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Notes on the Nesting Biology of *Amegilla florea urens* (Cockerell) in Iriomote Island, Southernmost Archipelago of Japan (Hymenoptera, Apidae)

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<Original Article>

Notes on the Nesting Biology of *Amegilla florea urens* (Cockerell) in Iriomote Island, Southernmost Archipelago of Japan (Hymenoptera, Apidae)

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Abstract: *Amegilla florea urens* is univoltine and overwinters at prepupal stage in Iriomote Island (N24° 15'-25'). Flying period is ca. one and half months from middle May to end of June (Maeta *et al*, 2010). Foraging activity of the bees commenced from very early morning and continued until late evening. They preferred to visit flowers with a long corolla tube, and were specialist pollinator of *Alpinia flabellata*, *A. intermedia* and *A. zerumbet* in this island (Maeta *et al*., 2010). Nesting sites were found at bare clayish bank in and margin of the subtropical forests. Nests were unicellular type. The burrows were excavated gently upward or nearly horizontally from the surface of the bank. A single provisioned cell with one "pre-chamber", which remained empty and unprovisioned, was constructed at the innermost of the burrow with 6.0-12.6 cm in straight length from the nest entrance. The inner wall of the provisioned cell and pre-chamber was lined thinly, but the former done doubly to form a membranous layer (0.01-0.10 mm thick) with the secretion from dufour's gland. Two species of cleptoparasite, *Thyreus takaonis* and *Zonitis okinawensis*, were newly recorded from nests of *A. f. urens*. Breaking the prepupal diapause was also mentioned.

Key words: Floral resources, nest architecture, nesting sites, diapause of prepupae, cleptoparsites, *Amegilla*, Iriomote Island

Introduction

The genus *Amegilla* is a group of Anthophorini of the subfamily Apinae with 253 described species. The distribution widely extended Old World (Michener, 2007). Three species, *A. florea florea* (Smith), *A. f. urens* (Cockerell), *A. senahai subflavescens* Yasumatsu et Hirashima, *A. s. senahai* (Yasumatsu) and *A. quadrifasciatus* (Villers) were recorded from Japan. *Amegilla f. urens* and *A. s. senahai* are siblings and sympatrically distributed in the Yaeyama Islands of subtropical zone (Hirashima ed., 1989). None of bionomical studies of these 3 species was done, except for the nest architecture of *A. s. senahai* (Maeta *et. al.*, 2001). In this paper, we have described the results of our survey conducted between 2002 and 2008 in Iriomote Island (N24° 15'-25').

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Materials and Methods

1. Nesting site and density of nests

Two nesting sites (site A, B) were found in Iriomote Island. Topography, vegetation and soil texture were examined around nesting sites. To show the nest density the number of nests within one square meter at the most highly aggregated spot was counted.

2. Flying period and floral resources

To examine the flying period and floral plants used by *A. f. urens*, sampling of adult bees was conducted on 91 floral species, belonging to the 43 families for 6 years (2002-2007) in Iriomote Island (Maeta *et al.*, 2001). Nesting sites were also checked often to examine the nesting situation of bees.

3. Nest architecture and cell contents

Nests were excavated on July 17, 2006 (4 nests at the site A), on May 18 and 20, 2007 (4 nests at the site A), on July 23 and 24, 2007 (88 nests at the sites A and B) and on July 25, 2008 (15 nests at the site B). Dimensions of various parts of nests, *e.g.*, entrance, burrow, provisioned cell and pre-chamber were measured at or after excavation of nests. Cell contents, including immatures and natural enemies, were also examined at the same time.

4. Ovarian state of nesting bees

Six females were captured at the nesting site A on May 23, 2007, and dissected to estimate their daily oviposition numbers. Ovarian development was expressed by stages of the basalmost oocytes in 4 pairs of ovarioles. They were classified into the developing and degenerating phases (Kurihara *et al.*, 1981). Stage I : Previtellogenic oocytes ; State II : Vitellogenic oocyte ; Stage III : Mature oocyte ; Stage IV : Chorionated egg ; and Stages I'-III' : Degenerating from stages I-III.

5. Breaking the prepupal diapause

Prepupal diapause is estimated to be broken by subjecting them under "low temperatures", below that of bees commence their foraging activity (ca. 24°C). Those prepupae obtained from nests excavated on July 23-24, 2007 were used. Each sample composed of 10 prepupae was subjected to 9°C, 12°C, 15°C, and 18°C on Augsut 11, 2007 for 2 months. Incubation after subjection to these low temperatures was conducted at 28°C. To prove low temperatures are essential to break diapause, 10 prepupae obtained on July 25, 2008 were kept at 28°C for 4 months. Subjection was done on August 27, 2008.

Figs. 1-7 Nesting sites, provisioned cells and male aggregation of *Amegilla florea urens*. 1 : Nesting site at A. 2 : Nesting site at B ; 3 : Provisioned cell with a full grown larva, paired with an empty pre-chamber. 4 : Provisioned cell, removed a feeding larva. Note an unconsumed pollen loaf remained at the bottom of the cell and 8-shaped cell plug. 5. Rear (left) and outer (right) surface of the plug. 6 : A pseudopupa of *Zonitis okinawensis* in a host cell. Note the provisioned cell wall which is coated membranously with the secretion from dufour's gland by the host bee. 7 : A sleeping aggregation of males.


1


2


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4


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6


7

Table 1 A list of floral plants visited by *Amegilla florea urens*.

Family / Species	Number of individuals collected	
Verbenaceae		
Stachytarpheta jamaicencis		1 ♂
Zingiberaceae		
Alpinia flabellata	20 ♀	17 ♂
Alpinia intermedia	8 ♀	3 ♂
Alpinia zerumbet	41 ♀	10 ♂
Total	69 ♀	31 ♂

Results and Discussion

1. Nesting site and density of nests

The site A : It was located at hilly side along the river Ohmisya. This site was relatively dark place throughout the day, because it was surrounded by dispersed wood. Nests were found on the bare clayish slopes with ca. 0.7 to 1.0 m height beside a narrow path in the wood (Fig. 1). Twenty nests/m² were aggregated at the highest density spot.

The site B : Contrary to the site A, this site was in a relatively bright place. It was located at the bare clayish bank of hilly side along the river Urauchi at ca. 2.5-3.0 m height and 40 degrees angle, facing to eastward from the forest road (Fig. 2). There was ca. 60 nests/m² at the spot of the highest density.

2. Flying period and floral resources

Flying of the bees started from middle May and lasted until the end of June, showing that *A. f. urens* is univoltine (Maeta *et al.*, 2010). This species is relatively scarce in this island. A total of 69 ♀♀ and 31 ♂♂ were collected from 2002 to 2007 on only 4 out of 91 floral species of which flower-visitors were examined. Most of them were obtained from *Alpinia* plants (Table 1), which are typically "hymenopterid flowers" (Knuth, 1906) and "gullet-shaped blossoms" (Faegri and Pijil, 1966), and are principally visited by bees with well developed glossa (melliphily). *Alpinia flabellata*, *A. intermedia* and *A. zerumbet* grow at or little inside of the forest margin under bit shady places or with little sun light throughout the day. *Amegilla f. urens* is regarded as a specialist pollinator of these 3 species of *Alpinia* (Maeta *et al.*, 2010 ; Maeta *et al.*, unpublished data).

Adults of the bees commenced foraging activity from early morning and continued until just before sunset. The last visit by bees to *A. zerumbet* was observed at 19 : 25 (24.1°C) as dark as 240 luxes on May 22, 2007. Foraging pattern of a sibling species, *A. s. senahai* was quite similar with that of *A. f. urens*, which is multivoltine (flying period : middle April to early November) and are relatively common in Iriomote Island.

Patrolling of *A. f. urens* males did not occur at the nesting sites, but was observed often on the flowering plants which were visited by females. Males formed a sleeping cluster before sunset near the patrolling sites, biting a stalk of various plants upward with their mandibles (Fig. 7) as

in *A. dawsoni* and *A. s. senahai* (Houston, 1991 ; Maeta, *et al.*, 2001). Similar male sleeping habits are reported in various taxa of bees (Evans and Linsley, 1960 ; Linsley, 1962 ; Sugiura, 1998).

Flower records for both of the species, *A. f. urens* and *A. s. senahai*, overlapped completely, but the latter one used more floral resources, including those grown at the sunny sides (Maeta *et al.*, 2010).

3. Nest architecture

A single main burrow was excavated nearly horizontally (Fig. 8B, D) or gentle upwardly (Fig. 8C) from the surface of banks, and was deepened nearly straightly, but sometimes slightly curved either left or right side (Fig. 8A). No lining was performed on the inner burrow. Nests of *A. f. urens* were unicellular type, only a single provisioned cell was constructed at the innermost of the burrow. An urn-shaped provisioned cell was formed followed by a "pre-chamber" which was similar in shape with that of the former. Provisioned cells orientated downward together with pre-chambers (Figs. 3, 8). Both cells had constrictions at their mouths. However, the constricted positions were always gapped between upper and lower parts, due to that the upper and lower halves is not symmetrical, as in *A. s. snahai*, which also has the same nest type (Maeta *et al.*, 2001). The adaptive significance of the pre-chamber is uncertain. Supposedly, a relic like exhibition of the plesiomorphic character which transited from multicellular to unicellular type.

The inner wall of both provisioned cell and pre-chamber were coated thin, but the former was done doubly to form a membranous layer (0.01-0.10 mm thick) with the secretion from dufour's gland. However, the coating differed betwen *A. f. urens* and *A. s. senahai*. The second

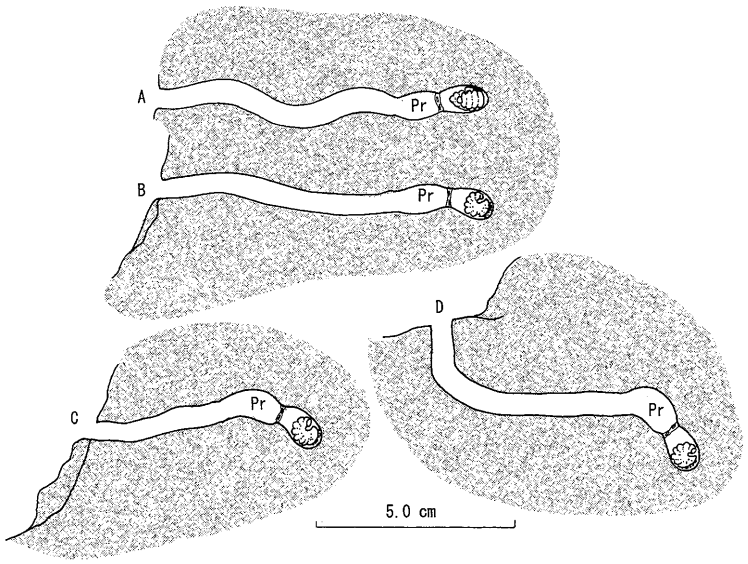

Fig. 8 Upper (A) and lateral (B, C and D) views of the three representative nests of *Amegilla florea urens*. A : The burrow in A was deepened toward either left and right, slightly curving. B : The burrow is in B the lateral view of that in A. C : The burrow in C was excavated upward from the declined soil surface. D : The burrow in D was excavated downward from relatively flat soil surface. Pr : Pre-chamber.

coating on the provisioned cell wall was light brown colored and done membraneously in the former (Fig. 6), while that is milky colored and wax-like and relatively thick layer (0.08-0.30 mm) in the latter (Maeta *et al.*, 2001). The lining of both Japanese *Amegilla* species was never eaten by full grown larva, but it was eaten as food by *A. dawsoni* (Rayment) and *Anthophora abrupta* Say (Norden *et al.*, 1980; Houston, 1991).

The closing of the mouth of provisioned cells was unique as reported in *A. s. senahai* by (Maeta *et al.*, 2001). Plug was made at the constricted mouth spirally and belt-like layer by spreading wet soil, presumably admixing liquid from dufour's galnd. The inner surface of cell plugs was slightly concave and smooth, but the outer one left a slit at the end of forming of the plug, because it was made double layers, looking like a 8-shaped form (Figs. 4, 8). A small interspace between the inner and outer plug walls was existed, but the central part was not detached. Contrasting to the inner layer, the outer one seemed to be continuously constructed from center to outer direction. The procedure to make cell plugs seems to be common to all species of *Amegilla*.

The frontal part of the pre-chamber is partially buried with soil, but often skipped as in *A. s. senahai* (Maeta *et al.*, 2001). In *A. pulchra* only frontal part of the last provisioned cells is roughly filled with soil (Cardale, 1968a), while the main burrow is roughly filled with soil until the nest entrance in *A. dawsoni* and *Amegilla* sp. which make a turret (Houston, 1991). From these facts it is understood that in *Amegilla* species, main burrows seem to be generally not filled with soil after completion of the nests. The comparison of the size dimensions of various parts of the nests between *A. f. urens* and *A. s. senahai* is shown in Table 2. To show the body size difference between both species, head widths of females were used. The values are 5.17±0.18 mm

Table 2 Measurement values of various parts of nests in *Amegilla florea urens* and *A. senahai senahai*.

Part (mm)	*Amegilla f. urens*			*Amegilla s. senahai*[1]	
	Range	Mean±SD	*N*	Mean±SD	*N*
Diameter of nest entrances	8.1-8.9	8.5±0.3	5		
Diameter of burrows	7.2-8.3	7.9±0.6	3	ca. 5	
Depth of burrows[2]	60.0-126.4	94.3±26.9	5	ca. 200	
Provisioned cells					
Length[3]	12.2-18.5	15.0±1.4	16	13.9±0.8	16
Diameter at center	8.6-11.6	10.3±0.8	20	9.4±0.6	16
Diameter at mouth	6.5-10.2	8.5±0.9	20	7.4±0.3	16
Pre-chamber					
Length[3]	14.6-17.1	15.4±1.4	3	14.8±0.3	3
Diameter at center	9.8-12.0	10.7±1.0	4	10.5±0.6	3
Diameter at mouth	9.4-12.1	10.9±1.1	4	ca. 8	
Plug of provisioned cells					
Width of outer part	1.8-2.4	2.1±0.2	8	4.0	
Width of central part	0.8-1.8	1.3±0.5	7	1.0	

[1] Cited from Maeta *et al.* (2001).

[2] Measured the straight line between the bottom of provisioned cell and the nest entrance.

[3] Distance from the bottom cell wall to the closing plug.

(N=10) in *A. f. urens* and 5.23±0.15mm (N=10) in *A. s. senahai*. The sizes of both provisioned cell and pre-chamber are little larger in those of the former, reflecting the difference of body sizes between both species. The depth of burrows of *A. s. senahai* (ca. 20 cm, Maeta *et al.*, 2001) was deeper than that of *A. florea urens* (6.0-12.6 cm). This may relate to the difference of nesting sites of both species.

Types of the nest architecture in the genus *Amegilla* are tentatively classified as follows (Maeta *et al.*, 2001).

Type I : Unicellular, the burrow is excavated horizontally or slightly upward and a single provisioned cell paired with a pre-chamber are arranged at the innermost position. Usually nesting at inclined bare bank in the natural field, no turret at the entrance (*A. s. senhai*, Maeta *et al.*, 2001 ; *A. f. urens*, present study).

Type II : Multicellular, the main burrow is basically excavated vertically and the lateral burrows derived from the main burrow irregularly and are deepened vertically or horizontally. Plural provisioned cells are arranged at the same direction of each lateral burrow. Nesting at artificial environment such as brick wall and presumably overhanged bank, no turret at the entrance (*A. pulchra* (Smith), Michener, 1960 ; Cardale, 1968a).

Type III : Multicellular, the main burrow is basically excavated vertically and several lateral burrows are made which were derived from lower part of the main burrow. Plural provisioned cells are arranged in each lateral burrow, as if they form a comb. Nesting at flat ground, Turret present at the entrance (*Amegilla* sp. (=*bombiformis*?), Cardale, 1968b ; *Amegilla* sp., Houston, 1991 ; *A. dawsoni*, Houston, 1991).

4. Immatures

Provision was deposited at the basal part of the cell to form horizontally flat surface, although provisioned cell was inclined downward. Pollen loaf was not wet. Position of an egg on the pollen loaf was not confirmed by the present study. Prepupa bents her body inwardly to place the dorsal body on bottom wall and fecal pellets were attached on the innermost basal wall.

5. Natural enemies

Two cleptoparasitic species, *Thyreus takaonis* (Cockerell) and *Zonitis okinaweneis* (Miwa) were found in cells of *A. f. urens,* when nests were excavated at sites A and B in 2007. A single individual of both cleptoparasites infested a single host cell. The former cleptoparasite overwinters at prepupal stage and the latter one at pseudopupae. Both cleptoparasites are also recorded from nests of *A. s. senahai* in the adjacent Ishigaki Island (Maeta *et al.*, 2001). *Thyreus takaonis* is multivoltine, but Z. *okinawensis* remained in prepupae, suggesting that this species is univoltine as in temperate *Z. japonica* Pic (Maeta and Sasaki, 2005). The rate of parasitism by both cleptoparasites in nests of *A. f. urens* is shown in Table 3, which is little higher in *Z. okinawensis* (10.2%, 9/88), but very low in *T. takaonis* (2.3%, 2/88). In *A. s. senahai*, 3 *Z. okinawensis* pseudopupae (17.6%) and one *T. takaonis* prepupa (5.9%) are found out of 17 host cells (Maeta *et. al.*, 2001). The parasitic rate of *T. takaonis* seems to be low in both host *Amegilla* species. Parasitism by *Zonitis* and *Thyreus* is also reported in Australian *A. pulchra* (Cardale,

Table 3 Percent rate of two cleptoprasitic species and *Amegilla florea urens* excavated at two nestig sites (A and B) in 2007.*

Species	No. of individuals obtained (%)		
	July 24 at A	July 23 at B	Total
Thyreus takaonis	0 (0)	2 (4.5)	2 (2.3)
Zonitis okinawensis	3 (6.8)	6 (13.6)	9 (10.2)
Amegilla f. urens	41 (93.2)	36 (81.8)	77 (87.5)
Total	44 (100)	44 (100)	88 (100)

*Nests excavated after cease of the nesting activity. Individuals found in provisioned cells were prepupae and newly eclosed adults in *T. takaonis*, pseudopuae in *Z. okinawensis*, and full grwon larvae and prepupae in *A. f. urens*.

Table 4 Ovarian states in six *Amegilla florea urens*.

Indi. No.	No. of oocytes in stages of I-IV and I'-III'[1)]			
	I	II	III	III'
1	5	2	1	
2	5	2	1	
3	6		1	1
4	5	2	1	
5[2)]	4	3		
6	5	1	1	1

[1)] Developing phase (stages I-IV). I: Pre-vitellogenic oocyte; II: Vitellogenic oocyte; III: Mature oocyte; IV: Chorionated egg. Degenerating phase (stages I'-III'). Stages I'-III': Degenerating oocytes from stages I, II and III (Referred Kurihara *et al.*, 1981). Stages of IV, I' and II' were not found.

[2)] One oocyte was lost at dissection.

1968c).

Adults of *T. takaonis* was attracted to the nesting sites when we were excavating nests, although the nesting period of *T. f. urens* was over and no flowering plants were around the nesting sites. About 10 females were collected in 10 minutes at the nest site A on July 15, 2006. However, bees were not attracted any longer after an hour of nest excavation. They seems to be attracted by acid-like odor emitted from host provisioned cells, when the nests were exposed by our excavation. The nesting females of *A. f. urens* were observed to chase and expel the cleptoparasitic bees who tried to enter the host nests.

6. Ovarian state of nesting bees

Table 4 shows the state of ovarian condition of *A. f. urens* which were captured at the nesting site A in a full activity period. Each founding female had only a single mature oocyte, suggesting that they can scarcely lay only one egg/day, although they foraged a full day from very early morning to nearly sunset. Oviposition numbers of *A. f. urens* seem to be fewer. On the

other hand, a megachilid bee, *Osmia corniforns* (Rdoszkowski) have 3 mature oocytes in their ovaries, and lay at least 2 eggs/day, spending for about 10 hours of the foraging activity in a day (Maeta and Kurihara, 1971 ; Maeta *et al.*, 2005). A similar case was also known in *Megachile rotundata* (Fabricius) (Maeta and Kitamura, 2005).

7. Breaking of the prepupal diapause

None of prepupae, which were subjected to 4 different low temperatures (9-18°C) for 2 months, pupated. Those prepupae which had been kept at 28°C for 4 months, also did not develop into pupae. All of them of the 5 treatments were dead during incubation. For temperate bee species to breake diapause subjecting them for 3-4 months at their dormant stages (prepupae and adults) is essential (Maeta *et al.*, 2009). The prepupal diapause of a subtropical megachilid bee, *Megachile esakii* Yasumatsu, can be broken effectively by subject them at low temperatures (15 -21°C), but for a very shorter duration (about one month or less) (Maeta *et al.*, 2009). To break prepupal diapause of *A. f. urens* it seems to be needed either to subject prepupae more longer durations or little higher low temperatures. However, further experiments are needed to determine the appropriate low temperatures and durations to break prepupal diapause in *A. f. urens*.

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