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Nesting Biology of a Solitary Andrenid Bee, *Andrena* (*Notandrena*) *richardsi* Hirashima on Mt. Daisen, South-Western Japan (Hymenoptera, Andrenidae)

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Abstract : Nesting biology of a solitary andrenid bee, *Andrena* (*Notandrena*) *richardsi* Hirashima, was studied on Mt. Daisen (35° 22' N, alt. 660 m), near Yonagao-City, Tottori Pref. in the years of 2001-2004 and 2006. Flying period was ca. 2 months from middle May to middle July. Foraging activity began from 7:00-8:00 and continued until 14:00 on sunny days when temperature went above 17°C. However, the number of pollen foraging trips/female per day was scarce, up to 6 times (mean±SD : 1.9±1.1, N=228), although flowering plants were abundant around the nesting sites. Each pollen foraging trip required 4-219 minutes (mean±SD : 55.4±48.4 minutes, N=126). Females principally visited flowers of *Swida macrophylla* (Cornaceae) as a major floral resource, and the periods of nesting activity of bees and blooming of flowers were overlapped each other. All immatures developed into prepupae in July, but not developed further. Two dormant overwintering stages, prepupae and adults, were recognized. Both the overwintering stages were determined innately, due to insufficient soil temperatures throughout the year at mountainous area. They overwinter at prepupal stage in the first year and again at adult stage in the following year, showing that *A. richardsi* is biennial. The nest structure of *A. richardsi* belongs to the single-series and multi-series types, each brood cell is arranged linearly from the innermost to upper parts of a single or more main burrows, respectively (Maeta, 2000). These brood cells were situated at the depths of 20-50 cm and up to 5 brood cells/nest (2.7±1.2, N=30) were found in developed nests. As natural enemies, *Meloe coarctatus* Motschulsky and *Bombylius* sp. were found in brood cells.

Key words : Nesting sites, nesting activity, development of immatures, 2 dormant overwintering stages, biennial, *Andrena*, floral resources, *Swida*

Introduction

In Japan, 84 species of the genus *Andrena,* belonging to 21 subgenera were known to occur (Tadauchi, 2001). Most of them are solitary, except one communal species, *A. lonicerae* Tadauchi et Hirahsima (described as *halictoides* in Takahashi, 1987). Till now nesting biology of only 15 out of 84 species were studied (Maeta, 2000 : Maeta *et al.,* 2004). *Andrena* (*Notandrena*) *richardsi*

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Hirashima is an endemic and solitary species. This species is relatively rare, although the distribution was recorded from various Prefectures in Japan, such as Aomori (Hirashima, 1962* ; Yamada, 1996*, 1998*) ; Miyagi (Gôukon, 1991*) ; Tochigi (Nakamura, 1989* ; Katayama, 2007*) ; Saitama (Nanbu, 1998*) ; Ishikawa and Toyama (Negoro, 1997*, 2003*) ; Fukui (Haneda *et al.*, 1998*, 2006* ; Haneda and Inoue, 2003) ; Yamanashi (Suda, 1980*) ; Kanagawa (Nagase, 2004*, 2007*) ; and Aichi (Ohkusa, 2007) (References with an asterisk show the individuals collected at mountainous areas). These records show that this species is habituated to nest at mountainous areas, but some are also collected at flatlands. Body color of adults collected at seaside differs from those collected at mountainous areas (Haneda and Inoue, 2003). Thus, there might be involved 2 different sibling species in *A. richardsi.*

Only Gôukon (1991) briefly mentioned the nesting site and nest architecture of this species examined in Miyagi Pref. northern Japan. We found 3 nesting sites of *A. richardsi* at halfway up Mt. Daisen, southwestern Japan and studied in 2001-2004, 2006 and 2008 so as to compared the nesting biology among the genus *Andrena.* The results are described as below.

Materials and Methods

1. Nesting sites

Three nesting sites (A, B and C) located closely were found on the flat ground and in a shady place with limited sunshine at halfway up Mt. Daisen, near Yonagao City, Tottori Pref. (35° 22' N ; alt. 660 m) in 2001 and 2002 (Fig. 1). To show the appearance of 3 nesting sites, topography, vegetation, soil structure, etc. were examined.

2. Male behavior

Patrolling and mating behaviors of males at the nesting sites, and the flying period of males were observed in 2003.

3. Nesting activity of founding bees

Nesting activity period of *A. richardsi* was studied at 3 sites (A, B and C) where found at Mt. Daisen, as described below. The nesting period was recorded in 3 ways : 1) Flying period (from appearance to disappearance of adults), 2) Nesting period (from appearance of conical-shaped soil masses=tumuli) to disappearance of adults), and 3) Foraging period (from appearance of foragers to disappearance of them). Daily foraging activity was observed 4 times at the site of A during the full blooming period of *S. macrophylla* on July 6, 2002 ; July 2, July 8, July 10, 2003. Some bees was marked with different color paints (brand name : Opaque color), so as to distinguish individuals. To record the time spent by a foraging bee, the nest was covered with a transparent plastic cup (diameter : 6.0 cm ; depth : 3.5 cm) after departure for a foraging trip. The cup was removed until the next departure of the bee. This procedure was repeated until the finish of foraging activity. Time spent for the following 3 tasks was calculated : 1) "Pollen foraging", from bees' departure to return with pollen loads ; 2) "Nectar foraging", from bees' departure to return without pollen loads (regarded tentatively as nectar foraging) ; and 3) "manipulation of pollen ball", from bees' return to the nests to departure for the next foraging trips. Relevant foraging behaviors observed around the nesting sites were also recorded.

4. Floral resources

Five females, which returned with pollen loads, were captured to examine the pollen species on June 29, 2002. The females were kept in small vials for a few minutes to force them deposition of pollen loads from their pollen baskets. The determination of pollen species was made under microscope by comparing them with the sample pollen grains obtained from various flowering plants, which grew around the nesting sites. Fecal pellets left in 3 brood cells were also additionally examined for pollen analysis.

5. Developmental duration in prepupae and pupae

For studying the development from prepupa to adult, we used prepupae obtained from nests excavated on April 5, 2004, presumably dormancy of this stage was already broken at this period. Incubation was made at 6 different temperatures (14°C, 16°C, 18°C, 20°C, 22°C and 24°C) following the day excavation. The values of threshold developmental temperature of prepupae and pupae were calculated from the regression lines, which were drawn based on the relationship between temperatures and developing rate of these stages (100/duration in days).

6. Developmental sequence of the immatures in nests

To follow the development of immatures and to confirm the overwintering stage, the excavation of nests was done 16 times in 2001-2004 and 2006, as described below. 1) October 20, 2001 (nesting sites A and B) ; 2) June 17, 2002 (C) ; 3) July 12, 2002 (C) ; 4) May 17, 2003 (C) ; 5) May 20, 2003 (C) ; 6) December 2, 2003 (C) ; 7)-15) March 29, April 5, July 12, 15, 16, 23, 26, August 27, and October 22, 2004 (all C) ; and 16) April 25, 2006 (C). Only immature stages and their numbers involved in brood cells were recorded.

Soil temperatures at the depths of 20 cm, 40 cm and 60 cm were recorded by 3 thermo-recorders (Brand name : Ondotori Jr., Thermo Recorder TR-52, T & D Cooperation), so as to analyze the development of immatures in relation to the soil temperatures.

7. Nest density and cumulative number of nests

Density of nests was examined at the sites of A and B in 2001, 2002, 2003 and 2004. Each nest tumulus was marked with the numbered tags at every time when new tumuli were formed, and presence and absence of bees were confirmed by observation of the foraging activity.

8. Nest architecture

For examination of nest architecture, a total of 16 nests were excavated in middle late July in 2002. Additional 30 nests were excavated on July 15, 16, 23 and 26, 2004. To facilitate the tracing of nest structures, powder of quicklime was blown on the wall of burrows by using a syringe. Major parts of nests, *e.g.*, diameter of main burrows, depth of brood cells, size dimensions of brood cells, etc. were measured with vernier calipers. Cell contents were also examined.

9. Sex ratio

Two overwintering stages, prepupae and adults, were found in nests. The sex of prepupae was indirectly determined by their sizes, whose weights were less than 74 mg and above 75 mg are tentatively regarded as males and females, respectively. Sex ratio was examined for 6 years (2001-2004, 2006 and 2008) and expressed by female ratio (females/females+males).

10. Natural enemies

All natural enemies were recorded at every excavation of nests. The percentage of parasitism was also examined, if available.

Results and Discussion

Maeta (2000) reviewed references on the nesting biology of andrenid bees in the world. We have compared the nesting biology among the species in this paper, however, species names are not described individually, when compared them generally. Other publications after 2000 were cited.

1. Nesting sites

The sites A and B (Fig. 1, A and B) were found near the building of the Chugoku-Shikoku Universities' Cooperative Training Center, with an area of ca. 15.2 m^2 (length : 8.0 m ; width : 1. 9 m), and ca. 4.5 m^2 (length : 5.0 m, width : 0.9 m), respectively. South and west sides of both A and B sites were surrounded with woods. The site C (Fig. 1., C) was found in the small garden of a private cottage with an area of 20.7 m^2, where was surrounded with woods. The site B was bare ground, but rocky soil, and the other 2 sites (A and C) were not. However, the ground of the sites A and C was a little grassy and completely bare, respectively.

Four similar examples of the nesting site of *A. richardsi* are reported from northern and central Japan. The first is found at Hanayama-mura, Kurihara-City (38° 45' N ; alt. 450 m), Miyagi Pref. (Gôukon, 1991), where a small nest aggregation (26 nests) was formed at loose sandy soil ground, including pebbles. The second is found at rocky ground beside the path in the Hakkoda-san Botanical Garden of the Tohoku University (40° 38' N ; alt. 900 m), Aomori Pref. (ca. 80 nests, Maeta and Gôukon, unpubl.). The third is found along the mountain trail on the slightly declining ground of rubble at Azami-daira (ca 200 to 300 nests ; 35° 23' N ; alt. 1,292 m) between Kagosaka-pass and Mt. Daido, Yamanashi Pref. (Suda, 1980). The fourth is found at a shady place on the slope with a very low height, facing a road (the number of nests undescribed ; 35° 40' N ; alt. 910 m), at Ikedori, Makioka-machi, Yamanashi Pref. (Suda, 1980). These findings show that *A. richardsi* seems to prefer shady bare and flat grounds or easy slopes at mountainous areas, as their nesting sites, where are usually intermixing with small rocks, pebbles and rubbles. They form relatively small nest aggregations.

2. Male behaviors

Males were observed at the nesting sites, but the numbers were alway few. Male patrolling was frequently observed at site B between May 20 and June 23 in 2003. Most males disappeared

Fig. 1 Views of the 3 nesting sites (A, B and C) of *Andrena richardsi* found on Mt. Daisen. Weeds were pulled up at the site A, so as to increase bare ground.

from the nesting site on June 26, after blooming of *S. macrophylla*. They were seen to fly repeatedly at 25-30 cm high above ground and searched females by walking. The earliest and latest patrolling times on day June 21 were 6:15 (June 23) and 18:25, respectively. The number of patrolling males at the site B varied from zero to ca 25 in a day, but most males turned to walk on the ground around 16:00. Figure 2 shows the schematic representation of male behaviors at the nesting site. Males searched females in 2 patrolling ways, 1) flying and 2) walking, to intrude themselves into nests for taking out females. Males pounced on the foraging females near their nest entrance. Sometimes, several males pounced on the same female and formed a ball-like mass. However, most of the females mounted by males were often rejected copulation by bending their abdomens inwardly and vibrating wings rapidly. Successful mating was observed only once at the site B on June 6, 2003. A pair of a male and a female were walking on the ground, who were connected with aedeagus, each of them kept reversed position.

Similar patrolling patterns as shown in Fig. 2 is reported in *A. prostomias* Pérez, however, "mounting on female in the air" and "mounting on female on the ground" are skipped in this species. Males of *A. prostomias* usually "dragging out female" from the nests, which were used for overwintering, and being excavated and provisioned (Maeta, 2000).

3. Nesting activity of founding bees

Formation of tumuli of *A. richardsi* at the site A was commenced on May 25, June 23 and

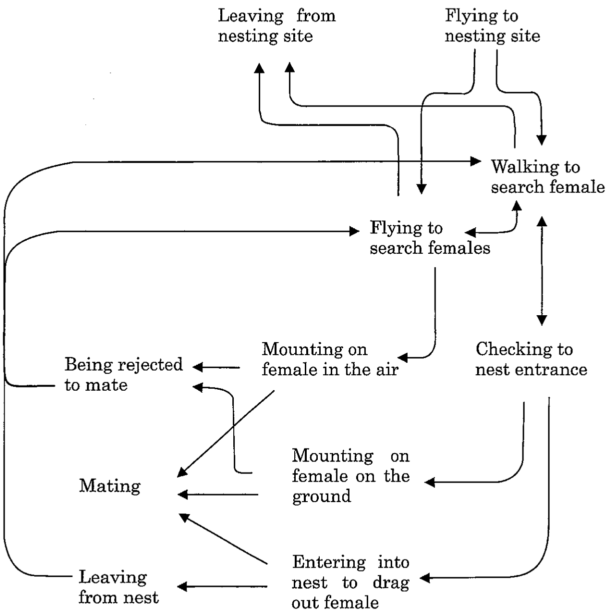

Fig. 2 Schematic representation of patrolling behavior of males observed at the nesting sites of *Andrena richardsi.*

June 29 in 2002, 2003 and 2004, respectively. Foraging by bees begun simultaneously with formation of tumuli. However, the first appearance of females at the nesting site A was on May 14 in 2002 and May 12 in 2003, suggesting that the pre-nesting period was unstable and very long, depending on the years. The causes were not analyzed, but this may relate to a mainly inclement weather at mountainous areas. An increase of the tumuli was observed no longer on July 8 in 2001, July 12 in 2002 (48 days from the first formation of tumuli, Fig. 6), and on July 10 in 2003 (17 days, Fig. 6). However, data for 2004 were obscure, because of few number of tumuli (30 nests). The cease of the nesting activity seems to be caused to the flower-fall of the major resource of *S. macropylla.*

Females departed from their nests with a zig-zag orientation flights through 20–50 cm above the ground, which was performed thoroughly at the first departure of a day. At every departing, bees closed nest entrance loosely with soil of tumuli by turning around their bodies. The entrance was also closed by carrying soil on the tip of dorsal abdomens from the burrow wall, when they returned to their nests every time. Bees begun to vibrate wings near of the entrances before the first leaving from their nests between 7:00 and 8:00. This behavior seems to be idling and sunning, so as to rise their body temperature. Idling and sunning were continued around the tumulus and on the plant leaves near the nests, while temperature were cool. Foraging started by *A. richardsi,* when temperature rose up above 17°C. Foraging hours were affected often by low temperature and fog at mountainous areas where weather was unstable. In *A. fenningeris* Viereck, females are staying at near the nest entrance where they get warmth by through basking, and thereafter they begin their foraging trips at/over 11°C on sunny days (Batra, 1999).

Daily foraging activity of *A. richardsi* was observed at the site A for 4 times on different sunny days. The number of bees' departures from nests and returns to nests are shown every hour between 6:00 and 16:00 in Fig. 3. The discrepancy between the number of departing and returning bees shown in the figure is due to either overlooking of departure (for July 8 and 10, 2002) or disappearance of bees (for July 10, 2003 and July 2, 2003). However, the number of returned bees were never overlooked, because we covered the nest entrances with cups during bees were absent.

The peak times leaving nests by bees for foraging were around 7:00, 8:00, 13:00 and 8:00 on July 6, 2002 (Fig. 3, A), July 2, 2003 (Fig. 3, B), July 8, 2003 (Fig. 3, C), July 10, 2003 (Fig. 3, D), respectively. On July 8, 2003, dense fog had been veiled around the nesting site until 10:00, and thereafter, bees gradually commenced their foraging trips. Each female carried a weight of 25-85 mg pollen load (mean±SD : 64±23 mg, $N=6$), when she returned to her nest.

The number of foraging trips performed by a single female per day is shown in Table 1. The value differed by observation dates, even in the full blooming time of *S. machrophylla,* due to fog condition. Bees sometimes returned to their nests without pollen loads (nectar foraging). Such bees were observed often at later foraging activities (Fig. 3, A-D), presumably, they carried only nectar. The maximum number of pollen foraging trips/day reached up 6 times, but the mean numbers were fewer, 1.9±1.1 ($N=228$, Table 1). Nectar foraging trips reached up 5 (mean±SD : 1.6±1.1/female/day, $N=228$, Table 1).

Time spent for a single pollen foraging trip was variable (55.4±48.4, $N=126$), depending on its orders performed in a day (Table 2). The longest was as much as 219 minutes, especially those records of individuals, who engaged in the first pollen foraging trip in a day, was the longest, but no clear tendency was recognized among orders (Table 2). On the other hand, time used for manipulation of pollen ball was stable, 16.8±14.8 minutes in combined all orders ($N=73$, Table 2). In *A. prostomias,* time spent for a single pollen forging trip is remarkably short in females of which number of foraging trips are larger than in those are fewer (Maeta, 2000).

In other andrenid bee species, the mean time spent for a single foraging trip is as follows : Less than 30 minutes for 6 species (19.4% ; 30-60 minutes for 10 species (32.3%) ; 60-90 minutes for 10 species (32.3% ; Exceed 90 minutes for 5 species (16.1%) (reviewed in Maeta, 2000), showing that most andrenid bees spend longer time for a single foraging trip. The number of foraging trips performed by a bee is scarce in all species of the genus *Andrena.* Reports on the maximum number of foraging trips performed/day in 20 species are as follows : Less than 5 times for 8 species (40%) ; 5-10 times for 12 species (60%) ; no species exceeds 10 times (reviewed in Maeta, 2000). In *A. vaga,* pollen and nectar is collected on different days with having 1-5 pollen foraging trips (mean : 3)/day on the pollen day (monopolized to carry pollen load only). Most of the flights take between 1 and 2.5 hrs on the pollen days, and 2 and 3.5 hrs on the nectar days (monopolized to carry nectar only) (Bischoff *et al.,* 2003). *Andrena prunorum* Cockerell females carried 5-6 pollen loads/day, spending 2.7-72.7 minutes (mean : 22.1 minutes) (Miliczky, 2008).

The number of foraging trips performed/female/day might be related to the making rate of pollen balls in a day, and is subsequently affected by reproductivity of bee species. In 2 andrenid bee species, *A. prostomias* and *A. japonica* Smith, the number of times of pollen foraging trips required to complete one pollen ball are calculated by the number of pollen grains which composed of one pollen ball for female (Af) and male offspring (Am), and of one pollen load (B).

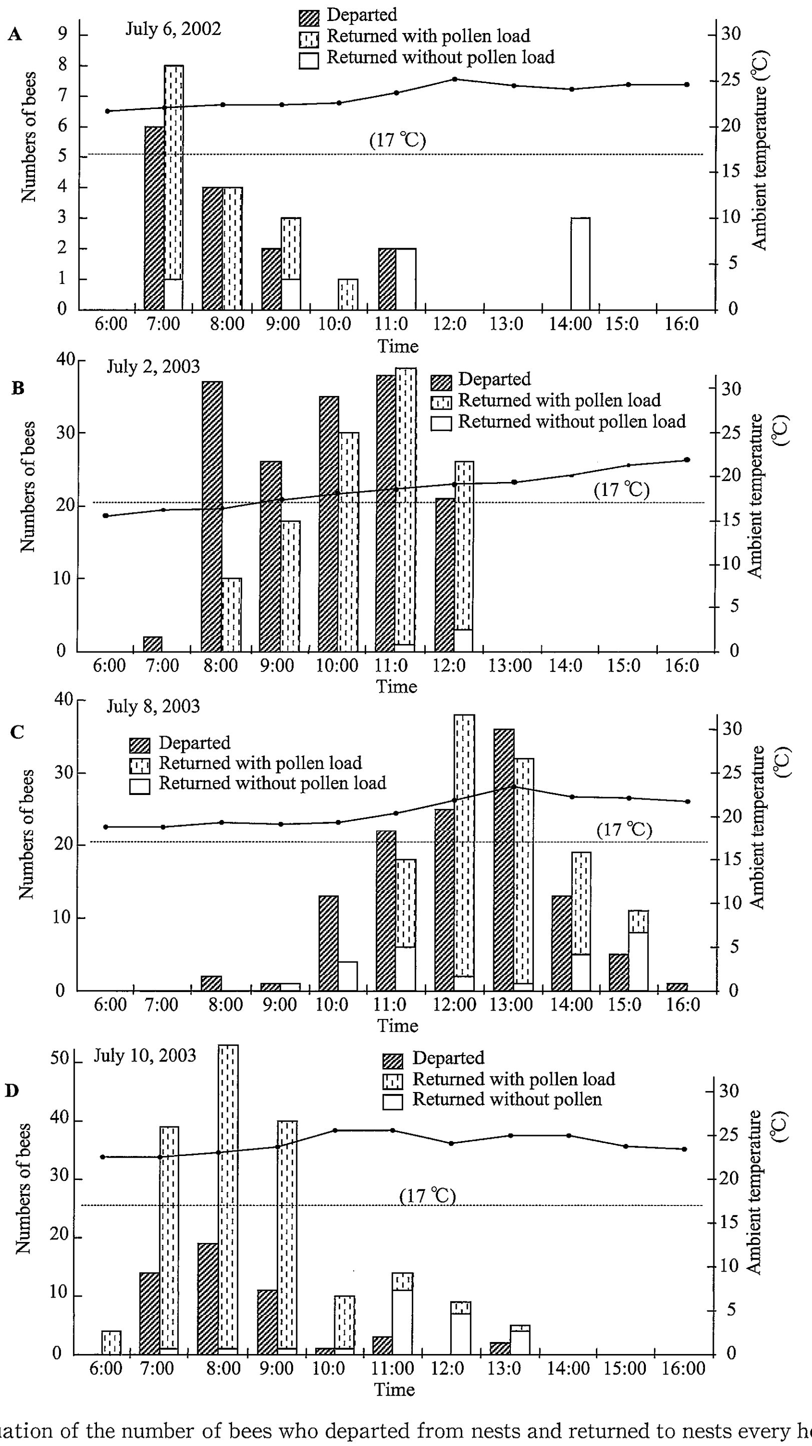

Fig. 3 Fluctuation of the number of bees who departed from nests and returned to nests every hour between 6:00 and 16:00. Observations were made on 5 different days during the full blooming of *Swida macrophylla*. A : July 6, 2002 ; B : July 2, 2003 ; C : July 8, 2003 ; and D : July 10, 2003. A horizontal dotted line drawn in the figure shows the temperature (17℃) at which bees begin their foraging activities.

Table 1 Number of foraging trips performed by a single female per day in *Andrena richardsi* observed on 4 sunny days.

Date	No. of females observed[1]	Number of returns/female					
		Range		Total		Mean±SD	
		A	B	A	B	A	B
July 6, 2002	10	0-5	1-5	17	21	1.7±1.6	2.1±1.4
July 2, 2003	71	1-4	0-4	123	119	1.7±0.8	1.7±0.9
July 8, 2003	63	1-6	0-5	125	96	2.0±1.3	1.5±1.2
July 10, 2003	86	1-6	0-5	180	144	2.0±1.1	1.6±1.2
Combined	228	1-6	0-5	445	380	1.9±1.1	1.6±1.1

1) Number of females returned to their nests with pollen loads (A) and without pollen loads (B). B seem to be that females carried only nectar.

Table 2 Time (min) spent for pollen and nectar foraging trips and manipulation of pollen balls in relation to the order of foraging trips performed in a day in *Andrena richardsi*.[1]

Task		Order of foraging trips and pollen manipulations performed in a day							Combined
		1	2	3	4	5	6	7	
Pollen	Range	6-219	12-184	4-107	9-136	14-66	9-104	—	4-219
foraging	Mean±SD	98.9±64.6[a]	43.6±7.9[b]	36.2±24.8[b]	42.9±46.7[ab]	35.5±23.6[bc]	52.3±48.0[ab]	—	55.4±48.4
trip[2]	*N*[5]	31	52	29	7	4	3	0	126
Nectar	Range	10-237	34-134	71-212	36-119	—	64	4-87	4-237
foraging	Mean±SD	77.9±94.8[a]	84.0±70.7[a]	142.0±99.7[a]	81.7±42.1[a]	—	64[a]	45.5±58.7[a]	87.0±75.4
trip[3]	*N*[5]	7	2	2	3	0	1	2	17
Manipulation	Range	3-121	6-81	8-21	6-18	5-87	12-12	—	3-121
of pollen	Mean±SD	17.5±17.9[a]	17.9±15.1[a]	12.1±4.0[a]	12.5±3.7[a]	23.3±31.2[a]	12.0±0.0[a]	—	16.8±14.8
ball[4]	*N*[5]	79	52	26	8	6	2	0	173

1) Summarized 220 individuals in total 3 days observations conducted on July 2, 8, 10, 2003. However, the cases of which durations recorded were selected. Significant diffrerence in time spent for pollen foraging trips is indicated by different letters (a, b, c) among different orders ($p<0.05$, Dunnet T_3 test). No significant difference was obtained in time spent for nectar foraging trips and for manipulation of pollen balls among different orders ($p>0.05$, one-way layout ANOVA).

2) Duration (min) from departure to return with pollen load.

3) Duration (mim) from departure to return without pollen load.

4) Duration (min) from returning with or without pollen load to leaving for the next foraging trip.

5) Number of cases recorded.

The value can be obtained by Af/B and Am/B. *Andrena prostomias* need 9.7 times of pollen foraging trips to make the largest pollen ball and 4.4 the smallest one (Maeta, 2000). *Andrena japonica* engaged in 6 times of the pollen collecting trips for making a female pollen ball and in ca 4 times for a male pollen ball, reflecting size difference between sexes (Maeta *et al.,* 2004). The number of foraging trips to be needed to form one pollen ball is estimated in 7 andrenid species. The range is variable (4-15 times), depending on the species examined, but for 5 species it is 4-6 times (reviewed in Maeta, 2000). Contrasting to andrenid bees, a mason bee, *Osmia cornifrons* (Radoszkowski), which has a high reproductivity (mean number of eggs laid/female : 43.3±7.3), one provision is made by ca. 28 pollen foraging trips (Sugiura and Maeta, 1989). One female engaged in pollen foraging trips for 44-86 times/day under favorable weather and floral resource conditions, spending only 4-5 minutes for each pollen foraging trip (Maeta *et al.,* 2005).

4. Floral resources

We collected females only from flowers of *Swida macrophylla* on Mt. Daisen. Analysis of pollen obtained from pollen baskets ($N=5$) revealed that all pollen loads examined were of *S. macrophylla,* growing abundantly on Mt. Daisen. Fecal pellets obtained from brood cells ($N=3$) were also composed of the same pollen species. These findings suggest that *A. richardsi* is oligolectic. However, Hirashima (1962) collected 5 females on flowers of *Ilex* sp. (Aquifoliaceae) on Mt. Hakkoda, Aomori Pref., and Yamada (1998) sampled each single female on flowers of *Salix* sp., (Salicaceae), *Prunus grayana* (Rosaceae) and *Acer* sp. (Aceraceae) at 3 different mountainous areas in Aomori Pref. The above mentioned flower records show that *A. richardsi* seems to be rather polylectic.

Flowers of *S. macrophylla* around the 3 nesting sites on Mt. Daisen starts blooming from middle May every year, showing that the blooming commenced the same period with the start of flying activity of bees. Majority of flowers of *S. macrophylla* around the 3 nesting sites had gone at the middle of July in usual years.

5. Developmental duration of prepupae and pupae

Duration of prepupae and pupae of *A. richardsi* incubated at 5 different temperatures are shown in Tables 3 and 4. No development of prepupae was occurred at 14°C, although this temperature is considerably higher than the threshold developmental temperature as described below. However, those prepupae developed into adults, when incubated them again at 28°C after keeping for 8 months at 14°C. Inhibition of development of prepupae was recognized above 18°C. Temperature zones without inhibiting prepupal development were very narrow in this species, between 16°C and 18°C in males, and between 16°C and 20°C in females. Developmental inhibition by temperatures above 18°C in male prepupae and above 20°C in female prepupae may function to retain them so as to overwinter at this stage. In a mason bee, *Osmia cornifrons,* thermal inhibition occurred at prepual stage above 22°C. The inhibition functions to retain their development during hot summer, because overwintering dormant adults are vulnerable against high temperatures (Maeta, 1978 ; Maeta *et al.,* 2006).

The regression line of the prepuapal development in *A. richardsi* was drawn excluding those temperatures at which developmental inhibition was occurred (Fig. 4). Threshold developmental temperature of prepupae, which was calculated from the regression line, was not clear in males, because only 2 temperatures (16°C and 18°C) were available to use for calculation, but it is 8.8°C for females. On the other hand, no thermal inhibition was occurred in pupae incubated at the 5 different temperatures. The developmental duration in days of this stage was the shortest at 24° C in both sexes. The threshold developmental temperatures of pupae are 7.6°C for males and 5. 6°C for females (Fig. 4). The threshold developmental temperatures in both prepuape and prepupae is lower in females than males. It suggests that *A. richardsi* is protogyny, although sex distribution in a burrow is estimated to be the ♀♂ type. This discrepancy between the sex distribution and protogyny in *A. richardsi* can be solved by more detailed studies.

In univoltine and summer species, *A. prostomias,* which nests at flatlands, the threshold developmental temperature of prepupae is 6.6°C for males and 9.4°C for females, and that of pupae

Table 3 Developmental duration in days of prepupae of *Andrena richardsi* reared at 5 different temperatures.[1)]

Temp. (°C)	Sex	Developmental duration in days[2)]			Mortality (%)
		Range	Mean±SD	*N*	
16	♀	57-73	64.0±5.7	5	16.7
	♂	41-83	69.0±24.2	3	57.1
18	♀	31-70	45.0±17.2	6	0
	♂	31-84	45.3±20.4	5	28.6
20	♀	33-63	40.5±12.3	6	14.3
	♂[3)]	38-56	53.0±10.6	4	42.9
22	♀[3)]	50-70	58.5±10.1	4	33.3
	♂[3)]	46-56	51.0±5.8	4	42.9
24	♀[3)]	49-63	53.0±6.2	6	14.3
	♂[3)]	47-63	56.8±6.6	5	16.7

[1)] Incubation was started on April 6, 2004.
[2)] Duration in days from the commencement of incubation to pupation.
[3)] Development was inhibited at this temperature.

Table 4 Developmental duration in days of pupae of *Andrena richardsi* reared at 5 different temperatures.[1)]

Temp. (°C)	Sex	Developmental duration in days			Mortality (%)
		Range	Mean±SD	*N*	
16	♀	40-53	47.3±5.6	4	20.0
	♂	38-47	42.5±6.4	2	33.3
18	♀	32-37	35.5±2.1	5	16.7
	♂	37-45	39.4±3.4	5	0
20	♀	35-38	36.4±1.3	5	16.7
	♂	38-38	38.0±0.06	2	50.0
22	♀	16-39	29.3±9.6	4	0
	♂	22-30	27.3±3.8	4	0
24	♀	24-28	25.7±1.7	4	33.3
	♂	23-24	23.3±0.6	3	40.0

[1)] Incubation of prepupae started on April 5, 2004. Thereafter, kept them at the same temperatures until eclosion.

is 9.1°C for both females and males, showing that this species is a typical protoandy (Maeta, 2000). These values are lower in *A. richardsi* than those in *A. prostomias,* reflecting a difference of their habitats.

6. Developmental sequence of the immatures in nests

In univoltine species of andrenid bees, occurring in temperate zone, those of vernal species overwinter as adults, while those species emerge from summer to autumn as prepupae (reviewed

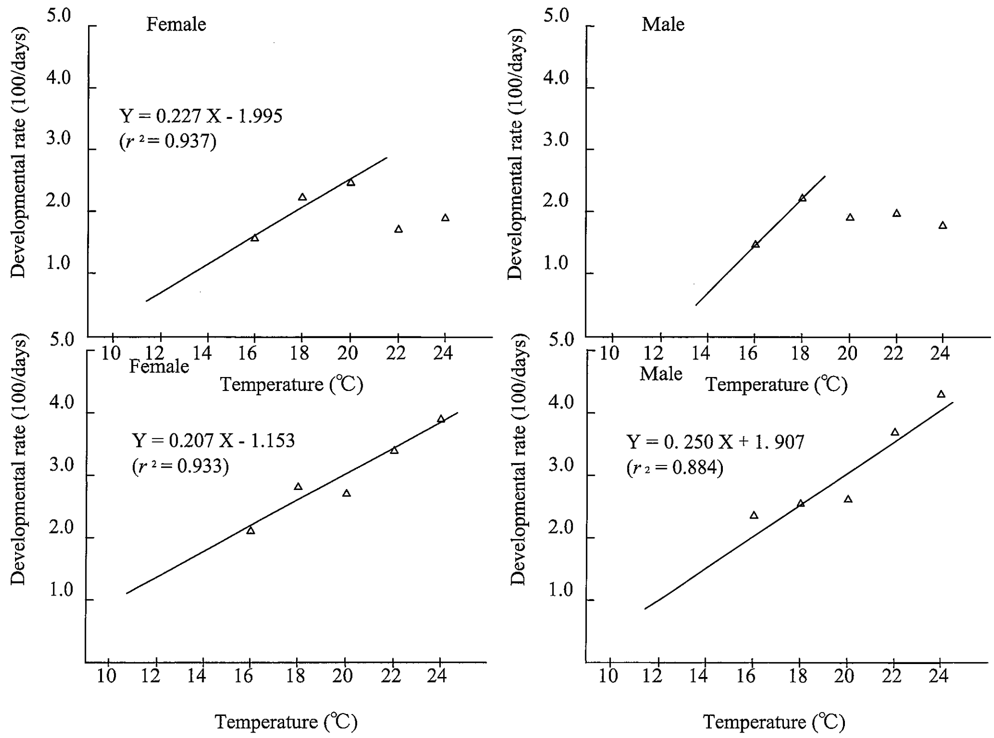

Fig. 4 Developmental rate (100/duration in days) of prepupae (upper) and pupae (lower) at 5 different temperatures in *Andrena richardsi.* Regression lines of prepupae were drawn by excluding the temperatures at which developmental inhibition occurred.

in Maeta, 2000). *Andrena richardsi* belongs to the vernal species, because they emerge in middle May at mountainous areas. Thus, ordinary overwintering stage seems to be adults (Fig. 5, B), but also prepupae (Fig. 5, A) are found together in the same year. First, we thought that difference of developmental patterns is due to parasivoltinism, as proposed by Torchio and Tepedino (1982) in 3 species of mason bees. Adults are one-year form and prepupae 2-years form in *A. richardsi.* However, such developmental polymorphism is not determined optionally, as described below.

Table 5 shows immature stages found in the nests of *A. richardsi,* which were excavated in various months. Foraging period of bees lasted up to middle July in usual years, as mentioned above. When nests were excavated from autumn to winter (October to December) of 3 years of 2001, 2003 and 2004, both prepupae and adults were found in 2001, whereas only either prepupae or adults in 2003 and 2004. Probably, because of small sample size both stages were not found at the same time every studied year.

The result of 2004 is the most informative to trace the development of immatures (Table 5). It is obvious that pupation took place from July to August and eclosion from August to October. Young larvae developed into prepupae in July. Those prepuape found in March and April seem to be born in the previous year and hibernated the winter of 2003/2004. To continue further development until adults, prepupae and pupae require ca. 41 days and ca. 26 days (total ca 70 days), even at the optimum temperature (20°C and 24°C for female prepupae and pupae, respec-

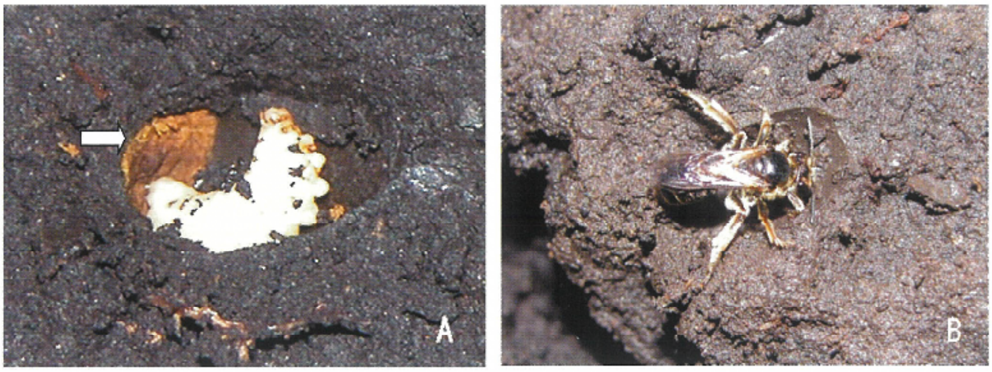

Fig. 5 The figure shows the brood cells of *Andrena richardsi* with an overwintering prepupa (A) and an adult (B). Feces attached on the posterior cell wall are shown by an arrow mark in the figure A.

Table 5 Contents in the nests of *Andrena richardsi* excavated at different months.[1]

Year	Stage	Nesting site	March		Apr.		May		June		Jul.		Aug.		Oct.		Dec.		Total	
			♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
2001	Prepupa[2]	A, B													16	8			16	8
	Pupa														0	0			0	0
	Adult														5	0			5	0
2002	Prepupa[2]	C							5	6	16[3]	2							21	8
	Pupa								0	0	0	0							0	0
	Adult								0	0	0	0							0	0
2003	Prepupa[2]	C					0	0									4	11	4	11
	Pupa						0	0									0	0	0	0
	Adult						15	6									0	0	15	6
2004	Prepupa[2]	C	13	6	18	21					32[4]	29	0	0	0	0			63	56
	Pupa		0	0	0	0					0	0	10	4	0	0			10	4
	Adult		0	0	3	0					0	0	0	0	21	8			24	8
2006	Prepupa[2]	C			9	6													9	6
	Pupa				0	0													0	0
	Adult				0	0													0	0
2008	Prepupa[2]	C					7	4												
	Pupa						0	0												
	Adult						0	0												
Total	Prepupa[2]	—	13	6	27	27	7	4	5	6	48	31	0	0	16	8	4	11	113	89
	Pupa		0	0	0	0	0	0	0	0	0	0	10	4	0	0	0	0	10	4
	Adult		0	0	3	0	15	6	0	0	0	0	0	0	26	8	0	0	44	14

[1] Months are not shown in the table, when no excavation was made.
[2] Sex of prepupae was indirectly determined by their sizes (see Fig. 7).
[3] Two of 16 individuals were full grown larvae, and 5 just defecating full grown larvae.
[4] Two of 32 were full grown larvae.

tively (Tables 3 and 4). However, actually such high soil temperatures are not existed during 3 corresponding months (March to May, Table 6), so as to meet the commencement of flying period,

Table 6 Monthly mean temperatures (°C) of ambient and in soil at 3 different depths on Mt. Daisen (alt. 660 m).

Ambient and soil temp.	Year[1)]	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Ambient	2004/2005	-0.2	-0.9	1.5	10.9	14.1	20.2	21.9	23.0	20.3	16.0	—	4.1*
20 cm	2006	2.8	1.9	1.1	3.2	12.8	16.3	20.1	22.4	18.3	14.9	10.2	4.9
40 cm	2006/2007	3.3	2.7	4.4	3.1*	11.4	14.9	19.0	21.4	18.2	15.1	11.2	6.9
60 cm	2005	4.4	3.1	2.1	4.0	10.7	14.1	18.1	19.7	19.3	15.7	11.1	6.3

[1)] Asterisk shows the month in which temperature was begun to record.

which begins at middle May. These prepupae will develop into adults in October, and those adults are obliged to overwinter in 2004/2005 in their brood cells. Only 5 months (from June to October) are available for development of prepupae and pupae, in which soil temperature at the depths of 20 cm, 40 cm and 60 cm exceeds 14°C (Table 6). Moreover, those overwintering individuals in temperate bee species, irrespective of prepupal or adult stages, need to encounter low temperatures for 3 to 4 months, so as to break their diapause (Maeta, unpubl.), *e.g.,* in *A. prostomias* 10–16°C for 4 months are necessary to break prepupal diapause (Maeta, 2000). These facts show that *A. richardsi* is biennial. However, voltinism of the bee populations which are inhabiting at flatlands needs to be confirmed, because sufficient soil temperatures are supposedly sustainable to maintain univoltinism in those circumstance.

In *A. rudbeckiae* Robertson and *A. macra* Mitchell, 2 overwintering stages (prepupa and adult) are known and these stages are suggested to be determined optionally (Neff and Simpson, 1997 ; Riddick, 1990), although the mechanism to determine the stages is not known. Other oligolectic species, *e.g., A. mojavensis* Linsley *et* MacSwain and *A. omninigara clarrkiae* Linsley *et* MacSwain can adjust their flying periods, depending on the blooming condition of their definite host plants (Linsley *et al.,* 1964 ; MacSwain *et al.,* 1973).

7. Nest Density and cumulative number of nests

Total number of nests (=tumuli) at the 2 nesting sites (A and B) attained a peak as follows : ca. 30 at the site A and 186 at B in 2001 (89 nests/m² at the highest spot) ; 156 at A in 2002 ; 281 at A in 2003 ; 30 at A in 2004. However, none of tumuli was found at the 3 nesting sites (A, B and C) in 2008. These aggregations seem to be ruined at all. Aggregations of some species of andrenid bees, *e.g., A. vaga* Panzer and *A. prostomias* were continuously observed for long years (Ulrich, 1956 ; Maeta, 2000), but usually found unstable in most species (reviewed in Maeta (2000)).

Figure 6 depicts the seasonal change of cumulative percentage of nests examined in 2002 and 2003 at the site A. The results of both years are contrasting. The nesting

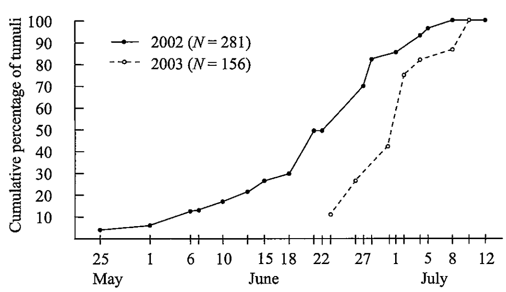

Fig. 6 Cumulative percentage curve of the number of nests in *Andrena richardsi* observed at the site A in 2002 (upper) and 2003 (lower).

period in 2002 was continued for 48 days, but in 2003 only for 17 days. The day on which the maximum number of tumuli was observed was on 33rd day (June 27) in 2002 and was 9th day (July 2) in 2003, since the first formation of tumulus. Gradual increase of nests for a long duration shows that re-excavation after renunciation of previously excavated nests occurs frequently in this species. As to the nest density of andrenid bees, many reports are published (reviewed in Maeta, 2000). Most species make relatively low density of nests even at the highest spot, composing of several decades to several hundreds nests per square meter. Two very high densities were known in *A. alleghaniensis* Viereck (666 nests/m^2, Batra, 1990) and *A. ovatula* (Kirby) (500 nests/m^2, Wafa *et al.,* 1972). Our study of the nest density in *A. richrdsi* was not high, but not seems to be low among andrenid bee species.

Survival rate of the nests in *A. richardsi* was not studied by the present study, because the bees did not participate in foraging every day. In *A. prostomias* and *A. japonica,* percentage of nests in which bees are present declines sooner before that the number of tumuli reached up to the maximum (100%) in both species (Maeta, 2000 ; Maeta *et al.,* 2004).

8. Sex ratio

Figure 7 depicts the size (weight) distribution of prepupae, combined data for 4 years from 2001 to 2004. There was 2 distinct groups, representing sexes of male and female. The prepupae with weight less than 74 mg and above 75 mg are tentatively regarded as males and females, respectively. The sexes of prepupae determined by their sizes were proved to be true by rearing them in March and April of 2004. Sex ratio was expressed by female ratio (females/females+males, Table 7). It was obtained from the individuals of prepupae and adults found in nests excavated for 6 years (2001-2004, 2006 and 2008). The values differed slightly by generation of the year, ranging 0.525-1.000, and the combined value for corresponding 7 generations (2002-2007 and 2009) was 0.611, showing that sex ratio is slightly female biased. The value of 1.000 in Table 7 might be due to a small sample size.

The reliable female ratio is only obtainable from the excavation of nests. Such cases are merely known in 7 solitary species as below : *A. crataegi* Robertson (0.48, Osgood,

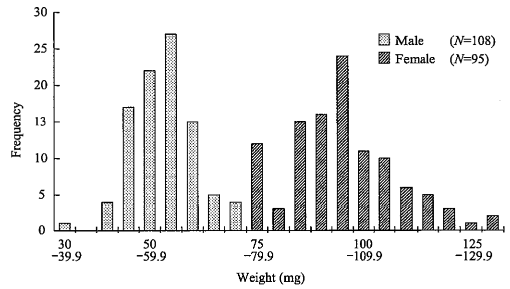

Fig. 7 Distributional frequency of the weight (mg) of prepupae in *Andrena richardsi.* Prepupae were obtained from nests excavated for 4 years between 2001 and 2004.

Table 7 Female ratio of *Andrena richardsi.*[1)]

Generation of year[2)]	Female	Male	Total	Female ratio
2002	5	0	5	1.000
2003	36	20	56	0.643
2004	19	2	21	0.905
2005	66	50	116	0.569
2006	32	29	61	0.525
2007	9	6	15	0.600
2009	7	4	11	0.636
Combined	174	111	285	0.611

1) Prepared based on Table 5.
2) The year in which the generation will emerge was determined by their developmental sequence. Sex of prepupae was determined by their sizes.

1989) ; *A. fenningeri* (0.5, Batra, 1999) ; *A. japonica* (spring and summer generations : 0.73 and 0.76, Maeta *et al.,* 2004) ; *A. placida* Smith (0.53, Thorp and Stage, 1968) ; *A. vaga* Panzer (≒0.50, Friese, 1882) ; *A. vicina* Smith (0.46–0.62, Miliczky and Osgood, 1995) ; *A. takachihoi* Hirashima (0.66, Göukon and Maeta, unpubl.). Female ratio is 0.68 even in *A. carantonica* Pērez (reported as *A. jacobi* Perkins, Paxton & Tengö, 1966), which is known as a communal and presumably local mating competition occurs. From these reports, the sex ratio of most andrenid bee species is found as almost half or slightly female biased, while male-biased sex ratio (0.32–0.35) is known in *A. prostomias* (Maeta, 2000).

9. Nest architecture

The size of tumuli formed on the ground was 37.2±8.6 mm (N=72) in diameter and 18.2±2.3 mm (N=6) in height. No turret at the center of tumulus was present. Tumuli were weak and easily broken by rain and wind. Broken tumuli were never rebuilt. Diameter of the nest entrance was 6.5±1.1 mm (N=28). The situation of brood cells was carefully examined. The main burrows were excavated by bees nearly vertically, more or less inclining toward various directions, until the depth of ca 20 cm. Afterward, these burrows turned nearly horizontally and then slightly inclined. The diameter of main burrows was ranging 5.0–8.0 mm (mean±SD : 6.1±0.7 mm, N=17), but stable throughout the burrows. No lining was made on the wall of burrows.

Figure 8 shows the situation of brood cells in the 2 representative nests. Three brood cells were linearly arranged from the innermost to upper parts of the main burrows. The brood cell was barrel shape, and the opening part was constricted (range and mean±SD : 5.0–7.5 mm and 6.1±0.8 mm, N=9), equivalent to the diameter of the main burrow. The size of brood cells was as follows (shown by range and mean±SD) : 10.0–16.0 mm and 13.6±1.8 mm (N=10) in length, and 4.5–9.0 mm ; 7.8±1.4 mm (N=9) at the largest part of diameter. Interspace between 2 adjacent brood cells was compactly filled by soil. The length of burrow filled with soil was ranging 10.0–14.5 mm (mean±SD : 12.9±2.0 mm, N=4). The brood cells were orientated slightly upward (Figs. 8A, B). The dimensions of brood cells reported by Gôukon (1991) are well coincident with ours. He also mentioned the sizes of pollen balls and eggs are as follows : Entirely round shaped with 3.8 mm (diameter)×3.8 mm (height) (N=10), and banana shaped egg (2.08 mm in length and 0.58 mm in diameter, N=5) placed on the central top of the pollen ball, situating the ventral side of egg curved inwardly. Only 4 brood cells in the maximum were found per main burrow, and 7 nests with ramified main burrow in *A. richardsi.*

The number of brood cells in those nests excavated after cease of the nesting activity in 2004 was 1–5/nest (mean±SD : 2.7±1.2, N=30) in *A. richardsi.* In 38 solitary andrenid bee species, the oviposition numbers (=the number of provisioned cells/nest) ex-

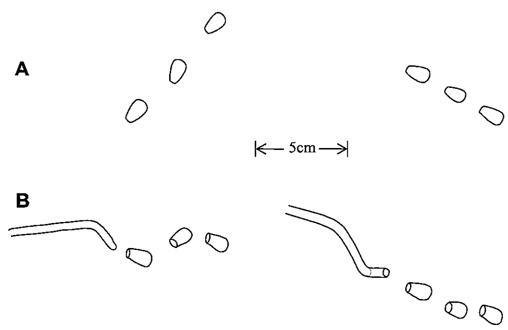

Fig. 8 Two examples of the nests of *Andrena richardsi,* showing the situation of brood cells in soil. A : Upper view ; B : Lateral view.

pressed by the maximum number of brood cells, including immatures and pre-and in-provisioning brood cells, were as follows : Less than 5 for 17 species (44.7%) ; 5–10 for 14 species (36.8%) ; 11–15 for 6 species (15.8%) ; and 16–20 for one species (2.6%) (reviewed in Maeta, 2000). In the following 3 communal species, the number of brood cells/nest was virtually larger than that of solitary species : *A. accepta* Viereck : 23 (Rozen, 1973) ; A. *crataegi* : 54 (Osgood, 1989) ; *A. labialis* Kirby : 36 (Sowa *et al.,* 1976). Apparently, the number of brood cells of *A. richrdsi* belongs to fewer group among andrenid bee species.

None of females among marked bees, which nidificated more than one nest (single-nests), was recognized in *A. richardsi.* Ten species of andrenid bees who make more than 2 nests (multi-nests) are confirmed by pursuing the marked bees (reviewed in Maeta, 2000). However, no increase of the brood cell numbers is seen in multi-nests of these species, as compared with those in single-nests.

In 2 nests of *A. richardsi,* the large-sized prepupae always situated at the innermost position, suggesting that sex distribution is a so called ♀♂ type (females arranged at inner- and males at the outer-part of nests), as in most megachilid bees which nidificate in the pre-existing cavities (*e.g.,* Malyshev, 1935 ; Krombein, 1967 ; Maeta and Sugiura, 1990). In *A. dunningi* Cockerell, 2 groups of the brood cells are arranged around the main burrow, formerly made the upper brood cells for males and later the lower brood cells for females (Johnson, 1981).

The brood cells in nests of *A. richardsi* were arranged linearly in soil between 20 cm and 50 cm in depth. The highest frequency of the cells was recognized around the depth of 25.0 cm (Fig. 9). Göukon (1991) described that the depths of brood cells in *A. richardsi,* excavated at Hanayama-mura, Miyagi Pref., northern Japan are 12.5–20.5 cm, suggesting that the depth of brood cells becomes shallower in northern districts. Soil temperatures were higher at shallower depth between May and August, but a little higher at deeper depth between September and April (Table 6). No clear relationship between the depths of brood cells and sexes of bees involved in them in *A. richardsi* (Fig. 9).

Matsumura (1970) and Maeta (2000) hypothesize the evolutionary process of nest architecture in bees of the genus *Andrena,* and latter author proposes 6 nest types (I–VI). The highest developed nests are single-series (IV) and multi-series types (V), of which brood cells are linearly arranged from the innermost to upper parts of a main burrow (IV), but the main burrow is ramified and repeats the same arrangement of brood cells in each burrow (V). The nest of *A. richardsi* corresponds to the types IV and V, as already reported by Gôukon (1991). Nine percent of 53 andrenid bee species of which nest types are studied belong to the types of IV and V (reviewed in Maeta, 2000). In addition to the above mentioned 53 species, the nest type of *A. (Plastandrena) prunorum* judged from the illustration (Fig. 5 in Miliczky,

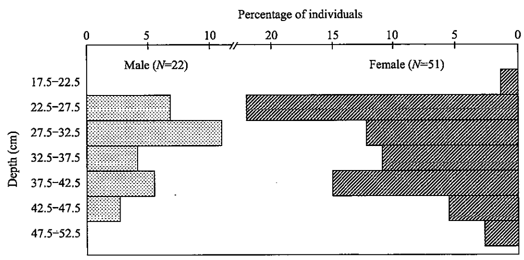

Fig. 9 Distributional frequency of the depths of brood cells of *Andrena richardsi* in soil, examined in 2004. No significant difference was obtained between the rates (%) of males and females at every depth of brood cells ($p > 0.05$, Fisher's exact test).

2008) seems to be IV, although the author did not described the type. This nest type is common among species in the subgenus *Plastandrena* (reviewed in Maeta, 2000).

10. Natural enemies

By excavation of nests at the site A on October 20, 2001, several deceased larvae by fungus, 3 adults of *Meloe coarctatus* Motschulsky and one pupa of bomylid fly (*Bombylius* sp.) were found in brood cells. The rate of parasitism was not examined by the present study. Two species of nomadine bees, *Nomada comparata* Cockerell and *N. alboguttata etizenesis* Tsuneki are reported as possible cleptoparasites, based on the circumstantial evidences (Suda, 1980 ; Maeta *et al.*, 1996).

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