *O. coerulescens*, which used leaf pieces for making partitions, the entrance was closed often with double or multi-layered closing plugs as in *M. spissula* (MAETA, 1978a, unpubl.). It might be used to strengthen the thin masticated leaf partition.

### 3.5. Closing plug

In multi-layered closing plug, the outermost partition was occasionally formed by a single leaf

Table 2. Types of nest entrance structures in relation to the length of vestibular space in completed nests trapped in Iriomote Island.<sup>1)</sup>

Types of nest entrance	Ranges of length of vestibular space									Total	
	0.0-0.9	1.0-1.9	2.0-2.9	3.0-3.9	4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	8.0-8.9		9.0-9.9
0ab( )	4	5	1								10
0abc( )	8	10	2	1							21
0abcd( )		9	1								10
0abcde( )	1		1								2
0abcdef( )	1	1									2
0abcdefg( )		1									1
0(a)	2										2
0(ab)	2										2
0(abc)	1	2	1	1	1						6
0(abcd)	2										2
0(abcde)	3		2								5
0(abcdef)			1								1
0(abcdefg)	2										2
0(abcdefgh)						1					1
Ia(b)		6	2								8
Ia(bc)	2	10	4	1							17
Ia(bcd)		13	8	4							25
Ia(bcde)	1	1	1		1						4
Ia(bcdef)		4	2								6
Ia(bcdefg)		2		1							3
Iab( )		1	3		1						5
Iab(c)	2	6									8
Iab(cd)	1	5	1		1						8
Iab(cde)	1	5	1								7
Iab(cdefg)			1								1
Iabc( )	4	6	10	4			1	1			26
Iabc(d)	2	1									3
Iabcd( )	1	4				1					6
Iabc(de)	1										1
Iabc(def)		1			1						2
Iabc(defg)	1										1
Iabcd( )			1	2			1				4
Iabcd( )			1								1
Iabcd(e)		2									2
Iabcde( )						2					2
Iabcd(ef)		1			1						2
IIab(c)	1	1		1				1			4
IIab(cd)				2	1	1		1			5
IIab(cde)			1			1			1		3
IIabc(d)	1		1	1	1		1			1	6
IIabc(de)	1	5		3			1				10
IIabc(cef)					1						1
IIabcd( )			1								1
IIabcd(e)			1								1
IIabcd(e)			1		1						2
IIabc(cef)		1	1	1							3
IIabcd(ef)		1	1								2
IIIabc(d)				1							1
IIIabc(de)			1								1
Total	45	104	52	23	10	6	4	3	1	1	249

<sup>1)</sup> Expression of the types of nest entrance structures see the text and foot notes in Table 3.

Table 3. Typical nest entrance structures in relation to the number of vestibular cells in tube-renting *Osmia* bees.<sup>1)</sup>

Subgenus/ Species	Material	No. of vestibular cells	Types of entrance structures <sup>2)</sup>
<i>Osmia</i> / <i>excavata</i>	Soil	1	Ia(b)*
		2	IIab(c)
<i>Osmia</i> / <i>pedicornis</i>	Soil	0	0(a)
		1	Ia(b)*
		2	IIab(c)
<i>Osmia</i> / <i>taurus</i>	Soil	1	Ia(b)*
		2	IIab(c)
<i>Osmia</i> / <i>cornifrons</i>	Soil	0	<u>0ab</u> ( )
		1	<u>Iab</u> (c)
		2	II <u>abc</u> (d)*
		3	III <u>abcd</u> (e)
		4	IV <u>abcde</u> (f)
		5	V <u>abcdef</u> (g)
<i>Osmia</i> / <i>lignaria</i>	Soil	1	Ia(b)*
		2	IIab(c)
		3	IIIabc(d)
		7	VII <u>abcdefg</u> (h)
<i>Helicosmia</i> / <i>imaii</i>	Leaf	0	0(ab), 0( <u>abc</u> )
		1	Ia(b)*, Ia( <u>bc</u> )
		2	IIab( <u>cd</u> )
<i>Helicosmia</i> / <i>coerulescens</i>	Leaf	0	0a(a), 0( <u>ab</u> )
		1	Ia(b)*, Ia( <u>bc</u> )
		2	IIab(c), IIab( <u>cd</u> )

<sup>1)</sup> Cited Maeta (1978a, 1988, 2016).

<sup>2)</sup> Represented by the highest number of nests, which were having respective number of vestibular cells. The most common type is shown with an asterisk. *Cornifrons* makes one thickest vestibular cell partition, which is always combined an usual partition. It is shown with a gothic letter.

The number of vestibular cells is shown by Roman numerals 0–VII, and partitions are named a-h from the last brood cell partition toward the closing plug. The closing plug is shown in parentheses. Sometimes a combination occurred with 2 vestibular cell partitions or the last vestibular cell partition and closing plug were found in a nest. These combined partitions are shown with an underline.

piece. Those nests closed with a single layered closing plug were only 14.9% (37/249, Table 2) in Iriomote, while it was 96.7% (326/337) in Nagano (MAETA, unpubl.).

#### 4. Natural enemies

Only following 4 associates were found in trapped nests in Iriomote Island. Parasitic rate of these associates is shown in Table 4. In temperate zone, infestation by *Zonitis japonica* PIC was

noticeable (MAETA & SASAKI, 2005; MAETA, unpubl.), but no infested cells by a sibling species, *Z. okinawensis* (MIWA) was found in this island.

#### 4.1. Fungus

Fungus seems to be undetermined *Ascosphearaea* sp. The rate of fungus was low except for the Mimikirihamama in 2006 (76.7%). These nests have possibly fallen from the nesting box because of scavenging by rats and force rain water.

#### 4.2. Molded pollen loaf

Molded pollen loaves were found in the brood cells, presumably immatures were dead at egg or very young stages. The rate of molded pollen loaves was generally low, but relatively high (25.7%) at Mimikirihamama in 2005. This place seems to be unsuitable for setting trap nests.

#### 4.3. *Melittobia sosui* DAHMS

Multivoltine *Melittobia sosui* was a serious parasite in Iriomote. The rate of parasitism always exceeded 25% in both places. The low rate in 2006 was due to the trap nests were withdrawn in mid July, whereas others were done in September and October (Table 1). *Melittobia sosui* invaded into the host brood cells in 2 ways, 1) during being provisioned in advance and stay there while hosts developed into prepupae, 2) either by gnawing a hole on the partitions or creeping into the interspace between partitions and the tube wall, as in *M. acasta* (MAETA, 1978b). Parasitization was repeated within the nests so far as fresh prepupae remained there. A single invasion hole was left on the cocoon wall where a lot of full grown parasite larvae were found, showing the infested host stage was prepupa.

#### 4.4 *Anthrax aygula* FABRICIUS

Infestation by *A. aygula* was not possible to detect during overwintering period, because of the parasite remained in host cocoons. We found infestation by this anthracine bee fly when incubated host prepupae at 27°C. Only 3 out of 294 cocoons obtained from 78 nests trapped in 2008 were infested by *A. aygula* (MAETA, *et al.*, 2009).

Table 4. Infestation rates of associates in the nests of *Megachile spissula* trapped in Iriomote Island.

Place and year	No. of brood cells examined	% of normal and infested brood cells by associates				No. nests examined	
		Normal prepupa	<i>Melittobia sosui</i>	Fungus	Molded pollen loaf		
Ohhara	2004	867	62.9	29.5	3.7	3.9	185
	2005	508	58.1	35.4	2.2	4.3	106
	2006	75	94.7	0	1.3	4.0	13
Mimiki-rihama	2005	222	46.8	25.2	2.3	25.7	51
	2006	43	18.6	0	76.7	4.7	8
Total	1715	59.7	28.7	4.8	6.9	363	

## Discussion

Bees of *M. spissula* seem to have an ability to measure the space where to construct brood cells in nest tubes, based on the number of eggs to be laid henceforth. They need to regulate the

extra space in tubes by empty space before the commencement of oviposition, by intercalary cells during oviposition, and subsequently by vestibular cells after oviposition, as suggested in *Osmia* bees (MAETA, 1978a, 2016). We compared nest characters between 2 populations that derived from subtropical Iriomote and temperate Nagano (MAETA, unpubl.).

The following remarkable differences on the nest architecture are recognized. 1) The number of brood cells per nest was significantly larger in Iriomote than in Nagano. 2) The extra space except for necessary length for accommodating brood cells was principally regulated by an empty space in both populations. Intercalary cell was less functioned to regulate space, but 44.5% of total nests in Nagano had one to 4 intercalary cells. In Iriomote only 7.7% of total nests had intercalary cell, but all of them had a single intercalary cell. The rate of existence of intercalary cells in Nagano was higher than that of Iriomote. 3) The entrance structure was constructed regularly according to the increase of vestibular cells in Nagano, and most nests were closed with a single closing plug. However, such regular patterns were not recognized in Iriomote. The entrance was usually closed by multi-layered partitions, composed of up to 8 partitions.

ISHII (2009) studied the comparative nesting behaviors and other associated matters of *M. spissula*, occurring in subtropical Iriomote Island and temperate Matsue. He reared separately 2 populations in cage houses set at the campus of Shimane University. Plenty of *Melilotus officinalis* were supplied there as floral resources. Two populations were also reared by him in the field of the campus. The differences of nest architectures between 2 populations were as follows. 1) The number of brood cells per completed nest reared in the field was  $4.2 \pm 1.3$  ( $N=100$ ) in Iriomote, and  $3.1 \pm 1.1$  ( $N=80$ ) in Matsue populations ( $p < 0.001$ ,  $t$ -test), but no significant difference in the cage houses. 2) The rate of completed nests reared in the field, which had intercalary cell(s), was 5% ( $N=125$ ) in Iriomote, while 14% ( $N=118$ ) in Matsue population ( $p < 0.05$ ,  $\chi^2$  test). 3) In the field nests of which entrance was closed with closing plug, the number of multi-layered partitions in a vestibular space was  $4.0 \pm 1.3$  ( $N=100$ ) in Iriomote population, and  $2.3 \pm 0.8$  ( $N=79$ ) in Matsue populations ( $p < 0.001$ ,  $t$ -test). A significant difference was recognized in the cage house, showing that the vestibular space was filled with more partitions in Iriomote than in Matsue populations. 4) In the field nests, the rate of nests of which closing plug was skipped was 12% ( $N=100$ ) in Iriomote and 3% ( $N=79$ ) in Matsue populations ( $p < 0.05$ ,  $\chi^2$  test). The comparative characters of 1) to 4) between Iriomote and Matsue populations reared in Matsue were well coincided with those among the field nests trapped at Iriomote and Nagano by us.

The differences in nest architectures between subtropical and temperate zones seem to have derived from the innate behaviors, not from the geographical variations. Identification of the species should be done not only by the morphological comparison of the specimens, but also by other supplemental methods, e.g., biological and molecular studies.

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