Bulletin of Insectology **77** (2): 229-237, 2024
ISSN 1721-8861 eISSN 2283-0332

Behaviour, ecology and development of the mud-dauber wasp *Sceliphron deforme*

Phong Huy Pham[1,2]
[1]*Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Ha Noi, Vietnam*
[2]*Graduate University of Science and Technology, Vietnam Academy of Science and Technology, Ha Noi, Vietnam*

Abstract

The solitary mud-dauber wasp *Sceliphron deforme* (Smith) (Hymenoptera Sphecidae) is distributed in the Oriental and the Palearctic regions. Despite a large geographical distribution, not much is known about its nesting biology. Here, the nesting biology of *S. deforme* is described with details on its ecology, nesting behaviour and development. The females built their mud nests in houses (both abandoned and occupied houses), usually on hall curtains, wall corners, and windows, sometimes on household appliances, screw recesses, crevices, and trap nests. One single observed female took 42 mud-carrying flights on average and 68.7 minutes to build completely a nest cell. *S. deforme* provisioned 8-11 paralyzed spider prey per nest cell, which belonged mainly to *Ptocasius strupifer* Simon (Araneae Salticidae) and sometimes to *Oxyopes* sp. (Araneae Oxyopidae), and sometimes left one empty cell in each nest. The total development time from the egg to emergence of the adult wasp was 26-28 days under laboratory conditions. The females copulated only once, just after emergence. With access to 50% diluted honey, adult males lived 3-10 days and adult females lived 5-27 days at the average room temperature and relative humidity of 29.8 °C and 78.8%, respectively. The date of initiation of the overwintering stage of *S. deforme* is unknown, but it ended about mid-April of the following year. *Chrysis* sp. (Hymenoptera Chrysididae), *Euchalinus* sp. (Hymenoptera Ichneumonidae), *Melittobia sosui* Dahms (Hymenoptera Eulophidae), and possibly two fly species (Diptera Sarcophagidae) were recorded as nest parasites of *S. deforme*. The emergence rate ranged from 66 to 71%, the developmental mortality of pupa was 12.5%, the nest parasitoid ratio was 37.5%, and the sex ratio of emerging adults was 0.75 (male/female). Findings in this study provide a better understanding of the biology and evolution of the nesting behaviour of the mud-dauber wasp *S. deforme*.

Key words: behavioural ecology, development time, mating, nesting biology, Vietnam.

Introduction

The solitary wasp genus *Sceliphron* Klug (Hymenoptera Sphecidae) is widespread worldwide and consists of 34 species (Pulawski, 2024). *Sceliphron* females build mud nests in a variety of sheltered situations, and many species are commonly associated with human habitations. Each nest usually consists of clusters of contiguous tubular mud cells attached to substrate and usually covered with a final mud layer. Each cell is provisioned exclusively with paralysed spiders, and a single egg is usually laid on the first spider placed in the cell (Bohard and Menke, 1976; Polidori *et al*., 2005; Chatenoud *et al*., 2012). *Sceliphron* wasps have been the subject of several studies in the past related to their nesting habit, prey, and parasites (Freeman, 1974; Callan, 1988; Polidori *et al*., 2007; O'Neill, 2001; Gess and Gess, 2014).

S. deforme (Smith) is distributed widely in the Oriental and the Palearctic regions, where five subspecies have been named. *Sceliphron deforme deforme* (Smith) is the most widely distributed subspecies. Since *S. deforme* was descripted more than 160 years ago, its nesting biology has received some attention from entomologists, such as Rudow (1912), Strand (1914), Williams (1919), Iwata (1939), Kazenas *et al*. (2005), Ćetković *et al*. (2011), and Kazenas (2013), who each contributed brief accounts of the nest structure, prey, and nesting sites. In addition, Basil-Edwardes (1921) reported observations on nesting sites, nest structure, provisioning, and development of larvae into nest cells.

The main aim of the present study was to determine nesting sites, nest structure, nest provisioning, development, mating, longevity, overwintering, nest associates, emergence rate, developmental mortality of pupa, and sex ratio of *S. deforme*. Data supported herein considerably enhance the current biological knowledge of the species.

Materials and methods

I carried out field observations and nest collections of the solitary wasp *S. deforme* in both abandoned and human houses and also used trap nests made of hollowed bamboo and reed, 1.0-2.5 cm in diameter and 10-30 cm long and placed on horizontal branches of random plants in the field to collect nests of the wasp in Vinh Phuc, Thai Nguyen, Cao Bang, Ha Giang, Son La, Hoa Binh provinces (Vietnam) from 2018 to 2023.

A total of 129 nests was collected, including 62 nests with final mud cover (mud-covered nests or complete nests) and 67 lacking the final mud cover (mud-uncovered nests or incomplete nests). Of the 129 collected nests, 26 were recently completed nests, 57 were old nests with emergence holes, and 46 were nests without emergence holes. I dissected 16 recently completed nests for aim of examination on nest structure, nest provisioning and nest parasites and took nest contents for examination of the development in the laboratory. The nest contents such as 1) eggs and prey, 2) larvae and prey, and 3) fully developed larvae or cocoons were put in glass tubes, 5 cm long and 1 cm in diameter. Out of the remaining 10 fresh nests collected in the beginning of winter (in

November), five were dissected in February and March to take overwintering cocoons of *S. deforme* for aim of determination of overwintering stage and the five nests were observed until adult emergence after overwintering.

For the 57 old nests with emergence holes (emergence holes of *S. deforme* were round-shaped and 4.2-5.5 mm in diameter; cells containing these emergence holes often contained *S. deforme* cocoon fragments, meconia, and excretory pellets of uric acid), I calculated the emergence rate of the wasp, it (%) = number of cells with emergence holes/total cells of the 57 nests × 100. Forty-three nests without emergence holes were placed intact into plastic boxes, where adults of *S. deforme*, nest parasites, and inquilines that emerged from the nests were allowed to emerge.

To assess longevity of *S. deforme*, an experiment was conducted by using adult wasps that emerged from treatments above. Each individual of *S. deforme* adult was confined in plastic box, 20 cm high and 10 cm in diameter. There were two experimental treatments: males and females without feeding (without food), and males and females with feeding (they were placed with 50% diluted honey). Lifespan was followed for individuals until their death.

To determine mating behaviour of *S. deforme*, newly-emerged adult wasps from treatments above were placed in plastic boxes, 20 cm high and 10 cm in diameter, each containing one male and one female. These wasps were fed on 50% diluted honey.

The sex of adult wasps was determined by counting antennal flagella (11 for males and 10 for females) and gastral segments (7 for males and 6 for females), obtaining the sex ratio = number of males/number of females.

The construction of a nest cell of *S. deforme* was observed in the field on 2 and 3 June 2018 at the Me Linh Station for Biodiversity, Me Linh, Vinh Phuc. After completion of the nest cell, it was picked up and its contents were kept in a glass tube as described above. Time for the construction of the nest cell was determined using a stopwatch SPT-20.

The program IBM SPSS Statistics ver. 26.0 with One-Way ANOVA ($P = 0.05$) was used to test for the longevity difference between sexes reared with 50% diluted honey and without food.

Room temperature and humidity were measured by a CT-138B Max-Min thermohygrometer. Pictures were taken in both the field and laboratory using a Canon camera SD3500 IS. The adult wasps of *S. deforme* were pinned, dried, and deposited in the Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam.

Results

Nesting site

S. deforme usually built its nests on hall curtains (28.7%) (figure 1A), in corners of room (34.11%) (figure 1B), or on the frames of windows (12.40%) (figure 1C). Less commonly they were built in screw recesses of television racks (1.55%) (figure 1D), in crevices between two speakers (3.10%), pantries (2.32%), refrigerators (2.32%), sack bags (3.10%) (figure 1E), trap nests (4.65%) (figure 1F), holes on wooden house poles (2.32%) (figure 1G), water purifiers (1.55%) (figure 1H) and in the sleeves of a coat (4.26%). The red or violet velvet hall curtains, about 6 m long and 4 m high, were usually located on the first floor of the buildings. Fifty-three mud-uncovered nests (both old and fresh) were collected at these sites. The nests were attached within grooves of the folded curtains. The lowest nests were 10 cm above the floor, whereas the highest were constructed close to the ceiling at a height of about 4 m. One hundred nests were collected at human habitations, 25 nests were collected at abandoned houses, and 4 were collected in trap nests (1.5-1.8 cm in diameter and 15-28 cm long) placed on forest trees. All nests were built at 0.5 to 11 m above the ground.

Nesting behaviour

A female of *S. deforme* was found building her nest at 16:56 hours of 2 June 2018. At this time, she had already put three mud balls in the wall corner of the second floor of a 3-story building (about 11 m high). The nesting site was about 8 m above the ground and about 3.2 m from the floor. The nest was contiguous with an old nest of the species. The female held mud balls with her mandibles during flight to the nesting site, sometimes this action being assisted with her forelegs, probably with larger mud balls. The mud balls were about 3 mm in diameter. After putting the mud ball on the cell, the female used her mouth to draw the mud ball out and then used her mandibles to smooth the inside of the cell. Each mud ball made a half of one ring around the cell wall, so that a complete mud ring consisted of two mud balls. At 17:14 hours the wasp stopped building, walked around the cell, as far as about 20 cm from the cell, used her mandibles to groom forelegs and her forelegs to clean her mouth, rested for about one minute, and then flew away. At this time, over third of the cell was completed and undoubtedly the wasp stopped the cell structure to find an overnight sleeping site. Eleven mud-carrying fights were recorded from 16:56 hours to 17:14 hours. In the morning of 3 June, at 8:20 hours the wasp returned to her nest cell without mud. She walked around the cell, used her mouth to revamp the cell, and flew away at 8:27 hours. At 8:29 hours she returned to the cell with nothing and remained there for about nearly two minutes. At 8:34 hours the wasp returned to the cell with a mud ball. At 8:54 hours, when the wasp was absent from the cell, it rained heavily and I did not see the wasp until the rain stopped at 10:00 hours. After that, the wasp continued to bring mud to the cell. At 10:35 hours, the cell was completed. Twenty-eight mud-carrying flights were carried out by the wasp in the morning. Overall, 42 mud-carrying flights were required to build a nest cell. The wasp spent an average time of 51.2 seconds (n = 39, range 24-87 seconds) to collect and transfer mud balls to the nest and then spent a mean of 46.9 seconds (n = 39, range 25-80 seconds) to sculpt the mud on the cell. Consequently, the wasp took a total of 68.7 minutes to complete that nest cell. The mud source that the wasp exploited was at a small pool (about 1 m in diameter) under a faucet in a flower garden, approximately 8 m from the nesting site. During structure of the nest cell, the mud-carrying female usually flew straight to its nesting site from the pool. Clearly, because the proximity of mud of the necessary quality must vary considerably among nest sites, the average time to complete a nest cell must also vary among females of this species.

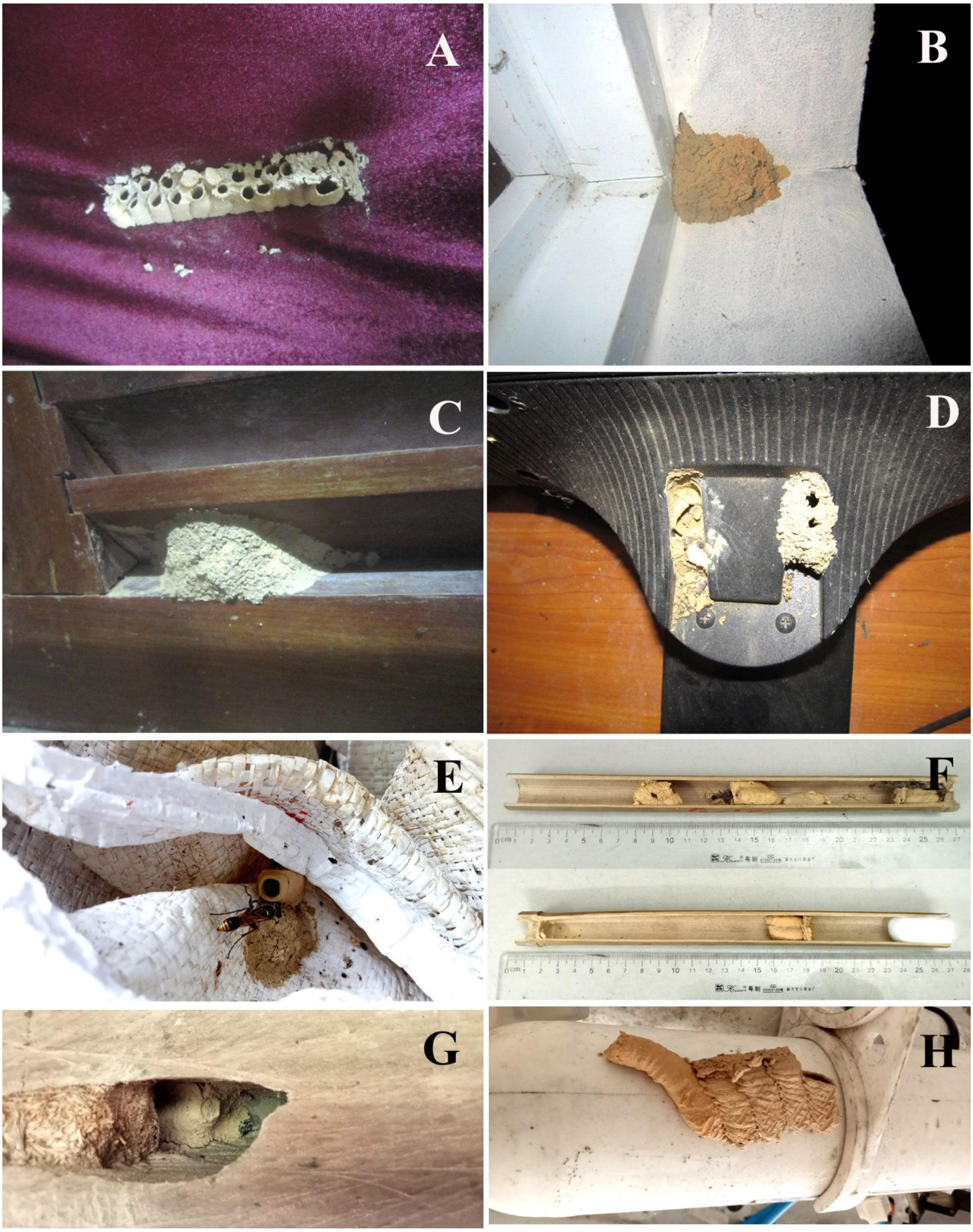

Figure 1. Nesting sites of *S. deforme*. (**A**) On the hall curtain; (**B**) on a wall corner; (**C**) on the frames of window; (**D**) in screw recesses of television rack; (**E**) in a sack bag; (**F**) in trap nests; (**G**) in a hole on wooden house pole; (**H**) on a water purifier.

Nest structure

Nests of *S. deforme* were usually made of the light-yellow mud, cell by cell. The number of cells per nest varied from 1 to 18 (mean = 5 cells per nest) (figure 2; figure 3A, B). Each cell from which a male offspring emerged was 15-23 mm long (mean = 20.17, SD = 1.71, n = 46) and 6-8 mm wide (mean = 6.91, SD = 0.86, n = 46) measured at the middle of the cell. Cells for female offspring were 22-27 mm long (mean = 24.15, SD = 1.61, n=26) and 9-11 mm wide (mean = 9.65, SD = 0.63, n= 26) measured at the middle of the cells. Cells were tubular in shape and cell walls were 1-1.3 mm thick. The inner surface of the cell was usually smooth, but sometime rough whereas rings associated with each mud load were visible as contiguous rings on the outer surface (figure 3C, D). Male cells had 13-15 rings and female cells had 16-18 rings. Cells sometimes varied in shape, being markedly curved because the mother built them on a curved surface. With external mud-covered nests, layers of mud were 3-15 mm thick.

Of 117 nests dissected, five contained a single uncompleted cell that was 50% or more complete (figure 3E, F). It appears that these probably are anomalous cells that the female abandons them when building because of either her death or her reacting to disturbance by people or natural enemies.

Nest provisioning

After completion of a nest cell described above, the *S. deforme* female perched on her nest cell, groomed her mouth and mandibles with the forelegs and her antennae with the mandibles for about two minutes, and then flew away. At 10:57 hours, she returned to the nest cell without prey, entered into it, head first, stepped backward, walked around the nest cell, and took orientation flight of two circuits, only about 15 cm away from the nest cell, and then flew away. At 11:05 hours, the wasp returned to the nest cell with a paralyzed spider prey which she held in her mandibles, entered into the cell, head first, and spent about 15 seconds depositing prey, and then flew away. At 11:25 hours, the wasp returned to the nest cell without prey, entered into for about 20 seconds, and then flew away. At 11:35 hours, she went back into the nest cell with another spider prey for near 20 seconds, and then left. From this time on to 15:06 hours, nine prey-carrying flights were recorded, each alternating flight in which no prey were brought to the cell. After placing the last prey into the cell, the wasp plugged the cell entrance with three mud balls, and rested for about 2 minutes, 5 cm away from the nest cell. At this time, I captured the female and collected the nest cell.

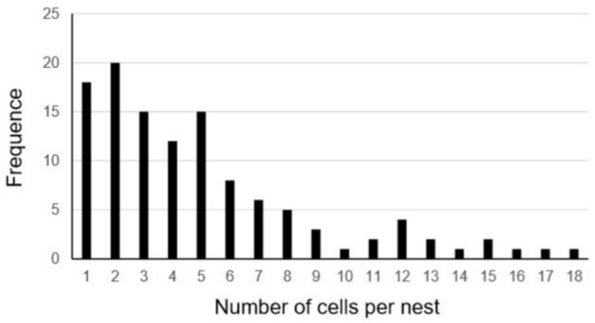

Figure 2. Frequency distribution of number of cells per nest of *S. deforme*.

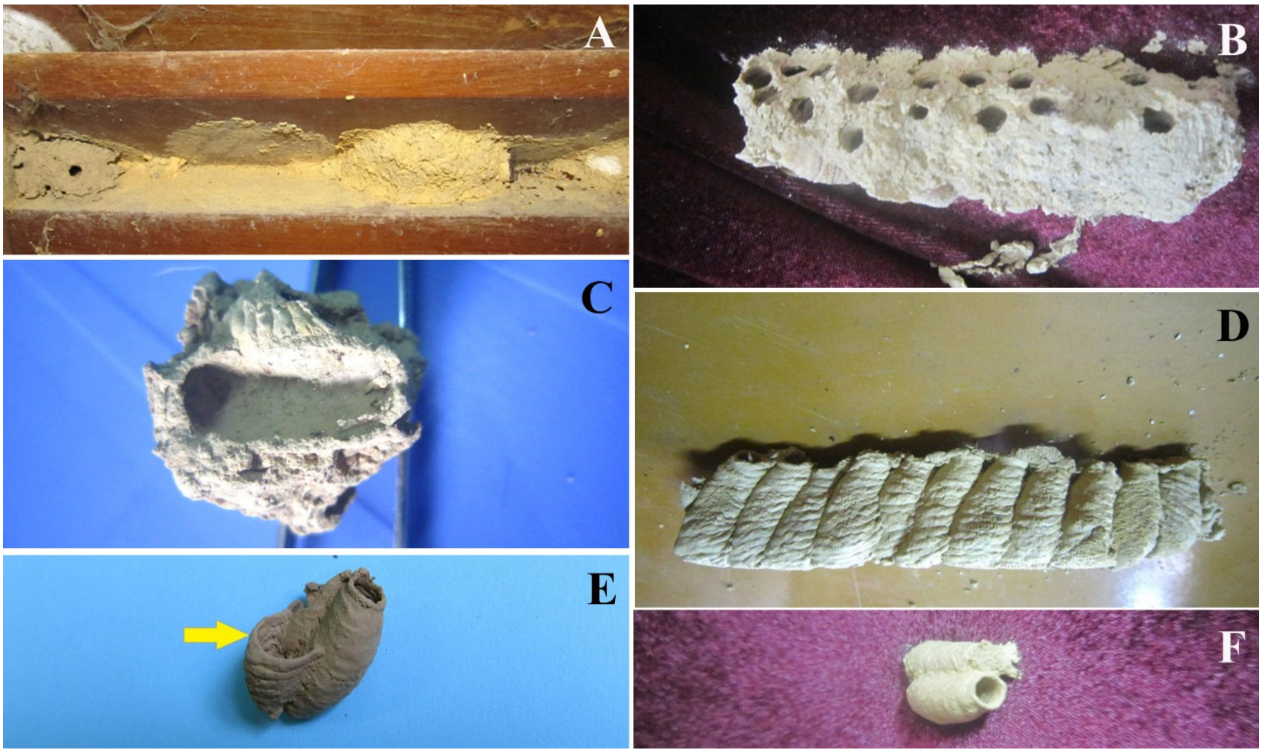

Figure 3. Nest structure of *S. deforme*. (**A**) Nest with one cell; (**B**) nest with 18 cells; (**C**) the inside of a nest cell; (**D**) the outside of nest cells; (**E**) incompleted nest cell; (**F**) completed nest cell without provisioning.

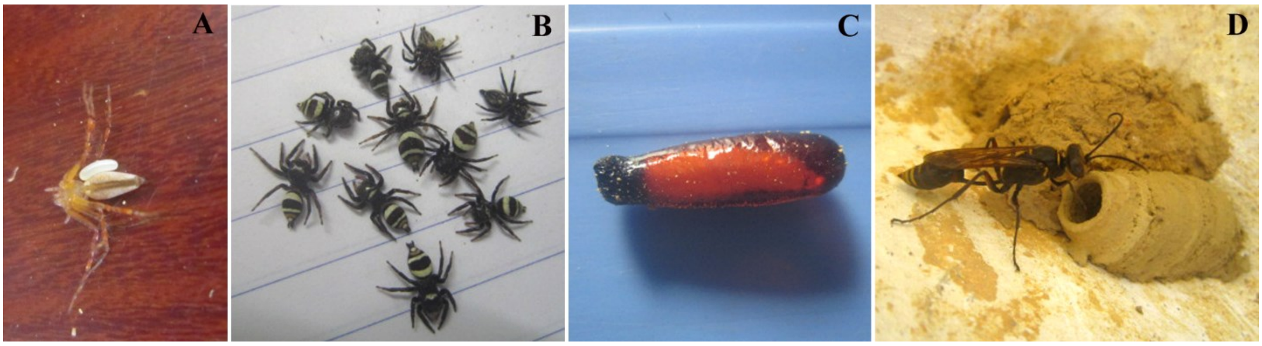

Figure 4. Nest contents and female of *S. deforme*. (**A**) Egg attached on prey; (**B**) spider prey *P. strupifer*; (**C**) cocoon; (**D**) female.

When the nest cell was opened on 4 June 2018 (two days after it was initiated by the female), it contained an egg and 11 spider prey, the egg being laid on the third prey counted from the inner end of the nest cell. The egg was attached to the left side of the prey's abdomen, but it extended backward (figure 4A).

Of five cases of other dissected nests, the eggs were all glued on the left side of the prey's abdomen. The prey's number of 10 other nest cells varied from 8-10 (mean = 9.5, SD = 0.27, n = 10). The spider prey were identified as follows: *Ptocasius strupifer* Simon (n = 95) (figure 4B) (a common spider species in North Vietnam), of the family Salticidae, and *Oxyopes* sp. (n = 38) of the family Oxyopidae. Prey provisioned in a nest cell were either only *P. strupifer* (n = 8) or both *P. strupifer* and *Oxyopes* sp. (n = 5).

Of 117 nests dissected, 33 contained one empty cell each (cells were not provisioned with spider prey). Of these, 25 were of mud-covered and eight were mud-uncovered nests.

Development

The egg, 2.2-2.5 mm long (mean = 2.3, SD = 0.11, n = 7) and 0.7-0.8 mm wide (as measured at the middle) (mean = 0.73, SD = 0.05, n = 7), was white, cylindrical, and moderately curved (figure 4A). Eggs hatched 2 days after being laid (n = 5). The larvae, translucent yellowish white, required 5-6 days (mean = 5.54, SD = 0.52, n = 13) to consume all provisions in the cell. The last instar larvae required more than one day to spin cocoons (n = 19). The cocoon was reddish brown, hyaline, and glossy (figure 4C). After completion of the cocoon, the larvae began to expel excretions at the bottom of the cocoon. This process took about one day (n = 25). The prepupa stage required about 3 days (n = 36). The pupa stage lasted 14-15 days (mean = 14.59, SD = 0.50, n = 32). Therefore, the total development time from the egg to emergence of the adult wasp (figure 4D) was 26-28 days (mean = 27.13, SD = 0.51, n = 32) under laboratory conditions.

Mating behaviour

In the laboratory, females of *S. deforme* each copulated only once (n = 21), just immediately after emergence. When placing a female in plastic boxes containing a male, he immediately pounced upon her with holding her pronotum with his mandibles (n = 21), placing his forelegs and midlegs on the both sides of her mesosoma just posterior to her forelegs and anterior to her hindlegs, respectively, and his hindlegs straddling her abdomen, just posterior to her hindlegs. The male bent his abdomen and attempted to clasp the female's genitalia from above. The copulation time ranged from 45 to 82 seconds (mean = 59.73, SD = 11.47, n = 15). In two instances, the male pounced upon the female with holding the base of her fore femora with his mandibles. In six cases, when two or three males were placed in a plastic box, conflicts usually took place. They pursued, grasped, and struggled each other, usually biting the hindlegs. As a result, smaller or weaker males were usually broken their hindlegs and died two or three days later.

Longevity

After emergence, under laboratory conditions, with no food provided, the adult males lived from 1-2 days (mean = 1.55 ± 0.52, n = 10) and adult females lived 1-2 days (mean = 1.80 ± 0.42, n = 10), and with 50% diluted honey, the adult males lived 3-12 days (mean = 77.98 ± 2.18, n = 20) and the adult females lived 5-29 days (mean = 20.08 ± 5.57, n = 20) at the mean laboratory temperature and relative humidity of 29.8 °C and 78.8%, respectively (table 1).

There were no significant differences between the longevity of males and females without and with food provided (SPSS statistics, One-Way ANOVA $df = 1$, $F = 0.46$, $P = 0.833$; $df = 17$, $F = 0.529$, $P = 0.908$, respectively), but there were significant differences between the longevity of individuals (both males and females) without and with food provided (SPSS statistics, One-Way ANOVA $df = 7$, $F = 1.102$, $P = 0.038$).

Overwintering

In North Vietnam, the winter and spring normally lasts about six months, from November to April of the following year, low temperatures range from 6 to 17 °C. The start of the overwintering stage of *S. deforme* was unknown. Five fresh nests (No. 31, 38, 91, 98 and 111) collected on 3 November 2018 and 9 November 2022 and dissected on 21 February 2019 and 2 March 2023, respectively contained 19 cocoons with prepupae suggesting that the wasp overwinters in the prepupa stage. Seven adult male and 10 adult female wasps emerged from the

Table 1. Longevity of *S. deforme*.

Treatment time	Longevity				Temperature (°C)	Humidity (%)
	without food		with 50% diluted honey			
	Male (n = 10)	Female (n = 10)	Male (n = 20)	Female (n = 20)		
May 2019	1-2 1.60 ± 0.51	1-2 1.80 ± 0.42	3-10 7.60 ± 1.93	5-27 19.90 ± 5.93	28.5	82.3
July 2022	1-2 1.50 ± 0.53	1-2 1.8 ± 0.42	4-12 8.35 ± 2.43	7-29 20.25 ± 5.21	31.2	75.4
Average (Mean ± SD)	1.55 ± 0.52 a	1.80 ± 0.42 a	7.98 ± 2.18 b	20.08 ± 5.57 b	29.8	78.8

Mean ± SD followed by the different letter in average differ by IBM SPSS 26 analysis test, One-Way ANOVA ($P = 0.05$).

Table 2. Nest construction and content of 16 fresh nests observed under laboratory conditions.

No.	Cell number	Emerged adult number		Empty cell	Failed cell	Pupal death	Parasitized cell
		Female	Male				
1	12	2	5	1	1	2	1*
2	3	1	-	1	-	-	-
3	9	5	-	2	1	-	-
4	3	1	-	-	2	-	-
5	2	1	-	1	-	-	-
6	4	1	-	1	2	-	-
7	7	3	1	2	1	-	-
8	8	5	1	1	-	1	-
9	2	1	-	1	-	-	-
10	2	-	-	1	-	-	1**
11	5	2	2	-	1	-	1***
12	8	-	7	1	-	-	-
13	4	1	1	1	-	1	-
14	5	-	3	-	-	1	1***
15	1	-	-	-	-	1	-
16	15	9	4	-	-	2	-
Total	90	32	24	13	8	8	4

* Cell parasitized by *Chrysis* sp.; ** cell parasitized by *C. japonicum*; *** cell parasitized by *Euchalinus* sp.

cocoons between 14 and 21 April 2019 and 19 and 28 April 2023 suggesting that this may be the typical end of the overwintering stage. Although many adults of five the other nests emerged in April 2019 and 2023, several emerged in June 2023 and this may be due to laboratory conditions.

Nest associates

Three parasitic wasps, *Chrysis* sp. (Chrysididae) (11 nests), *Melittobia sosui* Dahm (Eulophidae) (14 nests), and *Euchalinus* sp. (Ichneumonidae) (4 nests) were found from 23 of 129 *S. deforme* nests. All three were from 62 mud-covered nests and only *Euchalinus* sp. was picked up from eight of 67 mud-uncovered nests. In addition, many small dark brown cocoon shells, about 2 mm long and 0.6 mm wide, and three brown cocoon shells, about 6 mm long and 3 mm wide were found from at least six cells of five old mud-covered nests guessing that they probably are cocoons of parasitic flies (Sarcophagidae).

Whereas several dead adults (both brachypterous females and males) of *M. sosui* were picked up from one cocoon of an old nest, many adults and pupae of the parasitoid were picked up from two cocoons of a fresh nest (table 2). *M. sosui* parasitized on prepupae of *S. deforme* and completely consumed this host. An inquiline *Chalybion bengalense* (Dahlbom) (Hymenoptera Sphecidae) was found into two old mud-covered nests, one containing four overwintering cocoons that gave rise to adult wasps on 11 and 12 April 2019, one containing one cocoon shell and one dead adult wasp. A nest invader *Chalybion japonicum* (Gribodo) (Hymenoptera Sphecidae) was found in three fresh nests of *S. deforme*. Five adult wasps of the species emerged from two nests in July 2018 and two male adult wasps emerged from the other in March 2019. In one case of observation, when *S. deforme* was inspecting the nest cell observed above, a female *C. japonicum* came and attempted to enter the nest cell, immediately *S. deforme* rushed at her, and then pursued her, as far as about 5 m from the nest cell. During the trailing flight, *S. deforme* made a loud buzzing sound.

Out of 90 cells of 16 fresh nests dissected, seven cells belonging to six nests were taken by the four parasitoid wasps described above giving a nest parasitoid ratio of 37.5% (6/16) (table 2).

Emergence rate and developmental mortality of pupa

Out of 79 provisioned cells of the 16 dissected fresh nests (table 2) built on the wall corners and windows, 56 cells contained *S. deforme* cocoons that produced adult wasps, an emergence rate of 70.9% (56/79). Of 261 provisioned cells of 57 nests not covered with mud built on the hall curtain, 197 cells contained emergence holes of *S. deforme*, an emergence rate of 75.5% (197/261).

Out of 79 provisioned cells, except 8 failed cells and 7 parasitized cells, 64 cells contained pupal cocoons, of these 8 took dead pupal cocoons, resulting a developmental mortality of pupa of 12.5% (table 2).

Sex ratio

The emergence order of sexes on six nests was as follows: nest 1: ♂, ♂, ♂, ♂, ♀, ♂, ♀; nest 7: ♂, ♀, ♀, ♀, nest 8: ♀, ♀, ♀, ♂, ♀; nest 11: ♂, ♀, ♂, ♀; nest 13: ♂, ♀; and nest 16: ♀, ♀, ♀, ♀, ♂, ♂, ♂, ♂, ♀, ♀, ♀, ♀, ♀. Consequently, emergence of sexes follows no consistent order and the sex ratio varied among the nests. The sex varied among the nests, only male or female or both per nest (table 2). A total of 56 adult wasps, 32 adult females and 24 adult males, emerged from the 16 nests reared (table 2) giving a sex ratio of 0.75 (male/female).

Discussion

S. deforme uses a variety of sites in houses in which its nests are built. Rudow (1912) recorded the nesting site of this wasp (as *Pelopaeus tibialis* F.) on a wall in Tanzania, Strand (1914) observed a nest built in a house corner in Taiwan, and Basil-Edwardes (1921) showed several nests glued on various parts of the ceiling in India. Williams (1919) observed the mud-dauber wasp constructing nests after a book case and on wall poles in bamboo houses in Philippines. Iwata (1939) reported nesting sites of the species on the walls in Taiwan. Kazenas *et al.* (2005) and Kazenas (2013) showed numerous nesting sites of the wasp in Kazakhstan, such as under the beams in attics, in the room corners, under the eaves, in the closets, racks, shelves and boxes, inside rolled carpets, etc. Recently, Ćetković *et al.* (2011) reported nests of *S. deforme* in the room of a tourist resort house in Greece. In this study, *S. deforme* took many nesting sites, especially dark and hidden sites such as in the sleeves of a coat, on velvet hall curtains, in sack bags, and in trap nests, which are new nesting sites reported for the wasp. From nesting sites having been reported, it is clear that *S. deforme* is a common domestic sphecid wasp and its nesting sites are associated with human habitations.

The nesting sites of *S. deforme* are common in *Sceliphron* (mostly sheltered situations). Freeman (1974) and Hunt (1993) reported *Sceliphron assimile* (Dahlbom) building its nests on cliffs, in buildings, under bridges, on caves, and in a wooden cabinet housed in an open, roofed shed in Jamaica and Costa Rica. Callan (1988) observed *Sceliphon formosum* (Smith) nesting on walls of a garage and a human house in Australia. *Sceliphron caementarium* (Drury) builds its mud nests on walls of buildings and abandoned cars, in other human constructions, and under bridges in Missouri, USA (Ferguson and Hunt, 1989). Polidori *et al*. (2005) and Chatenoud *et al*. (2012) recorded nesting sites of *Sceliphron spirifex* (L.), *S. caementarium*, *Sceliphron curvatum* (Smith), *Sceliphron madraspatanum* (F.), and *Sceliphron destillatorium* (Illiger) in farms in Italy. Fateryga and Kovblyuk (2013) reported *S. curvatum* building its nests in human houses in Kiev and the Crimea. *Sceliphron asiaticum* (L.) nests in houses in Brazil (de Carvalho *et al*., 2014). Unusually, Gess and Gess (2014) recorded *Sceliphron quartinae* (Gribodo) and *Sceliphron fossuliferum* (Gribodo) building their nests on plant stems.

Except the nesting site on the hall curtains mentioned above, I found that *S. deforme* usually nests gregariously at wall corners, on walls or on wooden windows and it establishes a cluster of nests, usually 2-3 nests and sometimes up to 5 nests. Hunt (1993) reported *S. assimile* nesting aggregately in a wooden cabinet placed in an open, roofed shed in Costa Rica and he collected its 866 nests at this cabinet. Aggregative nesting in *Sceliphron* is not much known. The aggregative nesting of *S. deforme* may be only an instinctive action when its progeny emerges from a nest and take a similar site for building their nests. This action possibly leads to reducing energy for nesting females because they do not need spending many times to find nesting sites. However, a cost to be paid is that in three cases I found adult progeny of *S. deforme* emerging impossibly exiting their nests and died in their own nests because their nests had been covered by nests of other conspecific females. These emerging adult wasps cannot perforate mud walls of those nests.

Anomalously, I observed *S. deforme* adult females in four cases plugging pre-existing holes of old nests without provisioning them with spider prey. It may be to suggest that this action is either to deceive its natural enemies when it leads them to false nests or to react immediately to disturbance of natural enemies during nesting time of the wasp. At this time, no evidence is available and it needs, hence, to clear this in future studies.

More than 35% of collected nests of *S. deforme* contained usually one empty cell each (sometimes two). These empty cells may be "accessory burrows or false cells". The accessory burrow is reported for many ground nesting species of various genera of the family Sphecidae such as *Sphex argentatus* F. (Tsuneki, 1963), *Sphex sericeus* (F.) (Krombein, 1984), *Sphex ephippium* Smith (Evans *et al*., 1982), *Sphex ichneumoneus* (L.) (Brockmann and Dawkins, 1979), *Ammophila aberti* Haldeman (Parker *et al*., 1981), and *Ammophila harti* (Fernald) (Hager and Kurczewski, 1986). Several hypotheses relevant to the function of accessory burrows have been presented. Tsuneki (1963) stated that the function of accessory burrows is to overreach parasites. Tepodino *et al*. (1979) thought that abandoned cells may discouraged parasites from searching further in the immediate area. Hager and Kurczewski (1986) reported that species intend to cluster their nests in a small area, they then make usually false burrows or empty cells. This is to reduce parasitism.

The successful adult emergence rate of *S. deforme* in this study varied from 70.9% to 75.5%. I access that this is a rather high emergence ratio as compared to the emergence ratio of several other wasps, for example *S. assimile* being 59.9% in Jamaica (Freeman, 1973), various stem-nesting aculeates 50-60% in London, England (Danks, 1971) and the solitary bee *Osmia rufa* (L.) 58% in England (Rau, 1972). Explanations for the high emergence ratio in this study have possibly included 1) absence of natural enemies in the protected rearing environment (nest contents were kept in glass tubes and except for parasites already present, nothing can infiltrate into these nest contents) and 2) nesting-site change. Aggregative nesting of *S. deforme* at light sites such as on walls and windows lead to a successful emergence ratio of 70.9% compared to a higher successful emergence ratio of 75.5% when its scattered nesting is at dark sites on velvet hall curtains. Freeman (1973) showed that the mean mortality during development of *S. assimile* varying from 11.4% at sites with the least density of cells (<1/m^2) to 55.6% at those with the greatest cell density (>100/m^2). Freeman and Parnell (1973) stated that *Melittobia chalybii* Ashmead accounts for an average of 76% of the developmental mortality of *S. assimile* in Jamaica. In North Vietnam, *M. sosui*, a common parasitic wasp (Pham *et al*., 2023), attacked the prepupal stage of *S. deforme* and dense nest clusters of *S. deforme* at the same site may be a suitable condition for attacking a large number of cocoons by the parasitoid.

Conclusions

The present work produces biological data of *S. deforme* collected in many years in Vietnam. The wasp took a variation of nesting sites, mostly in sheltered situations associated with human habitations. Females spent more than one hour to build a mud cell and then provisioned it up to 11 paralyzed spiders. The total development time from the egg to emergence of the adult wasp was about one month. Whereas males lived only more than one week, females lived about four weeks with 50% diluted honey provided and copulated only once, just after emergence. *S. deforme* overwintered as prepupae and ended this overwintering stage about mid-April. The sex ratio was female-biased, the emergence rate was about 70% and the developmental mortality of pupa was up to 12.5%. Parasites of *S. deforme* included wasps and flies, and the nest parasitoid ratio was 37.5%. These data can be used to aid in phylogenetic studies and the evolution of nesting behaviour in *Sceliphron*.

Acknowledgements

The author is grateful to Kevin M. O'Neill, Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, USA for his comments, suggestions, and corrections of the English language on the manuscript, and to Khuc Thi Ut for her help in looking after bioassays in the laboratory. I thank Nhi Thi Nguyen and Luong Thi Hong Phung, Institute of Ecology and Biological Resources, Hanoi, Vietnam for the identification of spiders and an ichneumonid parasitoid wasp, respectively. I am greatly indebted to Stefano Maini and two anonymous reviewers for their thoughtful comments and suggestions, which greatly improved the original manuscript. This research is funded by Vietnam National Foundation for Science and Technology Development (NAFOSTED) under grant number 106.05-2021.26.

References

BASIL-EDWARDES S., 1921.- On the habits of a *Sceliphron* wasp (*S. deforme*).- *The Journal of the Bombay Natural History Society*, 28: 293-297.

BOHART R. M., MENKE A. S., 1976.- *Sphecid wasps of the world: a generic revision*.- University of California Press, California, USA.

BROCKMANN H. J., DAWKINS R., 1979.- Joint nesting in a digger wasp as an evolutionarily stable preadaptation to social life.- *Behaviour*, 71: 203-245.

CALLAN E. M. C. C., 1988.- Biological observations on the mud-dauber wasps *Sceliphron formosum* (F. Smith) (Hymenoptera: Sphecidae).- *Australian Entomological Magazine*, 14: 78-82.

ĆETKOVIĆ A., MOKROUSOV M. V., PLEĆAŠ M., BOGUSH P., ANTIĆ D., ĐOROVIĆ-JOVANOVIĆ L., KRPO-ĆETKOVIĆ J., KARAMAN M., 2011.- Status of the potentially invasive Asian species *Sceliphron deforme* in Europe, and an update on the distribution of *S. curvatum* (Hymenoptera: Sphecidae).- *Acta Entomologica Serbica*, 16: 91-114.

CHATENOUD L., POLIDORI C., FEDERICI M., LICCIARDI V., ANDRIETTI F., 2012.- Mud-ball construction by *Sceliphron* mud-dauber wasps (Hymenoptera: Sphecidae): a comparative ethological study.- *Zoological Studies*, 51: 937-945.

DANKS H. V., 1971.- Nest mortality factor in stem-nesting aculeate Hymenoptera.- *The Journal of Animal Ecology*, 40: 79-82.

DE CARVALHO L. M., BEVILAQUA V. O., QUERINO R. B., 2014.- An observation of the parasitoid *Melittobia australica* Girault (Hymenoptera: Eulophidae) and its host, the solitary wasp *Sceliphron asiaticum* (Linnaeus) (Hymenoptera: Sphecidae).- *Entomologica Americana*, 120: 43-46.

EVANS H. E., HOOK A. W., MATTHEWS R. W., 1982.- Nesting behaviour of Australian wasps of the genus *Sphex* (Hymenoptera, Sphecidae).- *Journal of Natural History*, 16: 219-255.

FATERYGA A.V., KOVBLYUK M. M., 2013.- Nesting ecology of the digger wasp *Sceliphron curvatum* (F. Smith, 1870) (Hymenoptera, Sphecidae) in Ukraine.- *Euroasian Entomological Journal*, 12: 309-314.

FERGUSON C. S., HUNT J. H., 1989.- Near-nest behavior of a solitary mud-daubing wasp, *Sceliphron caementarium* (Hymenoptera: Sphecidae).- *Journal of Insect Behavior*, 2: 315-323.

FREEMAN B. E., 1973.- Preliminary studies on the population dynamics of *Sceliphron assimile* Dahlbom (Hymenoptera: Sphecidae) in Jamaica.- *Journal of Animal Ecology*, 42: 173-182.

FREEMAN B. E., 1974.- The distribution in Jamaica of the mud wasp *Sceliphron assimile* Dahlbom (Sphecidae) and its associates.- *Caribbean Journal of Science*, 14: 115-124.

FREEMAN B. E., PARNELL J. R., 1973.- Mortality of *Sceliphron assimile* Dahlbom (Sphecidae) caused by the eulophid *Melittobia chalybii* Ashmead.- *Journal of Animal Ecology*, 42: 779-784.

GESS S. K., GESS F. W., 2014.- *Wasps and bees in southern Africa*. SANBI Biodiversity Series 24.- South African National Biodiversity Institute, Pretoria, South Africa.

HAGER B. J., KURCZEWSKI F. E., 1986.- Nesting behavior of *Ammophila harti* (Fernald) (Hymenoptera: Sphecidae).- *The American Midland Naturalist*, 116: 7-24.

HUNT J. H., 1993.- Survivorship, fecundity, and recruitment in a mud dauber wasp, *Sceliphron assimile* (Hymenoptera: Sphecidae).- *Annals of the Entomological Society of America*, 86: 51-59.

Iwata K., 1939.- Habits of some solitary wasps in Formosa (IV).- *Transactions of the Natural History Society of Formosa*, 29: 161-178. [in Japanese].

Kazenas V. L., 2013.- *Animals of Kazakhstan in photographs. Digger wasps (class Insecta, order Hymenoptera)*.- Tovarishchestvo s ogranichennoy otvetvennost'yu “Nur-print”, Almaty, Kazakhstan. [in Russian].

Kazenas V. L., Egorov P., Aldiyarov S., 2005.- Biology and ecology of digger wasp *Sceliphron deforme* Smith (Hymenoptera, Crabronidae) in Southeast Kazakhstan.- *Selevinia*, 2004: 163-165. [in Russian, with summary in English].

Krombein K. V., 1984.- Biosystematic studies of Ceylonese wasps, XII: behavioral and life history notes on some Sphecidae (Hymenoptera: Sphecoidea).- *Smithsonian Contributions to Zoology*, 387: 1-30.

O'Neill K. M., 2001.- *Solitary wasps. Behavior and natural history*.- Comstock Publishing Associates, Ithaca and London, UK.

Parker F. D., Tepedino V. J., Vincent D. L., 1981.- Observations on the provisioning behavior of *Ammophila aberti* Haldeman (Hymenoptera: Sphecidae).- *Psyche*, 87: 249-258.

Pham P. H., Nguyen H. T., Nguyen T. M., Truong X. L., Nguyen Q. C., 2023.- Redescription of the parasitic wasp *Melittobia sosui* Dahms, 1984 (Hymenoptera: Eulophidae), with records on its new hosts in Vietnam.- *Russian Entomological Journal*, 32 (2): 181-186.

Polidori C., Trombino L., Fumagalli C., Andrietti F., 2005.- The nest of the mud-dauber wasp, *Sceliphron spirifex* (Hymenoptera, Sphecidae): application of geological methods to structure and brood cell content analysis.- *Italian Journal of Zoology*, 72: 153-159.

Polidori C., Federici M., Pesarini C., Andrietti F., 2007.- Factors affecting spider prey selection by *Sceliphron* mud-dauber wasps (Hymenoptera: Sphecidae) in northern Italy.- *Animal Biology*, 57: 11-28.

Pulawski W. J., 2024.- Number of species in Sphecidae (sensu lato).- California Academy of Sciences. [online] URL: http://researcharchive.calacademy.org/research/entomology/entomology_resources/hymenoptera/sphecidae/genera/Sceliphron.pdf (last accessed March 8, 2024).

Rau A., 1972.- The biology of the solitary bee *Osmia rufa* (L.) (Megachilidae).- *Transactions of the Royal Entomological Society of London*, 124 (3): 213-229.

Rudow F., 1912.- Lebensweise und nestbau der Raub=, Mord= und Grabwespen, Sphegidae und Crobronidae (Fortsetzung).- *Entomologische Zeitschrift*, 26: 42-44. [in German].

Smith F., 1856.- *Catalogue of hymenopterous insects in the collection of the British Museum. Part IV. Sphegidae, Larridae and Crabronidae*.- Taylor and Francis, London, UK.

Strand E., 1914.- Ueber das Nest von *Sceliphron deforme* Sm.- *Archiv für Naturgeschichte (Abteilung A)*, 80 (10): 116-117. [in German].

Tepedino V. J., Mc Donald L. L., Rothwell R., 1979.- Defense against parasitization in mud-nesting Hymenoptera: can empty cells increase nest reproductive output?- *Behavioral Ecology and Sociobiology*, 6: 99-104.

Tsuneki K., 1963.- Comparative studies on the nesting biology of the genus *Sphex* (s.l.) in East Asia (Hymenoptera, Sphecidae).- *Memoirs of the Faculty of Liberal Arts, Fukui University (Series II, Natural Science)*, 13: 13-78.

Williams F. X., 1919.- Philippine wasps studies. Part II. Descriptions on new species and life history studies.- *Bulletin. Reports of Work of the Experiment Station of the Hawaiian Sugar Planters' Association. Entomological Series*, 14: 19-186.

Author’s address: Phong Huy Pham, Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Cau Giay, Ha Noi, Vietnam (phong.wasp@gmail.com).

Received April 15, 2024. Accepted September 24, 2024.