

Original Article

Nesting Biology and Behavior of *Euodynerus dantici* (Rossi, 1790) (Hymenoptera: Vespidae: Eumeninae) in Central Mongolia

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Abstract

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Nesting biology of *Euodynerus dantici* (Rossi, 1790) was studied in the Khugnu-Khaan Mountains of Khugnu-Tarna National Park, central Mongolia in 2014 using nest traps. *Euodynerus dantici* is univoltine in the study site, with one generation per growth season. Nest architecture and its structural parts were described in details. The inner cells of the nests were longer and contained a proportionately larger amount of food than the shorter outer cells. Females developed in inner cells and males developed in outer cells. Developmental stages of *E. dantici* is studied with details of pupation period. All basic behavioral elements of nesting females are described. A nest parasitoid, *Chrysis ignita* (Linnaeus, 1758) (Hymenoptera, Chrysididae) was reared from *E. dantici* nests for the first time. For provisioning, caterpillars of the family Noctuidae (Lepidoptera) were hunted by females. Diversity in nest architecture is possibly a result of nest parasite pressure.

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Introduction

Euodynerus dantici (Rossi, 1790) is a solitary wasp of the family Vespidae (Hymenoptera), widely distributed in the Palearctic region. In Mongolia, this species is recorded only from Khovd, Bulgan and Umnugovi provinces (Buyanjargal *et al.*, 2013). As all other vespid wasps, *E. dantici* provisions food in the nest after laying eggs. The egg is suspended from the ceiling by a thin flexible stalk (Krombein, 1967). As most other hunting wasps in temperate areas, *E. dantici* survives cold winters as prepupae within nest cells, emerging as adults only with the return of favorable conditions during the following summer. The nest of *E. dantici* consists of a consecutive row of provisioned cells

separated by transverse partitions made of mud as in other tube-renters (Blüthgen, 1961; Iwata, 1976; Fateryga, 2012). Nesting biology of this species was studied by Iwata (1976) in Japan and Fateryga (2012) in Crimea (formerly Ukraine, currently Russia). However, the nesting biology, including larval development of this species has still in sufficiently been studied, especially in the arid region. The main aim of this study is to reveal the nesting biology and behavior of *E. dantici* in a dry country, Mongolia. In order to achieve this aim, the following purposes were set up:

- to describe the nest structure,
- to measure the difference in cell size and

amount of provisioned prey in cells between the sexes of broods, and difference in the duration of pupal development between the sexes,

- to observe and explain main behavioral elements, and to quantify the diurnal activity of the female in the period of nesting.

Materials and Methods

The study was conducted in the Khugnu-Khaan Mountain of Khugnu-Tarna National Park in Rashaant district of Bulgan province, central Mongolia, from the beginning of July to the end of August in 2014; this period was chosen based on preliminary observations made in 2013. The study area belongs to the steppe region of Mongolia (Yunatov, 1977). For prey and parasitoid identification, we used keys by Medvedev (1978) and Mamaev (1972).

Nesting aggregations. Two nesting aggregations were found on walls (2 m wide and 4 m high) of ancient monasteries (from 16th century) made of yellow mud. The walls were faced sun exposure and sheltered from wind by sidewalls. The target species nests were located only up to 80 cm in height, where the density of holes and small cavities (5-7 mm in diameter) were highest. Origin of those holes is uncertain, but they were possibly bored by other species of wasp or bee.

Trap nest. Trap-nest technique is very efficient to study nesting biology of solitary wasps and bees. We prepared trap nests similar to those used by Krombein (1967). A hole, 5.5 or 6.5 mm in diameter and 90 mm or 152 mm in deep, was bored in a pine wood piece (25 mm x 25 mm x 165 mm). We rolled the traps

in a very shallow bath of melted paraffin so that the outsides were coated with wax. The wax protected them from molding caused by frequent rain. We bundled three to eight traps into a block and placed it in front of the first nesting aggregation (Fig. 1, left). We also prepared an artificial block made of yellow mud, measuring 80(height) x 18(depth) x 100cm (width). Twenty-four holes, 3.5(height) x 3.5 (width) x 16.5 cm (depth), were bored in the mud block to house wooden trap nests; the block was placed 10 cm apart from the second nesting aggregation (Fig. 1, right).

Nest study. When the traps were occupied by wasps, we replaced them with new traps of the same size. The collected traps were opened in the laboratory by inserting a jack-knife at the blind end of the trap and, by twisting the blade, to split the trap with the grain of the wood along the longitudinal axis of the boring (see Krombein, 1967). Egg or larval size was measured and the number of provisioned prey were counted for every brood cell. Also all nest architectural parts were measured with calipers and the data were filled in nest scheme sheets. After observations, nests were wrapped with tapes and located outside to supply normal diapausing. After the larvae changed to prepupae, we placed them separately into glass tubes of which both ends were closed with cotton. The nest and cell codes were written on each tube. The larvae in the tubes were observed under laboratory condition with 25-28°C and 30% humidity for subsequent development. When adults emerged, the sex was identified. Differences between measurements were tested with 2 sampled t-test using stat soft Minitab13.



Fig. 1. Bundled trap nests occupied by females of *E. dantici* (left), trap nests inserted in artificial mud block (right) set up in front of nesting aggregations of *E. dantici*.

Observation. We observed 19 trap-nesting females from 28th July to 8th August in the two nest aggregation sites. The nesting behavior was observed every day from 10AM to 06PM. To detect all the basic behavioral elements of trap-nesting females, we recorded the exact starting and ending time of every activity and their position when the activity is occurred.

Results

A total of 69 trap nests were occupied by nesting females of this species. However, eleven of the nests were just closed with plugs and empty inside.

Nest architecture. The following parts were built in the trap nest by the female: Preliminary plug, series of provisioned cells, cell partitions and closing plug. Females use mud as building material. The measurements for those structural parts are summarized in Table 1. A preliminary plug was made at variable distances from the inner end (in 23 nests), with an empty space left in the end of the boring.

After provisioning the first cell, a partition is built, followed by the provisioning of the next cell. Empty cells (intercalary cells) interspersed

between provisioned cells were found in five nests. When the female closed the last cell with a partition, she leaves an empty space, a vestibular cell at the outer end of the boring. We found four nests where a vestibular cell was divided into two sections. The vestibular cell was capped with a closing plug that is usually thicker than the partitions. In 22 nests the closing plug varied little in thickness (3-4 mm). Closing plugs may consist of 1-3 layers, which almost touched each other. The cell number observed was variable, from 1 to 6, with the most common number, 2 (in 13 nests).

Diversity in architecture was high in the nest of *E. dantici*. Sixteen different types of nest architecture were observed among 58 nests. The most common type was observed in 12 nests containing a vestibular cell and a closing plug, but without preliminary plug and intercalary cells (Fig. 2). The variation in nest architecture is summarized in Table 2. There was no observable relationship between nest architecture and success of nests.

Relationship between wasp sex and cell size and amount of provisioned prey. In total 45 individuals successfully emerged to adults. Among them 25 (55.5%) were males and 20

Table 1. Nest structure variables of *E. dantici*.

Variables	N	Min-Max	Mean±SD
Preliminary plug thickness (mm)	27	0.35-4.2	1.6 ± 0.9
Length of empty space (mm)	23	4.5 – 96	45.3± 33.9
Provisioned cell number	54	1-6	3.2 ± 1.6
Cell partition thickness (mm)	52	1-4.1	2.3 ± 0.9
Intercalary cell length (mm)	5	13.6-32.1	23.8 ± 7.5
Vestibular length (mm)	54	5.2-121.9	52.6±31.5
Closing plug thickness(mm)*	47	1.1-6.4	3.4±1.3

*Thickness of outermost layer when closing plug consists of 2 or 3 layers



Fig. 2. *Euodynerus dantici* nest; this type was common and seen in 12 nests. Eggs are seen in lower section of nest in cells 2, 4 and 5. The prey (noctuid caterpillars) are seen in upper section of nest.

Table 2. Variation in nest architecture.

Type of nest architecture	Frequency	Type of nest architecture	Frequency
cell/cells+ v+1clp	12	pp+ cell/cells+dv+1clp	2
e.space+pp+ cell/cells +v+1clp	9	cell/cells+ dv+1clp	2
e.space+pp+ cell/cells+v+2clp	5	without cell partition+1clp	2
pp+ cell/cells+v+1clp	4	pp+ cell/cells+dv+2clp	1
e.space+pp+ cell/cells+dv+1clp	4	e.space+pp+e.space+pp cell/cells+v+2clp	1
cell/cells+v+2clp	4	pp+ cell/cells+v+3clp	1
pp+e.space+pp+e.space+ cell/ cells+v+1clp	4	cell/cells+intc+ cell/cells+dv+2clp	1
cell/cells+intc+ cell/cells+v+1clp	3	e.space+pp+cell/cells+intc+ cell/ cells+v+2clp	1

e.space: empty space, *pp*: preliminary plug, *cell/cells*: provisioned cell(s) with cell partitions, *intc*: intercalary cell, *v*: vestibular cell, *dv*: divided vestibular cell, *clp*: closing plug.

(44.5%) were females. All nests are contained both sexes, and the inner cells were longer (12.1–28.9 mm) and contained a proportionately larger amount of prey (average 7.1 caterpillars per cell) than the shorter cells (9.9–27.5 mm) with fewer prey (average 4.3 caterpillars per cell) in the outer section of the trap nest. Females developed in the longer inner cells and males developed in the shorter outer ones. Difference between the length of cells ($t=5.52$, $p=0.00$, $DF=37$) and prey number in the cells ($t=3.90$, $p=0.001$; $DF=30$) was significant, and related to the sex of offspring (Fig. 3). Generally, the number of prey items per cell was 1–11 caterpillars/cell.

Life cycle. Some aspects of the development that we obtained are summarized in Table 3. Egg was ~2.8 mm long and ~1mm wide, and oval in shape. It was suspended from the north-eastward ceiling of the cell above paralyzed prey ($n=3$). Judging from the morphological changes of larvae, possibly, there are 4 instars.

First instar larva was about 2.8–3.5 mm long and 0.7–1.3 mm wide, reddish in color; head capsule was not distinguishable ($n=10$). Second instar larva was about 5.65–7.55 mm long and 2.50–3.85 mm wide, transparent whitish; head capsule was visible; abdominal segments not clearly distinguished ($n=24$). Third instar larva was about 8.10–11.40 mm long and 4–4.45 mm wide; abdomen with longitudinal grooves on dorsal and ventral sides ($n=43$). Fourth instar larva was 12.25–15.70 mm long and 4.85–5 mm wide, yellowish white; constrictions between the segments became very pronounced; lateral side of body had protuberances ($n=14$). Prepupal period occurred in 10–16 days after hatching. When feeding is completed (in 14 days), the larva put residuals (head capsule of caterpillars and excrement) at one corner of the cell and began to spin a cocoon. The cocoon was brown in color, delicate and incomplete, and was often firmly attached to a cell wall. After diapausing,

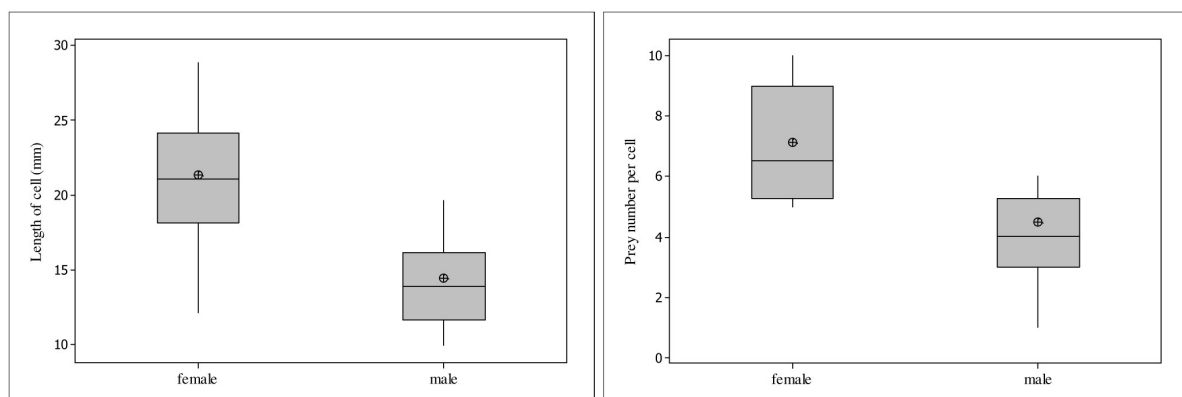


Fig. 3. Difference between the sexes in the cell length (left) and prey number per cell (right).

Table 3. The duration of the observed changes in pupal stage (in days).

Duration of changes	Mean		Range		T –test		
	Male	female	Male	Female	t-value	p-value> 0.05	DF
Pupation started in(after diapausing)	33.2	46.7	32-40	39-66	6.9	0.00	23
Pigmentation started in	5.6	9.3	1-9	7-11	6.1	0.00	33
Pigmentation completed in	2.2	2.9	1-9	2-4	2.0	0.05	35
Pupal skin cast at part of leg	2.0	1.9	1-4	1-4	-0.3	0.7	31
Complete casting of pupal skin	1.7	2.3	1-4	1-4	1.9	0.06	20
Total duration	45.2	59	37-61	53-66	9.5	0.00	41

the first pupation occurred in 32 days. During the pupation stage, the compound eyes were pigmented first, then black pigmentation of the body began in the thoracic region dorsally. While the pigmentation spreading throughout the thorax, the basal margin of the 2nd abdominal segment and head were pigmented. While the pigmentation continued to abdominal segments from anterior to end, the legs, mouthparts and antenna became pigmented. Future yellow areas of the cuticle appeared grayish white initially, until the black pigmentation was completed, and they then gradually became bright yellow. Once the yellow coloration was complete, the pupal skin began to tear off part of legs. Then pupae moved actively resulting in the complete casting of the pupal skin. When the skin was cast, wings were released. Duration of pupal period depended upon wasp sex. The pupation began 14 days earlier in male than in female. Female development continued longer than the male during pupation (Table 3).

Therefore, males flew before females in the middle of June and their abundance already declines sufficiently in the beginning of August. Females emerged in the beginning of July and disappeared in the end of August. Copulation took place shortly after emergence and then females started looking for nest sites. Females tended to nest in the place where they emerged. After that, they prepared nests for oviposition and provisioning. Females chose caterpillars of owl moths (Lepidoptera, Noctuidae) (n=30) for larval food.

Nest parasitoid. Mortality rate was very high in natural populations of *E. dantici* with a low number of successfully emerged individuals (29%). One of the obvious reasons was the presence of a nest parasitoid. We reared

Chrysis ignita (Linnaeus, 1758) (Hymenoptera, Chrysididae) from 33 cells of 22 nests (38% of obtained nests) regardless of the cell number and the location of cells in the nest. Parasitoid development was faster than hosts. Parasitoid larvae were already in condition of diapause 11 days after when the nests were opened for study.

Nesting behavior. From the observation of 19 females, the following basic behavioral elements were detected:

1. Pre-departure temperature testing: Nesting females stay within the nest at visible distance, till the air temperature becomes suitable for flight (10:00-11:00AM). They often crawl forward to the entrance to check the air temperature. They fly out if temperature is suitable, or crawl back and wait again if it is colder.

2. Basking: Basking can occur in any part of the day when the temperature is not sufficiently warm for flying. Basking is often part of the pre-departure behavior. In some cases females do not wait long enough for suitable temperature in the nest. Instead she directly drops on the earth from the nest and crawls to sun exposure for basking. This kind of basking may continue up to 40 minutes.

3. Departure: Depending on flight purpose, there are 3 kinds of departure:

a) For provisioning: this kind of flight is seen when females come back with paralyzed prey to the nest. While they carry a caterpillar, the sound of wings becomes very loud and distinct. They carry it longitudinally under the body, and the mandibles hold the neck of prey. During the loading, they rest several times on the way to the nest. Average time for hunting and carrying prey was 32 minutes (Table 4).

b) For collecting mud: females use yellow mud for building material. Every female has her

own site to collect mud. Range of searching for mud was 2.5- 4 m in 5 females.

c) For other purposes: Females often fly out for other reasons such as feeding, drinking and orientation. Majority of the daily activity of the female is of this kind of flight (Fig. 4).

4. Entering nest backward: This was a very common behavior after females carried prey to the nest. It may relate to locating prey in the nest properly using abdomen. Also during oviposition and after diurnal activity, they enter the nest backward.

5. Nest cleaning: when females successfully find a nesting site, they always prepare the nest for oviposition. If they decide to use old nests of the preceding year because suitable cavities for nesting are in short supply they need to remove residuals from the nest.

6. Capping the completed nest: After completing nest construction and provisioning, females close the nest entrance with mud firmly. This activity needed 28 min 30 sec – 59 min 30 sec for 7–10 times of flight for carrying mud.

7. Waiting: This activity is behaviorally similar to basking, but is distinguished from it in situations where warming up could not have a function, typically on very hot and sunny days. This behavior usually occurs after return into the nest with prey and carrying them into the nest. Females sit on a suitable place near the nest until departing again.

8. Floating: This is observed when females cannot find their nests. They fly around the nesting aggregation, often land on and enter a conspecific nest, but finally find their own nest.

9. Searching for a new hole for nesting: When females complete one nest, they start to find another hole for nesting. This behavior is

connected with floating.

10. Nesting in old nests: When empty holes for nesting are in short supply, females often adopt old nests used in the previous year. This occurs frequently in the beginning of August. 'Nest cleaning' usually follows it.

11. Throwing prey away from nest: Females occasionally throw away the prey just brought into the nest. This unusual behavior occurs possibly due to the death of the prey. During handling prey, females may have used an excessive dose of venom to them.

12. Mating attempt: Mating attempts by males often occur when females are nesting. Females aggressively reject this.

13. Aggressive behavior: This behavior is often observed when other insects such as the parasitoid *Ch. ignita* visit the nest. Females attack them very aggressively often to their death. Sometimes conspecific females compete for nesting site during a short period of time with no observable injury.

14. Closing empty trap nest: Eleven trap nests were closed by females without provisioning.

Generally, the weather condition directly affects the day time activity of the female, especially during the time zone when foraging trips are made. Under favorable conditions, up to seven caterpillars were taken by a female (Fig. 4).

Discussion

Euodynerus dantici is a tube-renter, and utilizes pre-existing cavities of variable origins (Blüthgen, 1961). Females also use abandoned nests of other wasps and bees, such as *Sceliphron destillatorium* (Illiger, 1807)

Table 4. Duration of the observed behavioral elements (hour.:min.:sec.)

Counted durations	N	Median	Mean	Max	Min
Total duration of staying in nest	516	0:01:12	0:04:02	1:31:25	0:00:01
Total duration of extranidal activity	490	0:03:10	0:14:22	2:31:40	0:00:01
Hunting trips	81	0:21:50	0:32:13	1:46:50	0:03:40
Staying in nest with caterpillar	81	0:01:00	0:01:20	0:08:10	0:00:15
Mud-collecting trips	29	0:01:35	0:02:23	0:11:10	0:00:15
Staying in nest with mud	23	0:01:45	0:04:22	0:39:00	0:00:05
Staying in nest for uncertain reasons	85	0:00:45	0:01:48	0:33:50	0:00:01
Entering nest backward	72	0:01:15	0:03:26	0:26:25	0:00:05

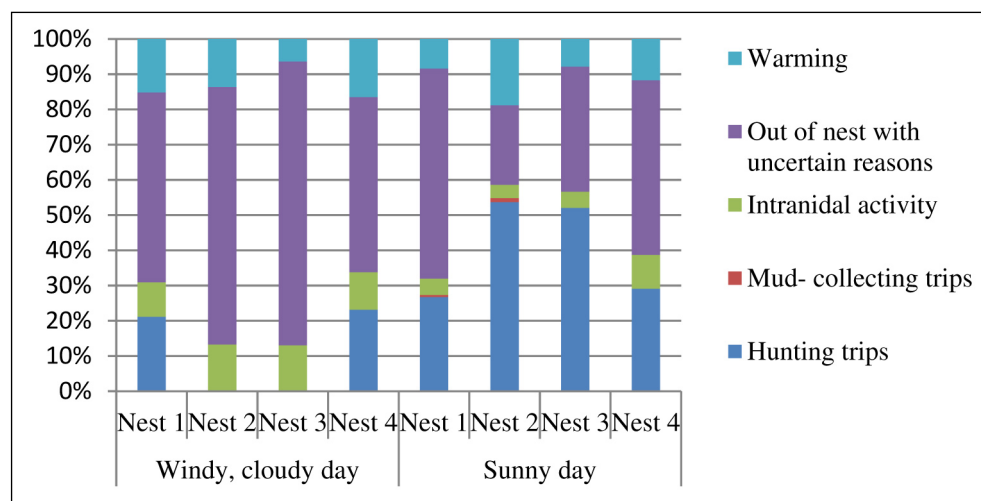


Fig. 4. Diurnal activity of *E. dantici* females in four nests.

(Sphecidae) (Fateryga, 2012) and *Megachile* sp. (Megachilidae) (Blüthgen, 1961).

Fateryga (2012) reported that *E. dantici* makes nests without intercalary cells, but we found 5 nests with them. Stimuli to build intercalary cells could have arisen as a result of parasitism, interference with the preceding cell, or contamination of its contents (Spradbery, 1973). Krombein (1967) suggested that they may be a relict from the evolutionary past when wasps made single cells with a protective vestibular cell in the outer part of the boring. With increasing specialization, the wasps have placed several of these single cells together to produce a series of brood cells, interspersed with empty, intercalary cells. Lengths of provisioned cells were larger for both sexes than those Fateryga (2012) reported for the same species.

The females of *E. dantici* are often construct a preliminary plug in their nests. There was no apparent reason why this plug was made at the inner end of the boring or at variable distances from the inner end. But individual idiosyncrasies of the nesting wasps and bees may have been the determining factor in the positioning of this partition some distance from the inner end, or the nesting females may have detected some adverse condition in the boring walls which caused them to set the preliminary plug some distance from the end (Krombein, 1967).

Construction of cell partitions may serve several purposes. First, they offer the occupant degree of protection from parasitoids and predators. Second, they insure each larva an adequate amount of food. Third, they prevent

cannibalism between the larvae in adjacent cells. Fourth, their surface facing the stored cell is roughened and convex, whereas the outer surface is smooth and concave because the wasp can compact and form the material with her head. Cooper (1957) showed that larvae orient with its head toward convexity (to nest entrance) and spin cocoons. When the adult developed with the head toward the entrance and eventually could escape from the nest. We found two nests which had only closing plug and no cell partitions at all. We think it could be also one of the facts of relict habit from evolutionary past.

We found five nests with a divided vestibular cell as Krombein (1967) and Fateriga (2013) reported for some other species of the same family. The maximum cell number was rather few compared to eight cells reported by Fateryga (2013) in Crimea and nine by Iwata (1976) in Japan. Resource availability is always insufficient in harsh conditions like Mongolian dry areas. For hunting wasps, possibly prey availability is the limiting resource. It could be reason why the species built nests with relatively few cells. For individual females, in order to ensure successful surviving of their broods, it could be a better way to build many nests with a few cells than build a few nests with many cells during the flying season. Besides that, high parasite pressure made them build nests that are structurally diverse, and the cell number tends to be fewer in those nests.

Strangely, the cuckoo wasp, *Chrysis ignita*, a common nest parasitoid of many species of potter wasps had not been found in the *E. dantici*

nesses (Spradbery, 1973), but we confirmed its presence in this study. Other species of this parasitoid genus such as *Ch. germane*, *Ch. succincta*, *Ch. sexdentata* were observed from the nest of *E. dantici* (Amolin, 2009).

Cells with brood, which gave rise to females were longer and received more prey than those which gave rise to males, and were located toward the inner end of the nests. The males developed in outer cells of the nests and emerged earlier than females. It is because of their larval and pupal stages shorter than those of females (Evans & West-Eberhart, 1970).

Generally, space efficiency was very unstable for the species because of diverse nest architecture, which is contrary to the situation reported by Fateriga (2013). Diversity in nest architecture could partly result from the high pressure of parasitism (almost half of the cells were infested in the nests obtained). Development stages are not fully studied for Eumeninae, except in particular species such as *Ancistrocerus antilope* (Cooper, 1953, 1966; Spradbery, 1973). For this species, up to five instars were described. We obtained 4 instars for *E. dantici* based on morphological changes. However more specific observation and method would be needed in the future, using measurements of head width and detailed characters of mouthparts.

The results of our study showed that *E. dantici* is univoltine in the study area, agreeing with observations by Fateriga (2013) in Crimea, but disagreeing with study results of Amolin (2009) in southeastern Ukraine. *Euodynerus dantici* females hunt only caterpillars of Noctuidae (Lepidoptera) for provisioning in Central Mongolia. However, the same species hunts caterpillars of Pyralidae in Japan (Iwata, 1976; Itino, 1992), and Tortricidae (Blüthgen, 1961; Iwata, 1976) in Europe and Japan. Such differences must often result from spatial and temporal variation in prey availability, but it could be also caused by variation in genetically based prey preferences (O'Neill, 2001). Further, the number of prey items per cell was fewer in Mongolia (1-11 noctuid caterpillars/cell) than in Japan (19-50 pyralid caterpillars/cell; Itino, 1992); this difference can be explained by the size of prey hunted, noctuid caterpillars being conspicuously larger than pyralid caterpillars. Generally, variation in the number of prey

items per cell within a species can result from differences in allocation of resources to male and female offspring and to variation in the availability of prey of different sizes (O'Neill, 2001).

Euodynerus dantici is possibly a phylopatric species, females nesting in the place where they emerged. So they form aggregations, but there is no evidence of co-operation among nesting females or between parents and emerging offspring, although some collective protection from predators may occur in these associations (Spradbery, 1973). For females, the time spent inside the nest was shorter than that outside the nest. But it is dependent upon the weather condition; when it is cool and cloudy, females occasionally stay in the nest whole day.

Unexpectedly, rather many nests (11 out of 58 nests observed) were empty or rarely with uncompleted partitions and sealed with thick closing plug. Such an anomalous behavior was also recorded by Krombein (1967) for species of spider wasp, who supposed it might be analogous to the behavior of wrens in willing up all kinds of cavities with leaves or twigs to deny nesting site to other birds. It could be a kind of nest reserving behavior when nesting site is not sufficient for all individuals as we observed *E. dantici* frequently reused abandoned nests of the preceding year. We encountered another situation, where an adult female triggered by another female. The nest contained 10 caterpillars, larvae of *E. dantici* and a dead adult female, and was sealed with a closing plug. We do not have any solid explanation for it. Maybe the female died in the nest because of night chillness or for other reasons, and then another female sealed the nest led by a relict or reserving behaviors.

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