Comparative Studies on the Nesting Biology of the Genus *Sphex* (s. l.) in East Asia (Hymenoptera, Sphecidae)

By Katsuji TSUNEKI
(Biological Laboratory, Fukui University)

(With 15 Text Figures and 6 Plates)

Contents

Reprinted from *The Memoirs of the Faculty of Liberal Arts, Fukui University*
Ser. II, Natural Science, No. 13, Part 2, pp. 13–78, 1963

FUKUI, JAPAN
(October 30, 1963)

Comparative Studies on the Nesting Biology of the Genus *Sphex* (s. l.) in East Asia (Hymenoptera, Sphecidae)*

By Katsuji Tsuneki
(Biological Laboratory, Fukui University)

SYNOPSIS

Tsuneki, Katsuji (Fukui Univ., Japan). Comparative studies on the nesting biology of the genus *Sphex* (s. l.) in East Asia (Hymenoptera, Sphecidae). Mem. Fac. Lib. Arts, Fukui Univ., II, 12 : 13–78 (1963).

Nesting biology of eleven species of *Sphex* observed by the author in Japan, Korea, North China and East Mongolia was described; the species : (*Sphex*) *argentatus fumosus* Mocs., (*S.*) *flammitrichus* Str., (*S.*) *maxillosus* F., (*S.*) *fukuianus* Tsun., (*S.*) *haemorrhoidalis* F., (*Palmodes*) *occitanicus* Lep. et Serv., (*Prionyx*) *albisectus* Lep. et Serv., (*Harpactopus*) *subfuscatus* Dhlb., (*Isodontia*) *harmandi* Pérez, (*Isodontia*) *maidli* Yasum., and (*Isodontia*) *nigellus* Sm., of which *haemorrhoidalis* has a habit of progressive provisioning and *harmandi* of gregarious rearing of multiple larvae in a brood-chamber. A tentative dendrogram, independent of morphology, was given based on their nesting substratum, types of the nest structure, the time of burrowing in relation to prey hunting, method of oviposition, kind and number of the prey and other special characters of each species.

The nesting biology of *Sphex* in Japan has been comparatively well studied through the efforts of several investigators. Unfortunately, however, nearly all of the papers published were in Japanese and could not reach understanding of the western biologists. Especially, it is most regretted to me that my two books, 'The Japanese Hunting Wasps' and 'A Naturalist at the Front' have had no opportunity to be prepared for readable to the western entomologists. In this paper I rearranged my field and laboratory notes and memoranda concerning the biology of the genus *Sphex*, adding some unpublished data, and attempted the comparative considerations on their phylogenetic relationships viewed from the characters of their biology and behaviour. The species contained in this paper are not only those occurring in Japan, but also some which live in Korth North China or Mongolia, the biology of which was sometimes well investigated in western countries.

In describing the following accounts I restricted the data to my own observations, since the other persons' papers concerned only a few common species and, moreover, they involved no particular facts worthy of addition to my own. Only occasionally I have referred to some of them for the sake of comparison.

As to the East Chinese forms two valuable papers were published by 0. Piel (1933, 35). However, some of the species (e. g. *haemorrhoidalis*) were very inadequately dealt with by him, being looked over as to its most interesting and most important point in biology.

---

* Contribution No. 69 from the Biological Laboratory, Fukui University, Japan

Mem. Fac. Lib. Arts, Fukui Univ., Ser. II, No. 13, 1963

The representatives of *Sphex* in our region contain two particular species which merit a special attention from the biological point of view. One is *S. haemorrhoidalis* which feeds her young progressively and the other *S. harmandi* which rears her young gregariously in a chamber.

Finally I must mention that the biological dendrogram tentatively presented in this paper was based on the knowledge regarding the Palaearctic species only, and some day this must be added or emended by other persons or by myself under the worldwide scale.

I. BIOLOGY OF EACH SPECIES

I. *SPHEX (SPHEX) ARGENTATUS FUMOSUS* MOCSÁRY

1. THE NEST AND BEHAVIOUR RELATING TO IT

1. Emergence and period of activity

In Japan, except for the southern islands, this species appears from late in July to early in August. Like other species, the male comes to the world first and the emergence of the female is delayed about a week or so. The male disappears usually during August and the female rests to continue the nesting activities up to the end of September or early in October.

2. Nesting ground

The place where the nest of this species is made is usually a sandy ground, but not less frequently the ground of loamy or clayey soil is selected. In such a place several to some ten individuals of wasps gather together and form a colony. I have seen the colonies of this species in various localities of Japan and Korea. Very frequently they were settled on sea shore or river bed, on the play-ground of the schools and the garden of the human houses. The place where the surface is sparsely covered with weeds is particularly preferred by the wasp. The habits of their settling colonies are due to their homing instinct, a natural tendency to return to their native place to make their own nests.

3. Ecological relation among the colony inhabitants

The nests are sometimes located close together, being only 20 cm or so apart and frequently give rise to confusion or contest. The inhabitants, despite they form a colony, have not an intimate relation among them. They are only casual neighbours, retaining obstinately the nature of the solitary ancestor. Each of them does not tolerate the presence of other wasps within a certain boundary around its nest. It can therefore be called a territory. But the territoriality is shown only temporarily during the time when the owner is present in or near the nest. When two neighbours encounter near the entrances of their nests each of them flings upon the other and both wasps fly up in the air to fight furiously with buzzing sounds. However, they do not fight exhaustively to drive away the seeming intruder. If the other wasp disappears from the direct sight the fight is at once ceased. The remainder returns to its own nest and will not search the other to drive it out of its own nest boundary. Furthermore, the wasp does not stay at its nesting site to defend it from the tresspassers or apparent intruders of the same species. Such being the case fighting behaviour between the neighbours of a colony has no practical bearing on the defense of their nests. Rather we are impressed by such behaviour that the wasp is insisting by such a protective movement the rightful possession of the nest.

4. Nest burrowing

Selection of the nesting site in this species is performed never so nervously as observed in some other hunting wasps such as many species of *Ammophila* (Sphecidae) or *Batozonus* (Pompilidae). The wasp determines a certain spot to nest and at once begins to dig the ground. Mandibles and fore legs are used as digging tools. She does not lay aside the débris at the entrance, but carries them backwards for some distance and then slowly pushes it posteriorly through the underside of her abdomen. As the tunnel grows deeper the intervals between her appearances out of the burrow becomes naturally longer. Frequently the wasp carries out a pebble holding it between her mandibles. The soil is held with her mandibles and fore legs, but during the time she passes to the refuge-heaps it slips out of her hold and is scattered over the pass. Thus the way on which she regularly goes to and fro becomes gradually heaped with débris and turns into a small bank. Since the sand drops more abundantly as she proceeds further and, moreover, as she used to rakes away the load at the end of the highway, the bank becomes higher backward and becomes longer in proportion to the depth of the tunnel. Finally the wasp begins to unload before she reaches the end of so lengthened the bank by turning sideways, so that the bank becomes broader backward. Sometimes it is slightly curved leftwards or rightwards in accordance with the turning inclination of the wasp. This bank is always left as it appears even after a brood chamber is made and is quite of use to lead the human observer to the entrance of the nest and to show the direction of the entrance gallery of the tunnel, how elaborately she conceals the nest by closing the entrance and by digging the side holes.

5. Temporary closure of the nest entrance

When the wasp digs up the tunnel and probably a brood-chamber at the end of it, she closes the entrance temporarily with a part of the soil taken out. Sometimes this is performed in the course of burrowing and later further digging is resumed. The manner of temporary closure is different from that of *Ammophila* or of *Bembix* and very characteristic. The wasp faces to the entrance, curls her front tarsi inwards to form a rough basket and pushes the soil forwards with it. She drops the burden in the entrance gallery, turns round to go to the bank. There she rakes the soil backward through the underside of her body, turns round again and goes to the entrance pushing the soil forward collected there. The same procedure is repeated several times and the entrance is completely closed.

6. Side holes and their biological significance

When the entrance is completely closed after 3 or 4 soil-carrying journeys the wasp begins to dig two further blind tunnels, usually one at each side of the concealed entrance.

Manner of digging The manner of work at this time of the wasp appears quite interesting. Her movement is inactive, sluggish and idle. Apparently her work has no definite orientation whatever. She carries out a burden of soil in quite an idle manner from a hole she has begun to dig. Soon, however, she ceases the work, walks about aimlessly around the nest, and then commences to big another hole at the other side of the concealed nest entrance. After a while she stops the work, turns back to the first hole and resumes very sluggishly the digging work. She thus goes to and fro between the two holes, always with intervals rambling idly around the nest. The manner is quite contrastic with the active, diligent and speedy manner of digging of the true nest. It appears as if the wasp is tired of the work after several failed trials of nest construction and is continuing reluctantly the search for the proper place for her nest. Despite such an appearance, the holes are simultaneously deepened to about 7 to 8 cm and then abandoned with the entrance left open.

External appearance The side holes thus made have a complete appearance of the abandoned half dug burrows, usually met with on the nesting ground of various species of the sand wasps. However, if we remove them out of the place either by filling them with sand or closing the intrances with pebbles, the wasp always reconstructs them or uncovers the entrances as they had been.

Variation in location As described above the side holes are usually dug at each side of the true burrow seen from the bank side. They penetrate into the ground somewhat divergently up to 7–8 cm from the surface, with an inclination of about 70°–80°. Sometimes, however, they are ended at about 3–5 cm from the entrance. The tunnels are not always equal or nearly so in depth. Rather, difference in depth is usual. This seems to contribute much to make it appear as stopped and abandoned burrows. Occasionally the side holes are made two at one side of the burrow, or three in number. In the latter case the location of the holes show some variation as given in Figure 1.

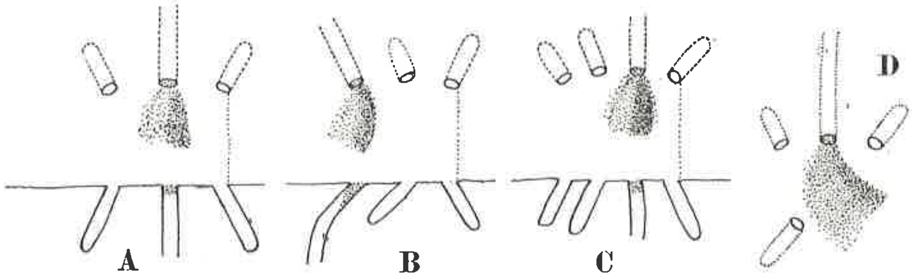


Fig. 1. Side holes. A, the commonest type; B, C and D, variations.

Consideration on their biological significance Different opinions prevail in Japan as to the significance of the side holes. Iwata and his followers insist that the appearance of the holes is a meaningless development of that digging habit which is sometimes shown by some sand burrowing wasps when they take soil to close the nest from a certain limited spot, and it has a danger to commit an error to give the holes any biological significance. Indeed, some wasps have an inclination to make a hole as a result of their taking the nest closing material from a limited place around the nest. Yasumatsu and myself independently observed that the Japanese *Bembix* made a considerably deep tunnel by removing the sand from a certain spot in front of her nest in order to close her nest permanently, and I further saw that such a tunnel was utilized by a wasp for her new burrow. In view of these observations the origin of the habit of digging the side holes is apparently explained by this hypothesis. On the other hand, others, including myself, consider that the holes may be of some use to mislead the parasites or to give a landmark to the wasp, apart from their origin.

In my present opinion the two hypotheses are different in the level or the dimension and by no means the ones to be set up in opposition. The biological significance of a phenomenon is the ultimate outcome and the human evaluation of the phenomenon from the view point of ecology or evolution. Fundamentally it does not concern with the causation of the phenomenon, although in some cases causation itself has some biological significance toward the animals concerned. Therefore there is no inconvenience to admit the maybe origin of the side holes on the one hand and to discuss the biological significance on the other.

At least it is true that I myself was deceived at first by the holes and was led to belive that they were abandoned half-made burrows. But it is decidedly a mistake to take up the human being as an object of the wasp's behaviour or its result. Let us see the insects. It is a very usual occurrence that we observe the parasitic flies circling above the holes and sometimes penetrating into them. We can also see the Mutillids and ants frequently crawling into the tunnels. However, there is a question as to these insects. Can they be the objects of the construction of the side holes? The Mutillids, so far as have been known, are not parasitic on this species. The ants rarely give damage to the nests, but their injury is too little and too weak to be contrasted with the existence of the holes. The parasitic flies are indeed, the most dangerous and formidable enemy to the wasp. But they have apparently no direct connection with the side holes in the methods of their parasitizing. When they want to send their maggots to the brood-chamber of the wasp they need not penetrate into the tunnel of the wasp's nest. It is sufficient to them only to wait the returning wasp by the side of its nest. The wasp carrying a prey will always give them a chance of larviposition by laying aside the carried insect guardlessly during the time when she clears the entrance stopper and inspects the brood-room conditions. The maggots, as soon as they are deposited directly or dropped from in the air by the mother fly, crawl over the body of the insect and quickly conceal themselves usually under the wing or its bud by the aid of their negative phototaxis. When the prey is dragged in the nest without being taken notice of the parasite by the wasp they are promised to receive ample food supply, with no risk of their mother to penetrate into the burrow.

Such being the case, we cannot simply ascribe the presence of the side holes to a result of natural selecction through the host-parasite relationships.

On the other hand, there is also a question as to the hypothesis of the landmark. It is certainly true that the wasp need not such a landmark to find out her own nest. The débris in front of her nest will sufficiently afford her the clue to find the precise position of her nest-entrance. Moreover, the very fact that the wasp can reconstruct the holes when they were removed tells us most eloquently that she can discover the nest with no aid whatever of such an accessory.

With regard to the origin, there is also some problems. First, the time of digging the holes is *after* closing the entrance, and moreover, for *the temporary closure* the wasp does not necessitate such a large amount of soil. Second, the wasp of this species need not gnaw off the material from the ground, since a mound of soil is piled up in front of the entrance, and indeed, a part of this mound is utilized by the wasp to close the entrance. Accordingly, the construction of the side holes has nothing to do with the closure of the entrance pouch. Third, this becomes most clear by the fact that the wasp when they are destroyed at once reconstructs them with no connection at all with burrowing or closing of the nest.

When we thus consider the significance of the side holes becomes far more obscure than has been supposed. However, there is an important point of which we must reconsider more prudently. That is a problem relating to the parasitic fly, since this is the most powerful enemy of the wasp.

As discussed in the foregoing page, apparently the mode of sending the maggots by the fly into the nest of the wasp has no direct bearing upon the presence of the side holes. We must, however, take into considertion of the fact that the fly frequently visits the holes, soon comes out and flies away. I have not as yet ascertained whether or not the parasite lays her larvae at the bottom at such a time. But I observed twice that the fly dropped the maggots into the empty burrow of *Ammophila sabulosa infesta* while the wasp was absent or while she was at work at the bottom. Apart from such observations, at any rate it is certain that the parasitic flies are strongly attracted by the hole. Moreover, it is most probable that some of them mistake the holes as abandoned burrows, since they fly away after such an inspection. This seems important, since it is of definite use to lessen more or less the number of the most dangerous enemies from around the nest. There is a collaboration that favours this consideration. In the southern parts of our region the black Sphex in question lives in sympatric with the golden haired Sphex, *S. flammitrichus*, which has a similar ways of life but which does not provide the nest entrance with the side holes. In such districts it comes always into notice that the former is more abundant and prosperous than the latter. And the examination of the nests by digging reveals that the latter species suffers severer damage from the parasitic flies. While the damage suffered by the black Sphex through the intrusion of the parasitic flies is on an average comparatively small, though it may be different with the district studied. According to my investigation (Table 1) rate of damage with reference to the nest is

Table 1. Contents of the nests of *Sphex argentatus fumosus* Mocs.

Loc	Nest No.	Cell No.	Prey ♀	Prey ♂	Prey Ima	Prey Nym	Prey Total	Wasp-ling	Para-site
I	1	1	–	–	–	–	–	–	+
		2	1	–	1	–	1	E	–
		3	–	–	–	–	–	–	+
	2	1	–	–	–	–	–	C	–
		2	–	–	–	–	–	–	+
		3	3	–	3	–	3	L	–
		4	2	–	2	–	2	E	–
	3	1	2	–	2	–	2	E	–
	4	1	–	–	–	–	–	–	+
		2	2	–	–	2	2	E	–
	5	1	–	–	–	–	–	–	+
		2	–	–	–	–	–	–	+
		3	–	–	–	–	–	C	–
		4	–	–	–	–	–	C	–
	6	1	1	–	1	–	1	E	–
		2	3	1	?	?	4	E	–
	7	1	3	–	3	–	3	L	–
		2	4	–	4	–	4	L	–
		3	5	–	5	–	5	L	–
		4	–	–	–	–	–	–	Empty
	8	1	3	1	4	–	4	L	–
		2	2	2	3	1	4	L	–
		3	3	1	4	–	4	L	–
		4	3	1	4	–	4	L	–
		5	3	1	4	–	4	L	–
		6	4	–	4	–	4	L	–
		7	5	–	5	–	5	E	–
		8	2	1	3	–	3	–	+
II	9	1	2	–	2	–	2	L	–
		2	–	–	–	–	–	C	–
		3	–	–	–	–	–	C	–
		4	–	–	–	–	–	C	–
		5	–	–	–	–	–	C	–
	10	1	3	–	3	–	3	D	–
		2	–	–	–	–	–	C	–
		3	3	–	3	–	3	D	–
		4	–	–	–	–	–	C	–
		5	–	–	–	–	–	C	–
	11	1	5	–	3	2	5	L	–
III	12	1	1	–	1	–	1	E	–
		2	3	–	?	?	3	D	–
		3	5	–	?	?	5	L	–
		4	5	–	?	?	5	L	–
		5	5	–	?	?	5	D	–
		6	–	–	–	–	–	–	Empty
	13	1	2	–	2	–	2	E	–
		2	2	1	3	–	3	–	Ant
		3	–	2	2	–	2	L	–
		4	2	2	4	–	4	E	–
	14	1	1	–	–	1	1	L	–
		2	2	2	4	–	4	L	–
		3	–	1	1	–	1	E	
III	15	1					1	E	–
		2					2	E	–
		3					2	L	–
		4					3	L	–
		5					3	–	+
		6					?	–	+
		7					?	–	+
	16	1	1	–	–	1	1	E	–
	17	1	1	2	3	–	3	L	–
		2	0	3	3	–	3	L	–
		3	2	1	2	1	3	L	–
		4	2	–	–	2	2	L	–
	18	1	2	3	3	2	5	L	–
		2	–	2	2	–	2	E	–
		3	3	1	1	3	4	E	–
		4	–	–	–	1	–	–	Empty
	19	1	3	–	3	–	3	E	–
		2	4	–	3	1	4	E	–
		3	4	–	3	1	4	L	–
		4	3	–	2	1	3	L	–
		5	1	–	1	–	1	E	–
	20	1	1	2	3	–	3	L	–
		2	–	1	1	–	1	E	–
		3	2	1	1	2	3	L	–
		4	3	–	1	2	3	E	–
	21	1	2	1	2	1	3	E	–
		2	1	–	–	1	1	E	–
		3	2	1	3	–	3	E	–
	22	1	–	–	–	–	–	–	Empty
		2	–	–	–	–	–	C	–
		3	–	–	–	–	–	C	–
		4	–	–	–	–	–	C	–
	23	1	1	1	2	–	2	L	–
		2	5	2	5	2	7	E	
		3	–	–	–	–	–	–	Empty
	24	1	2	–	2	–	2	E	–
		2	2	2	3	1	4	E	–
		3	3	2	5	–	5	L	–
		4	2	3	5	–	5	L	–
		5	–	3	3	–	3	E	–
IV	25	1	–	–	–	–	–	C	–
		2	–	–	–	–	–	C	–
		3	–	–	–	–	–	C	–
		4	–	–	–	–	–	C	–
		5	–	–	–	–	–	C	–
		6	–	–	–	–	–	–	+
	26	1	–	–	–	–	–	C	–
		2	–	–	–	–	–	C	–
		3	–	–	–	–	–	C	–
		4	3	1	4	–	4	D	–
		5	2	1	3	–	3	L	–

Remarks. Locality : I, Saitama Pref. ; II, Chiba Pref. ; III Utsunomiya; IV, Tsuruga.
Waspling : E, egg; L, larva; C, cocoon; D, dead (unhatched).
Parasite : +, parasitized by Tachynid fly: –, not parssityzed.

5/10 (50 %) in Yorii (Saitama Pr.), 0/3 (0 %) in Chiba, 1/10 (10 %) in Utsunomiya and 1/2 (50 %) in Tsuruga (Fukui Pr.). If viewed with reference to the brood-cell it comes respectively 7/33 (21 %), 0/11 (0 %), 3/55 (6 %) and 1/11 (9 %). On the other hand, in the golden haired Sphex the rate of damage through the parasitic flies is, with respect to the nest, 4/4 (100 %) in Tsuruga, 1/1 (100 %) in Amami-Ohshima and with respect to the brood-cell 15/34 (44 %) in Tsuruga and 2/5 (40 %) in Amami-Ohshima. According to the records of Iwata in which he referred to the parasitic flies, 2 out of 6 brood cells were invaded by the fly maggots (33 %). The difference of damage between the two species seems to have some bearing on the side holes, especially the difference in Tsuruga seems suggestive.

In conclusion we may say : The side holes must have some important significance towards the wasp itself, since they are soon reconstructed when destroyed. But as to their biolgical significance or survival values there is no definite evidence. It seems most probable that it may serve to some extent to deflect the attention of the parasitic fly. But the significance in this line cannot be too much exagerated, since the species without such are able to survive with no serious inconvenience nor hindrance in the competing world. This may be an instance of the fact that there is sometimes a phenomenon in nature which has no strong direct connection with the survival values or natural selection.

7. Orientation flight

Obeying the general rule of the nest making Hymenoptera, the black Sphex, too, makes the so-called orientation flight that must serve to study the locality of the nest. The pattern of the flight in this species, also observed by 0. Piel in China, is considerably different from that described in the well-known observation of the Peckhams on *S. ichneumoneus* of N. America, and is considered much more excellent in inprinting the general sceinic pattern* of the nesting site from various directions. An instance which was observed on August 10, 1936, in Saitama Pref. represents a typical case of the flight in this species.

When I took notice of the wasp she was flying about above the surface of the ground at about a meter high. The range of her flight was restricted to a certain narrow locality and she was frequently flying back to a certain spot on the ground to depart there again without alighting. I approached and found there a just dug up nest. She was certainly trying the orientation flight. I retreated several meters and observed and noted the behaviour of the wasp. She started from the nest site in a straight line, without drawing circles, turned round and stopped at a distance of 2–3 m from the entrance and at about 1–2 m above the ground, then continued a stationary flight for several to some ten seconds, with her head kept towards the nest, as if staring there. During the time she very slowly shifted her position to the right or the left for quite a restricted range. Then she suddenly dashed forwards to the nest entrance, but without landing there flew off from just above it to repeat that apparently gazing behaviour from a similar distance and height. At this time, however, the direction of her suspended flight was slightly changed against the

* The pattern must be a vague mosaic of brightness and colour, if colour is perceivable to the wasp. Details on this problem were discussed in my previous paper on the biology of *Bembix niponica* (1956).

nest. The behaviour was repeated over and over again and as times were multiplied the direction of the flight as against the nest was gradually changed from right to left, and the distance and height were also gradually increased in connection with the direction, and finally after about 10 minutes, she flew to about 30–50 m away from the nest and at about 20 m high above the earth surface. Towards the time the wasp hovered in the air for 10 m or so to the right and left, and without trying that stationary flight swiftly came back towards the nest. In such a case her flight was not in a straight line, but waved as if to regulate repeatedly the deviated direction. The pattern of the flight can be represented schematically as given in Figure 2. Repeated return to the nest from various directions, distances and heights gave me an impression that the wasp was training herself for her succeeding homing performance. In this case, her movement was restricted to the range from northwest through west to southwest. This seemed to have bearing on her later hunting field, since in the directions she tried the training flight there was a broad grassland, while the opposite direction was covered with the wide river bed and the stream.

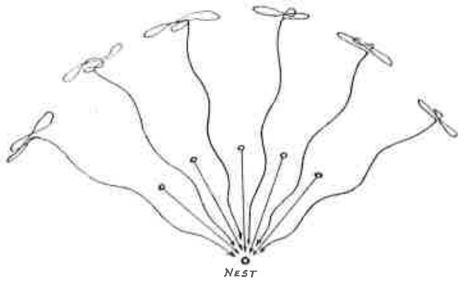


Fig. 2. Orientation flight.

8. **Structure of the nest and its dynamic aspect**

Structure Apart from the side holes, the structure of the nests of this species belong to the compound or branched type, containing several brood-cells, one at each end of the branch tunnels (Fig. 3). The main burrow enters the ground, as a rule, with a gentle inclination at first for several to some ten cm. Then it describes a parabolic curve and steeply penetrats into the earth, forming an angle of 60°–90° with the surface. Rarely it goes in the earth with a steep slope from the first, or continues a gentle inclination (about 40° or less) to the end. It has the length of about 25–70 cm and the depth of 15–50 cm. Generally it is deeper and steeper in the nests made in the soft soil. From the bottom region of the main burrow are given off several branch tunnels usually horizontally. They are 5–15 cm in length, sometimes only 2–3 cm or attaining 25–30 cm. The branch tunnels are given off at different heights in various directions. General tendency is from lower to higher, but regarding the direction quite inconstant. Of course there are many exceptions. Sometimes several tunnels are branched off from the same height. The branch tunnel is always completely closed when the brood-cell at the end is fully provisioned.

The larval cell is always placed horizontally, even when the branch tunnel leading to it is slightly inclined. It is elliptic in the longitudinal section, usually 35–50 mm in length, and 20 mm or so in maximum width with the hight slightly less than width. In some exceptional cases the length is increased to about 70–80 mm. The number of the cells involved in a nest when it is accomplished is from 4 to 8 (Table

2). The figures in this table contain those of the unfinished nests. Some of the

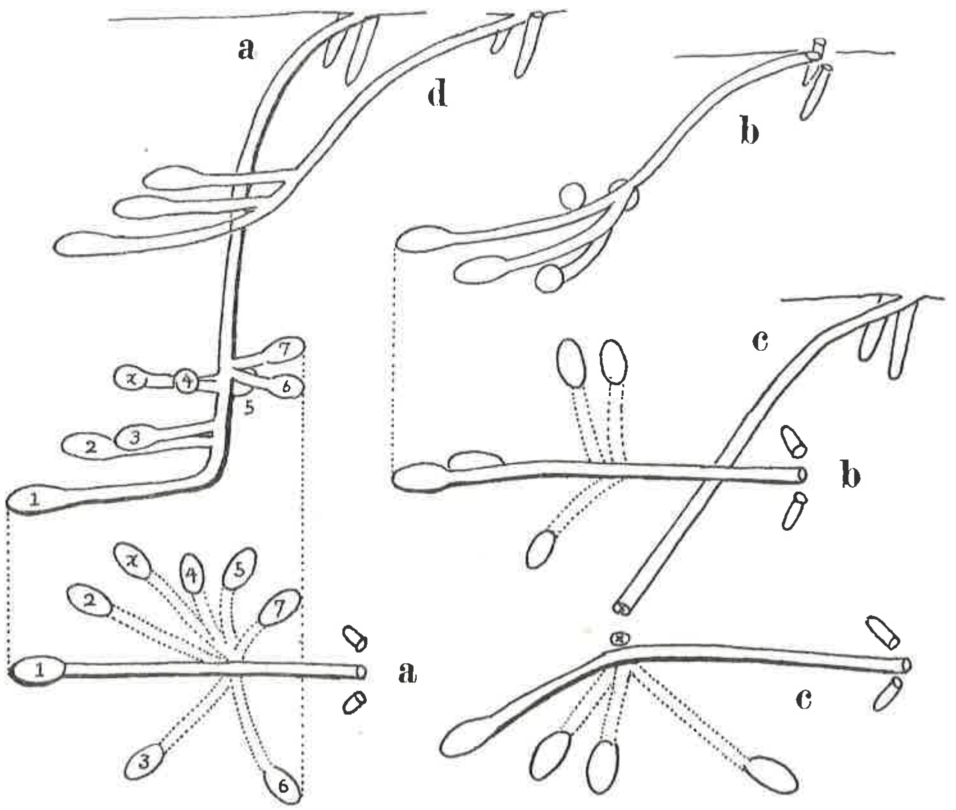


Fig. 3. Structure of the nest. The same letters indicate the same nest seen from different direction.

structure of the nests are illustrated in Figure 3.

Table 2. Number of brood-cells in the nests examined

Number	1	2	3	4	5	6	7	8
Freq.	2	2	4	8	5	2	1	1

Order of construction The main tunnel is usually dug up at a breath. At times, however, the wasp stops the work on the way. In this case the entrance is temporarily closed. When the first brood-chamber is fully stored with food for the larva the branch tunnel leading to it is compactly closed with earth. The material must be taken from the 2nd branch tunnel which is to lead to the next larval cell, since it is not observed that the wasp carries material in the burrow from outside the nest. Thus, closing of the previous brood-cell and digging to the next cell is carried out at the same time. In this order the cells are successively constructed and provisioned. When the tunnel leading to the final cell is closed, she also closes the bottem part of the main tunnel permanently, but never the whole or nearly the whole of the burrow. Rather in most cases it seems that the wasp omits the closing work of the main tunnel except for the entrance closure. The wasp that has completed a nest soon begins to make the next nest. But it is not certain how many nests are constructed by a single wasp during her life time.

The side holes are usually dug when the first brood-cell is made up and in some time during the later course they are emended, probably just after some brood-cell is dug up. During the provisioning of a cell when the wasp goes out the tunnel in front of the cell as well as the entrance of the nest is roughly closed with sand.

2. THE PREY AND BEHAVIOUR RELATING TO IT

1. Range of the prey

So far as my examination goes, the prey captured by the wasps of this species are restricted to four species of Tettigoniidae, namely, *Phaneroptera nigroantennata* B. v. W., *Ducetia japonica* Thun., *Hexacentrus japonicus* Karn. and *Homorocoryphus lineosus* Walk*. There is an interesting problem with regard to the selection of the prey as dealt with in the next paragraph. As to the sex the female occupies a greater part in the first 3 species, while in the last both sexes are approximately equal in number. Moreover, in this species there are two colour forms, the green and the testaceous, but both are indifferently captured. As to the growth degrees imagoes are far larger in number than nymphs. Such relations are given in Table 3. However, it is doubtful whether or not the results were based on any selection on the part of the wasp. At least as to the growth degree of the prey it seems only a question of the time.

Table 3. Species, sex and growth degree of the prey

Species of prey	♀	♂	Ima.	Nymp.	Total
Ducetia japonica	39	0	37	2	39
Phaneroptera nigroantennata	43	1	37	7	44
Hexacentrus japonicus	30	8	37	1	38
Homorocoryphus lineosus	55	41	79	17	96
Total	167	50	190	27	217

On the other hand, there is no definite relation observed between the first victim to which the egg of the wasp is attached and its sex or its growth degree. In the observed egg-carrying victims the proportion between the female and the male is 24:6 (♀ 80 %) and that between the imago and nymph 22:8 (imago 73 %). The fact does not indicate that the female and the imago are prefered respectively to the male and the nymph. Strictly, rather reverse is the case. This is quite obvious in the comparison of proportions shown in Table 3.

2. Individual preference for the prey and its evolutional significance

Actual fact The prey stored in 26 nests directly examined by me were as given in Table 4. At a glance every one will perceive that the prey is limited to a single species in most of the cases. Further, greater part of the exceptions involves only few

* Fujimatsu (1937, observation in Sendai) recorded as exceptions *Kuwayamaea sapporensis* Mats. et Shir. and *Xyphidion* sp. and Iwata (1935, observations in Osaka) similarly *Holochlora japonica* B. v. Watt. as exception.

Table 4. Species distribution of prey in the nests examined

Nest No.	Duc.	Phan.	Hexac.	Homor.
1	1	–	–	–
2	–	3	–	–
3	5	–	–	–
4	–	–	–	3
5	–	–	6	–
6	15	–	–	–
7	–	12	–	–
8	–	–	32	–
9	–	2	–	–
10	–	–	–	6
11	5	–	–	–
12	–	1	–	10
13	18	–	–	1
14	–	1	–	8
15	–	–	–	11
16	–	–	–	1
17	–	–	–	13
18	–	2	–	9
19	–	13	–	2
20	–	–	–	10
21	–	1	–	6
22	–	–	–	–
23	–	4	–	5
24	–	5	–	11
25	–	–	–	–
26	–	–	–	7
Total	44	44	38	103

of another species, and moreover, of another single species. Only nest 23 and 24 form exceptions in which two species of prey approximately match in number with each other. The observations of other Japanese authors do not touch upon this interesting preference of mother wasps regarding their larval food. However, from the list of the prey made by them we can presume that the same may be true in their cases also. But the material from my own observations is sufficient enough to show the phenomenon.

The fact above mentioned shows that, apart from the reason, some sort of selection is made on the part of the wasps concerned. There are not less number of the hunting wasps that show somewhat a similar sort of selection among various species of prey which are on the official list of diet of their larvae, *e. g.* other Sphecine wasps, Bembicine wasps, Crabronids, Mud-daubing wasps, etc. However, few of them is so strict as in the case of this species. It seems of interest, therefore, to pay some attention to this problem.

Various hypotheses As probable reasons of this apparent preference several cases can be assumed. First, it may be that only the single species that was captured by the wasp occurred in the locality. Second, the wasp may have a strong tendency to cling to the species that happened to be caught in her first hunting excursion. Third, the wasp may have continued to visit to her first hunting ground where the same species of prey lived in abundance. Fourth, this may represent the first step towards an inheritable preference for a certain species of prey in the differentiation of instinct.

Consideration Among the reasons the first assumption is obviously unapplicable. Instances observed in Yorii well indicate the relationship, where various species were caught by the wasps, yet each of them showed a strong preference for a species selected by her. The second is sometimes strongly insisted by some entomologists. However, can we entrust this curious phenomen on to such a simple explanation alone ? Usually when such a tendency is observed in some species, it appears per day, that is to say, in most cases per cell. Moreover, it becomes possible only when combined with the third case. In the Sphex in questin, whereas, the preference is not per day, but throughout her life. Had it been due to a simple inclination can we consider that the wasp which had captured a certain species of the prey avoids another species within her menu even when she meets with the insect during her hunting excursion ? We can not suppose that the wasp which captured 32 *Hexacentus japonicus* alone did not encourter with another prey species during her field activities. We cannot presume also that so many of the same species of prey assembled in a restricted area. The same can be held with respect to the wasps that captured *Homolocoryphus lineous.* Furthermore, if stress is placed on the tendency of adhering to the first species of the victims, it seems that similarly the tendency should appear with reference to the colour of the species when it has two colour forms as in this species, since the wasp is considered to have a colour sense of a certain degree (cf. Tsuneki, 1961), at least to have an ability to distinguish the brightness difference between green and brown. Whereas, such is not the case. Instances observed in Utsunomiya showed that the two colour forms were indifferently taken in one and the same brood-cell*. Still further, in some cases the wasp first captured *Phaneroptera* as the egg pedestal and later collected *Homorocoryphus* alone. It seems to go too far, therefore, to explain such individual preference as mentioned by a simple inclination of adhering to the first prey species.

I believe that the phenomenon affords us an instance of the actual specialization of instinctive behaviour, that is to say, the preference is based to a considerable extent on the hereditary inclination. The difference with the locality observed in the range of the prey selection and in the percentage occupied by the exception seems to indicate that it is just in the course of differentiation and is not as yet fixed firmly. To speak to the extreme, apparent adhering to the first prey is nothing else than the manifestation of this hereditary tendency. Without such a basis we can not consider such an absolute adhering to a certain species of prey.

Discussion on the evolutional trend As an evolutional trend it seems possible that two different opinions are opposed to each other. Some one says that in the general trend of evolution the kind of food is from restricted to unrestricted. This is directly connected with the survival values; and in the higher animals the trend is fairly striking. Even in the solitary hunting wasps the advanced insects such as *Bembix* and especially *Microbembex* have a large extent in the kind of food. Accordingly, in the Sphex in question, the individuals that show a limited preference in the species of prey represent the primitive groop, while those which mingle several different species of prey belong to the advanced group. The more the species number of the prey, the higher in the evolutional level.

While, others insist that the general trend of evolution is a differentiation and it means a specialization without doubt; this is a dynamic aspect in nature and at the step before natural selection; it is a problem different in the level from survival values accordingly; those which were specialized in improper direction will be swept out from the world through the agency of natural selection; and the relation is well

* The 50 insects of *Homolocoryphus* taken out of the nests contained 80 % of green. This agreed roughly with the percentage of the two colour forms in nature confirmed by a random collection by pupils.

shown by the ancient animals now remain in fossils. Therefore, among the individuals of the Sphex those which show a definite preference towards a certain single species of the prey come to represent an advanced group, while those mix several species an undiferentiated, that is to say, primitive group, apart from the survival values.

The first opinion is mainly insisted by Iwata, a well known habits investigator of Hymenoptera. But I am inclined to support the second opinion in this case, though I do not deny the possibility of the first case in some other animal groups. Had the first opinion been true it becomes that the Spex in question must be a mixed group of the representatives of 4 independent lines, namely, *Phaneroptera*-hunter, *Ducetia*-hunter, *Hexacentrus*-hunter and *Homorocoryphus*-hunter, because among the four species of the prey there is no chiefly prefered insect which is supposed to be the original stem of the prey species. This is very strange and does not consist with the opinion itself. If the range of food-species is enlarged, there must be a chief species and some additional varied species, and there must be no specialization towards each of the four different species. On the other hand, if the preference has been specialized it is quite natural that the result reaches the present staus. Moreover, there is no doubt as to the fact that specialization is the general rule of evolution. Without this idea we can not realize the differentiation in evolution. And the case in the Sphex cannot be an exception to this rule, I believe.

3. Carriage, storing and number per cell of the prey

I have not observed the hunting behaviour of this species. Carriage is performed on the wing, holding it by the antennae with the mandibles, usually supporting it with the middle pair of legs, but sometimes hanging down freely from the mouth. Near the nest the wasp lands on the ground and goes walking towards the nest entrance, dragging the prey under her body. The prey is always dorsum-up. The wasp stretches her legs and straddles the prey, catching it by the base of the antennae, without holding it with any of the legs. In front of the entrance she lays it aside, removes the entrance closure, enters the tunnel empty-handed to clear the branch tunnel leading to the just provisioning larval cell. She then comes out of the nest, head first, carries the prey to the entrance in the usual manner, lays it aside again, enters the nest head first, turns round in the burrow, protrudes her anterior body out of the entrance, catches the prey by the antennae and pulls it backing into the tunnel. The manner is quite streotyped.

In the brood-cell the prey is placed venter-up, head-in and the egg of the wasp is always laid on the first prey carried in. The prey successively brought in are piled up in the chamber. The number per cell is usually from 2 to 5. In one exceptional case I found 7 prey in one cell. In this case, however, there is a doubt whether they are really stored by a single wasp, since occasionally some neighbour by mistake, and some abnormal wasp intentionally (it seems) carries the prey into the nest of other wasp (see p. 29).

4. State of the prey

The prey robbed of the wasp while it is carrying, or taken out of the nest are all alive. They can slowly move the antennae and palpi in reaction to the stimulus. Their abdomens are slowly distended and contracted for respiration, their hearts slowly pulsate and they excrete regulary for several days. But they cannot move for themselves. An instance, of which I took a record, distinctly reacted to the stimulation for 8 days by moving its palpi; from the 9th day, however, it did not show the reaction, but its articulation is pliant and its fresh coloration was unaltered, only the abdomen being strikingly shrunk. After remaining for 5 further days in such a state it began to harden, but no sign of putrefaction could be observed. Obviously the insect starved to death.

In the brood-cells I not unfrequently found the prey putrefied. In such a case the egg of the wasp did not hatch and the feces piled up at their posterior ends were covered with mould and thence they became putrefied. Probably high moisture in the cell accelerated the corruption.

3. THE EGG, LARVA AND THE LARVAL BIOLOGY

1. The egg

As above mentioned the egg is laid on the first victim carried in each larval cell. It is attached to the anterior part of the mesosternum just obliquely inside one of the front coxae, lying somewhat obliquely crosswise and protruding its caudal portion sidewards from the opposite side. Which side of the sternum is selected to glue the egg is quite uncertain. In 24 instances observed by me each side occupied a half of the total number. The egg is markedly long, measuring 5.5–6.0 mm in length 1.0–1.3 mm in width, with both ends rounded and slightly bent. In colour it is pale yellow and has a waxy lustre.

2. The larva and the cocoon

The egg hatches after 20–30 hours after being laid. The difference in time is directly affected by the temperature of the period. This is also the case with regard to the growth of the larva. The hatched larva begins to eat the prey from the very spot to which the cephalic pole of the egg has been attached. The head of the larva penetrates into the body of the prey by the aid of the lengthened neck-like thorax, with the posterior portion of the body remained outside and swollen rapidly. When the first prey is consumed for which 2 or 3 days are needed the larva pulls its head out of the corpse and begins to eat the 2nd victim. At this time the place from which it gnaws into the victim's body is uncertain. The time required to devour up the 2nd, 3rd and 4th victims is usually 3–4 days. When the amount of food provided by the mother wasp is inadequate the larva after eating the final victim returns to the remaining corpses of the already eaten victim and perfectly sucks up every bit of flesh, leaving only the uneatable chitin sclerites. Usually five days are necessary to consume the full provision (4–5 prey) under the laboratory rearing in August. Then it begins to spin the cocoon.

I frequently reared the larva in a tube bottle having a diameter of about 15–20 mm and packed with cotton plugs at both ends (Pl. III, Fig. 1). The full-grown larva placed in it soon began to spin the cocoon. In nature the cocoons are always spun with its cephalic end, that is to say, rounded end directing towards the entrance of the chamber. In the tube bottle, too, the cephalic end is always directed towards the mouth of the tube, though the place is closed with a cotton plug, with but a single exception among about a score of trials. The cocoon is lengthened egg-shaped, 30–40 mm in length and 8–10 mm in width and fairly deep yellow in colour. It has a duplicate structure, the outer layer being thin and compact fibrous in tissue and the inner layer hard, rigid, showing a considerable resistance against the pressure between fingers. By cutting open we can see the cocoon is smeared inside with a dark brown plastic substance, believed since Fabre to derive from the excrement of the larva.

3. An experiment on the larval preference of food

Since the remote days when the prey species are determined to the wasps of this species the larvae have continued to eat food limited to a certain narrow range. It seems therefore quite probable that they also show the same kind of food preference, as their mothers do, for some restricted prey species, somewhat similar to the cases of Lepidopterous larvae. Or do they still remain in the plastic state, capable of receiving any eatable meat if a chance is given to them? In summer of 1929 I tried to give them various kinds of insects and other small animals. I selected several larvae that reached the final instar when their appetite became most hightened. They were reared in basins filled with wet sand.

First I gave to a larva a female adult *Gampsocleis burgeri* de Haan (Tettigoniidae) which was artificially paralyzed by injecting a drop of acetic acid. The larva cut open the abdomen of the prey, thence thrust its head and completely devoured it. I again gave it another specimen of the same species. The larva ate it up and spun the normal cocoon. To the second larva was given an adult *Gryllus mistratus* Burm. (♀) (Gryllidae) and to the third a large adult mantis, *Paratenodera sinensis* Sauss., filled with eggs. Both were accepted by each larva without a sign of the least hesitation and completely eaten up, only the eggs being left untouched. The fourth and fifth larvae ate respectively *Locusta migratoria* L. (Locustidae) and *Phraortus elongatus* Thum. (Phasmida, Prisomeridae) quite indifferently. Among the Orthopterous insects given only the example of *Acrida lata* Motsch, and *Xiphydion* sp. were refused after long trial. Both the species were not welcomed even by the ants, in the comparative observation. I then gave each one of the larvae a caterpillar (a larva of Noctuidae) robbed of *Ammophila*, spiders deprived of *Pompilus* and *Anoplius*. All of them were accepted and devoured. So I turned my attention to the insects that have not been captured by the fossorial wasps of our country. The dragonfly, *Anax parthenope* Selys, the cicada, *Meimura opalifera* Walk. and the beetle, *Anomala cuprea* Hope were selected. Their heads and abdomens were cut off and the thorax alone was given with the sclerite cut open. The larvae ate them one after another with apparently the same appetite as shown to the normal food and spun the cocoon normally. Finally I crushed a snail (*Euhadra peliomphara* Pfeif.), pulled out the meat and gave it to a larva. The larva tried to eat, but the tough tissue of the meat refused the larva to tear off. After the obstinate trial for 20 min. the larva gave it up and began to search for another prey.

Judging from the results it seems to be concluded that the stomach of the larva has never specialized for the particular prey given by the mother wasp.

4. NOTES ON SOME ABNORMAL BEHAVIOUR OR EVENTS

1. Two wasps fighting around a nest

On August 23, 1929, I found a wasp of this species searching something near her nest which was dug by the side of one of the sleepers of a light railway. She did not fly far away, though repeatedly driven off by the observer, but at once turned back and walked about there. I retreated several steps and began to observe her movement. She did not enter her nest, but went in the bush of weed on the road side and after a while came out carrying a long-horned grasshopper (*Hexacentrus japanicus*). She approached her nest, when I frightened her and deprived her of her game. At that moment a strange wasp suddenly appeared from the side bush and entered the nest which I believed to be a possession of the first wasp. She soon came out and attacked the first wasp which was searching about the lost game. The two insects flew up fighting in the air with strong buzzing. At last the first wasp was driven away. But she soon came back and repeatedly tried to enter the nest and every time a fight broke out. At times, a wasp entered the nest while the other was digging within and was furiously driven out. Every time at the end of a contact, the first wasp was driven away. The procedure gave me an impression that the second wasp was the rightful owner of the nest. I carefully searched for another nest that might be forgotten (!) by the first wasp. But no nest could be found around the place. I thought that it might be that the burrow was dug by the two wasps at the separate time, one at the time of absence of the other. Of course, there was no evidence of my assumption. It seemed certain, however, that the second wasp was not a labour parasite of the first.

2. Strange behaviour of a wasp in her prey storing

The same day I saw another wasp at another colony of the wasps carrying a victim on foot towards nest E through the grass field. At times she crimbed up the stem of a shrub or a grass and flew for some distance. Her movement was very slow and apparently tedious. She frequently stopped her progress and stood still, stretching her antennae forwards and trembling the tips nervously, as if she were on the watch of something unknown to me. After spending a long time she arrived at the nest which was, strange enough, left open. She dropped her burden in front of the entrance, but without entering the tunnel at once, ran about somewhat promptly and sometimes climbed the grass to take the same apparent watching posture as done before. After a while, she returned to the nest entrance, but again she did not enter there at once. She stood still in front of the entrance, with her abdomen towards the nest orifice, and stretching her antennae forwards, apparently in the highest tension. Again she walked about around the nest. During the time she happened to touch the insect she placed, but she passed over them quite indifferently. She then came back to the nest, again took the same watchful posture towards exterior. In spite of my careful search, however, there was no living form that might be the cause of such strange bchaviour of the wasp, except myself, and it was certain that I was not the object that could attract the attention of the wasp on such an occasion. Indeed, around the nest there was no dangerous living thing such as the parasitic flies which sometimes gave rise to a cautious movements in the wasp. Finally the wasp turned round and entered the burrow. However, after a moment she came out, walked about once more around the nest. Then she hurried in the nest head first, turned round in the tunnel, produced her head out of the entrance and this time caught the grasshopper by the antennae and pulled it in the burrow. To my surprise, a moment later the wasp ran up out of the tunnel and took that alert posture for a while. At last she entered the nest to stay for about a minute and a half, probably for oviposition. When she reappeared at the entrance she raked the sand together a little, but without closing the entrance, climbed the grass near-bye and flew away.

According to my long intercourse with various species of sand burrowing solitary wasps, such behaviour as mentioned above can be observed only with the individual that are in the act of labour papasitism — not as yet fixed hereditarily (in the fixed state the parasite is very audacious), but occasionlly appearing among the comrades that are otherwise diligent and independent labourers.

I at once dug open the nest. The tunnel showed the ordinary type of structuse and the branch tunnel at the bottom (10 cm in length) was not as yet closed. The larval cell at the end had, however, already invaded by a troop of maggots of the parasitic fly which were devouring the victims belonging to *Phaneroptera.* The victim carried in by the wasp a short while before was an insect of *Hexacentrus.* Therefore, this was not her cell. A second cell discovered was also invaded by maggots which were larger than the preceding. The cell was an accomplishcd one, since the branch tunnel leading to it was completely packed with soil. Slightly above this I found a third cell, with its branch tunnel roughly closed. The *Hexacentrus* that I saw was laid singly in the cell, with the egg of the wasp attached to it. The informations obtained from digging can be summarized as follows:

(1) The prey in the first two cells were all *Phaneroptera nigroantennata.* (2) The prey in the third cell belonged to *Hexacentrus japonicus.* (3) The tunnel to the second cell that I examined first was left unpacked.

Probable explanations: (1) The first two cells invaded by mattots were made by a wasp other than that observed by me and the latter was an intruder. (2) The wasp observed was the owner of the nest, becoming nervous against the parasitic fly. To me the first seems most probable, since (a) the prey species carried by her was different from others provisioned in other cells, (b) cell 2 was imcomplete and there is no reason to be abandoned by the owner to construct a third cell.... usually the wasp continues her provisioning work without reference to the parasite invaded.

3. Two eggs found in a cell

During my investigation of the nests of this species in Utsunomiya in 1936 I found a larval cell containing two eggs of the wasp attached respectively to a separate victim. In the cell in question 1 *Phaneroptera* and 4 *Homorocoryphus* were laid. The former was found separately at the interiormost portion of the cell and being eaten by a 8 mm larva of the wasp, while the latter were piled at the entrance portion in a mass and on one of them was found the wasp's egg. The nest contained three other cells, respectively provisioned with 2, 4 and 0 prey, all but one belonged to *Homorocoryphus*, the exception being *Phaneroptera*. These cells were normal, having respectively a single egg laid on one of the prey, except the empty (not as yet provisioned) one. The branch tunnels leading to these cells were given off nearly at the same level in different directions from the main tunnel and that to the first cell in question alone lay by about 7 cm below the others.

Now, with regard to the first cell how and why have the two eggs been laid ? We can presume the following two cases:

(1) The mother wasp dug up the first cell, took in the first prey and laid the egg on it, but by some reason or other (probably bad weather) she could not continue her successive work or provisioning. When she resumed her work after 2 or 3 days her next egg had already been maturated and she started all the work to the cell once again. (2) Either of the prey on which an egg was laid was carried in by some individual other than the mother wasp, either by mistake or intentionally.

Judging by the fact that the *Phaneroptera* bearing the larva on it must be carried in the cell at about 2 or 3 days earlier than others, the first assumption may appear probable. But to me it seems that the general linked nature of the instinctive behaviour system will oppose the occurrence of oviposition without the preceding burrowing work of the cell. Moreover, apparently the insect are able to accommodate the oviposition in the case of delay of only a few days, since, if such is unable, abnormal events such as an inadequately provisioned cells, must be met with very frequently after the continued rainfall.

With respect to the second assumption the probability seems higher. I have already described observations on the one hand upon the two wasps contending one and the same nest, and on the other hand upon the individual who has, it seemed, intentionally carried her victim in the nest of other wasp to lay her egg.

As to the casual intrusion to other's nest we not less frequently observe instances in the dense colony of many species of the sand burrowing hunting wasps (e. g. *Bembix* and *Cerceris*). As to the intentional intrusion in the species that usually do not live a parasitic life two instances have been known, namely, *Ammophila sabulosa infesta* Sm. and *Batozonus annulatus* F. (Tsuneki, 1935). In both instances some wasp of the same species digs the buried prey out of other's nest, destroys the laid egg, emends the nest, retransports the prey into the nest and lays its own egg. The behaviour after removing the egg of the rightful owner of the nest follows the normal course of the habits of the species.

If the case in question belongs to the casual intrusion there arises no special problem. But if the case is based on the intentional intrusion, it comes to furnish another instance of the most primitive parasitism. It is performed motivationally as a parasitism on the larval cell alone, since the wasp carries in her victim to lay her egg. But as a final result it becomes parasitic on whole the contents of the cell, since the hatched larva after eating the prey on which it was laid devours the later hatched larva and the provision of the rightful owner of the nest.

To me it seems most probable that the two eggs laid in one chamber were brought about through either of the two cases of the second assumption.

II. *SPHEX (SPHEX) FLAMMITRICHUS* STRAND

This is a large beautiful species, adorned on the face, clypeus and propodeum with long, dense, golden pubescence. The wings are ambur yellow and slightly clouded on the apical margin. The species is distributed over Formosa, the Ryukyus, Kyushu, Shikoku and southern half of Japan proper, ranging easterly to Shizuoka Pref. and westerly along the coast of Japan Sea as far north as Tsuruga, Fukui Pref.

This species is very similar in nesting habits to *S. argentatus fumosus* Mocs. They prefer sandy area for nesting site, they live in colony, they make the branched compound nest and they catch also the long horned grasshopper as food for the young. The modes of their burrowing, carriage, placement of prey, oviposition and closing of the nest are also similar to those of the compared species. The structure and the form of the nest, egg and cocoon are also very similar, but the wasp of this species does not construct the side holes at the entrance. Generally the nest is slightly grander in scale in proportion to the size of the body of the wasp.

1. The prey

I have observed a number of colonies of this species in Honshu, Shikoku and on the Island of Amami-Ohshima (Ryukyu). Everywhere the wasps hunt *Holochlora japonica* Br. v. Watt. (Tettigoniidae) exclusively. But Iwata recorded that he found *Ducetia japonica* exceptionally stored in one of the nests in the district of Osaka. Generally the imagoes and nymphs are indifferently captured. Early in the season nymphs are mainly caught, but later gradually the proportion of the adults is increased and finally it occupies whole the part. This is only due to the relation between the growth degrees of the prey and the periods of the wasp's activity, as was pointed out by Iwata.

The number of the prey stored in one cell ranges from 2 to 6. I have not confirmed that the number per cell has an inclination of decrease from the interior cell to the exterior, parallel to the order of construction. This was reported by Iwata and was accounted for as connecting with the sex and size of the adult insects future emerging. In my opinion, however, if such is really the case, it seems to have no ecological significance, since in the branched compound structure, different from the tube-renting linear one, the earlier or later of the emergence of the adult wasps has nothing to do with the order of passing the tunnel to the external world. At most it may show the general fundamental rule of oviposition in the wasps' world.

The state of the paralysis of the prey is similar. They can live over one week in the laboratory rearing.

2. Structure of the nest (vide addenda)

One of the nests that I have dug open was an accomplished one and had 9 larval cells inside (at Matsubara, Tsuruga, Fukui Pref., on Sept. 7, 1957). The branch tunnels were all compactly stuffed with sand and could not be persued in detail. The distribution of the cells seen from above was as given in Figure 4, and their depth from the earth surface was shown in Table 5. The number of the prey in each cell was counted from the remains of wings, head capsules and hind legs mainly. It is presumable from the figure that in this nest the main tunnel is comparatively short and long branch tunnels are given off at different levels. The order of construction was difficult to presume. The number given in the figure is only the number of discovery in digging. If the cells located deeper were made earlier as was the general rule in *S. argentatus*, then the horizontal distribution becomes irregular and there is no connection between the order of construction and the number of the prey. The cells are somewhat varied in size, the smallest are measured 60 mm in length, 25 mm in maximum width and 20 mm in maximum height, while the largest are respectively 80, 35 and 27 mm.

Table 5. Depth of larval cells from the earth sruface and thenumber of prey

Cell No.	Depth (cm)	Prey
1	30	4
2	35	1
3	40	4
4	45	3
5	38	2
6	30	6
7	37	2
8	40	4
9	40	6

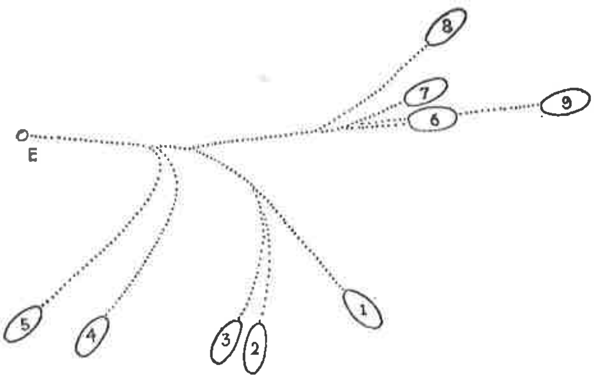


Fig. 4. A nest of *S. flammitricus* seen from above.

There is no side holes in the nest of this species. The sand dug out was heaped in front of the entrance. In the nest above mentioned the heap occupied an elliptic area of 25×13 cm. In Tsuruga the surface sand was greyish, while below 10 cm the sand turned yellowish. Therefore, the heap of the dug-out sand made a strong contrast against the surface sand. But it was left as it was quite indifferently.

In the instance above given 6 out of 9 cells were damaged by the parasitic fly, only 2 cocoons being found in cell Nos. 1 and 8. In cell 2 the prey was only one and remained putrefied. Probably the egg did not hatch. The cocoon is beautiful orange yellow in colour just after spinning, but turns into brownish later.

3. Curious behaviour of a male

A farm yard in front of a cottage in Kachiura on the Island of Amami-Ohshima, the Ryukyus, was occupied by a flourishing colony of this species. Some thirty nests were crowded within an area of about 50 square meters. The females came flying one after another, hanging their heavy victims by the antennae and landed near each nest. Landing was performed rather in the manner of falling. After standing on the earth the wasps always took a short rest before carrying the prey to each nest. Over the ground the abandoned victims were scattered hither and thither, some of which were half-dried up, some remaining yet fresh. This was caused chiefly by the attack of the ants and partly by the intrusion of men and animals. The ants, though they deprived the wasps of their prey, frequently abandoned it because of difficulty of carriage and too abundant bait. The insects transported by the wasps belonged all to *Holochroa japonica*, chiefly females and imagoes (July 3, 1961). During my work of taking the colour photograph I took notice of a wasp that behaved quite curiously. It could not be other than the male, judging from its pale golden hairs on the propodeum and the small size of the body. It walked about on the earth, took up a victim that was temporarily laid aside by some wasp during her inspection of the interior of the nest and carried it about in the same manner as females did. It walked about on the earth dragging the prey, turning round and round without reaching any nest. When approached by me, the wasp left the prey, flew up in the air and made a short pendant flight in front of my face and finally flew off. After a while I found a male wasp carrying about a victim, probably the same individual as I saw before. It aimlessly dragging about the grasshopper for about 5 minutes. Then I approached and directed my lens towards the wasp. Suddenly it turned its way towards me and began to follow me as I moved. Whenever I moved sideways in order to catch its profile it at once turned its way and faithfully followed after me, so that I could not take photograph from the side. I retreated several steps and left it alone. After walking round and round over the ground, dragging the prey, it finally left it on the earth and flew away. About ten minutes later I again took notice of it dragging another victim. This time I caught it to ascertain its sex. Doubtless it was a male. The prey that he carried about was, of course, not the one he himself captured. I saw once that he walked about empty-handed and began to carry about a prey with which he met during the course.

It seems interesting that the male still retains the same instinct of carrying the victim in the same nammer as the female does.

III. *SPHEX (SPHEX) MAXILLOSUS* FABRICIUS

1. AN OBSERVATION IN THE MONGOLIAN STEPPE (at Apaka, July 19, 1939)

I turned back from the Ephedra-Hill to a small valley and was sweeping my insect net on *Astragalus tenuis* Turcz. which was in full bloom of the tufts of pretty little flowers. Again I had a fortune to capture a red banded Sphex. To my surprise, the wasp came flying one followed by another, so that I could collect as many specimens as I would. The female of this species is somewhat larger and more beautiful than the male, for she has the four posterior legs also adorned more broadly with red. I was tired with the long continued walking and went leisurely down the valley to the small delta where the waterless brook opened into a flat grassland. There, quite unexpectedly, I discovered the hermitage of the wasp.

At a few meters in front of me a wasp landed on the ground covered sparsely with weed. She was just a red-banded Sphex! Further, she held a greenish insect under her body. Lucky enough! She has just come back from her hunting journey. Her nest must be concealed in the neighbourhood. Careful follow will lead me to her retreat! With the utmost care not to frightened the wasp I approached her. She was dragging the victim among grasses, capturing it by the bases of antennae and straddling it from the back. From time to time she crimbed the grass. From the top of the grass which was rocked and bent by the weight of her and her burden she flew for about 2 m or so with her game hanging down and landed among the grasses. Thus mixing her walking with short flights she crossed the delta and reached the foot of one of the hills. There, her domicile was concealed. The wasp laid aside her prey and penetrated into a burrow which was opened at that place. On one side of the entrance was heaped the débris taken out of the burrow, but there was no side holes. It seemed strange to me that the entrance to her burrow was left open during she was absent, since all the Japanese species that I knew closed it carefully every time she left the place. After a moment the wasp made its appearance at the entrance hole, but soon retreated without catching the prey lying there. Again she betreyed her head at the door, but again backed without touching the victim. At a third time she finally caught it by the antennae and pulled it backing into the burrow. During the time when the victim was left alone I could confirm that it was a nymph of some species of the long-horned grasshopper belonging to Phaneropterinae having a short, acutely reflected sword-shaped ovipositor.

1. **Mode of burrowing**

I looked around and as I expected could find another three wasps burrowing their nests. They thus lived in colony as allied species did. The mode of their digging is much the same as in the Japanese black Sphex (*S. argentatus fumosus*). The wasp carried out backing armful of earth from the bottom of her burrow, holding it against her breast with the mandibles and fore legs which were curled up inwards to form a rough net work. When arrived near the entrance she pushed the burden backwards from under her body and at once went in the tunnel. After 5–6 times of such a carriage the entrance was completely closed with the earth brought out, since the wasp pushed back the burden before she completely appeared out of the entrance. Thus, her movement was only supposed by the intervalic stirring of earth stopper formed at the entrance. After a while the wasp came out of the burrow backing through the stopper and carefully cleaned her antennae and wings with her fore and hind legs. Then she carried backing the earth piled up at the entrance one armful after another for about 10 cm or so and scraped it backwards. No hurried manner was observed as usually done in the species of the spider wasps.

Turning back to the first wasp I found that she had already started to her next hunting journey and the entrance was left open as before. It seemed too early to open the nest. But I was unable to rule freely my time. The chance must not be allowed to fly away. I began at once to dig the burrow. My digging tool was, as usually the case, a pocket-knife only. But I succeeded in uncovering the nest by patience and carefulness. Patience was needed not only in the slow pace of digging, but especially in enduring the attack of a host of the blood-sucking flies and mosquitoes which were the only but the most disagreeable living things in the grassland of Inner Mongolia. The nest had the following structure:

2. Structure of the nest

See Figure 5. The entrance is about 8 mm in diameter, the tunnel penetrates into the earth at a steep slope, nearly vertically, for about 4 cm, then turns almost horizontal and goes for 6 cm, Thence it turns through about 90° in the horizontal plane and proceeds for 1. 5 cm, then it suddenly inclines downwards again in nearly a vertical line and ends after entering to 8 cm. No temporary closure was made anywhere in the tunnel. By searching at the bottom, two horizontal branch-tunnels were discovered, each being ended with a larval cell after running for about 2–4 cm. Slightly apart from these, another short tunnel was given off from the middle of the second vertical portion which also led to a end cell. At each base the branch tunnels were closed with earth. The brood cell is slightly enlarged than the tunnel and about 3. 0–3. 5 mm in length, placed horizontally, and in cells 1 and 3 the length axis made a certin angle with the branch tunnel whith ran straight. (The cells were numbered provisionally from below.)

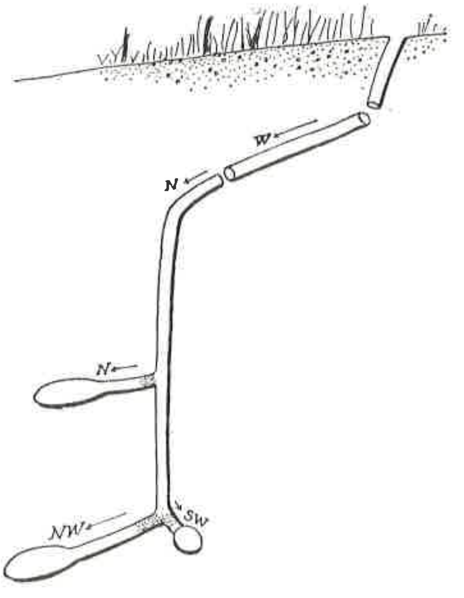


Fig. 5. A nest of *S. maxillosus.*

3. Contents of the cells

In cell 1 one nymph (♀) of *Phaneroptera* sp., about 25 mm long (probably final instar) was placed, venter-up and head-in. An egg was attached to the inside of the left fore leg, slightly deviated towards the mid leg. It crossed the thorax of the prey, with its apex slightly produced sideways from posterior to the right fore leg. It is cylindric, slightly bent, with both ends rounded, but relatively shorter than in the Japanese black Sphex and much paler in yellow coloration. In cell 2 two nymphs (♂♂) of the same species was similarly laid. The egg could not be discovered, but it might be fallen off during it was taken out. In cell 3 the nymph that I saw carried in by the wasp was laid, but without the egg, in spite of my careful handling.

4. Some problems

This wasp is, so far as observed, strange in three points in habits. The first is the fact that despite there were three larval cells none of the tunnels leading to them was completely closed with earth. All the three were closed at the entrance portion only. In the Japanese black Sphex the next larval cell is prepared just when the preceding cell has completely provisioned and the branch tunnel has thoroughly and compactly closed with earth which is probably taken from the branch tunnel of the next larval cell. The second is that apparently there was no connection between the provisioning and oviposition in some cells. Apart from cell 2 from which the egg might have lost, cell 1 contained a single egg-bearing grasshopper only, while cell 3 also a single victim, but to which the egg of the wasp was not deposited. The third point is that the branch-tunnel leading to cell 3 was opened in the mid way of the vertical main tunnel.

How we explain these strange points? Has the wasp a hibit of burrowing several cells at first and later making provisioning and oviposition without order? I cannot imagine such a disorder in the life of a member of *Sphex*. Then what is told by the queer facts above mentioned? My tentatve explanation is as follows:

Cell 3 would have been made at first, probably being given off from the then bottom of the main tunnel. By some reason the wasp could not work after finishing the cell construction, and when she resumed the work, the cell was already out of her working schedule. She further dug the main tunnel downwards and completed cell 2 (construction, provisioning, oviposition (?) and additional provisioning). She then construct cell 1, carried in the first prey and laid her egg on it. When I found her, she was engaging in the additional provisioning work to the cell. During the course of carriage of the prey to the cell, however, she discovered the entrance to cell 3, and she dragged the victim into the cell, probably with the intention to take it to cell 1. That the single prey in the cell was not attached the wasp's egg is due to that it is in reality the additional prey to cell 1*. If cell 2 really lacks the egg of the wasp, the state comes more interesting, that is to say, the wasp stored the additional prey in the cells other than that in which the egg was laid, in cell 2 two and in cell 3 one.

The prey were all alive, with the abdomen slowly pulsated for respiration, with the antennae tediously moved and when stimulated they could move the mouth parts.

* * *

After the examination of the nest I turned back to my barrack, with a happy expectation of uncovering the other three nests on my next visit. However, when I went there again after several days, to my disappointment, I found that all of them were left abandoned without being completed. Even the main tunnel was not dug up. Why they stopped their work I could not know. But I found anew the nests of another in-

* Later when I investigated in the suburbs of Sapporo behaviour of *Bembix niponica* within the nest, I frequently observed that the wasp backing in the branched glass-tunnels carried in her victim to the tunnel and cell other than that to which she intended to take it. The wasp can not control the direction of her backing progress.

teresting wasps and my interest was turned to them, so that no further pursuit was made with respect to the red-banded Sphex. (Later when I came back to Japan I knew that my red-banded Sphex was nothing but "le Sphex à ailes jaunes" of J. H. Fabre.)
(Translated from my *A Naturalist at the Front*, 1943)

III. *SPHEX (SPHEX) FUKUIANUS* TSUNEKI

I already reported an instance of the nest of this rare species* which was observed on August 8, 1953. First I will give abstract of the paper and then will describe the observations further carried out.

1. SUMMARY ON THE FIRST NEST

The nesting site was an area sparsely covered with weed and surrounded by tall trees. The nest was apparently of the compound branched type, containing 3 larval cells inside. But the detailed structure could not be clarified, since the tunnels leading to the cells were compactly closed with the same soil as that of the surroundings. The brood-cells lay shallow, about 8 cm below the surface of the ground. The main tunnel leading to a provisioning cell was 23 cm in length, curved, fairly steep for the first 8 cm and then ran nearly horizontally. It was temporarily closed in front of the brood-cell which was 55×20×15 (h) mm in dimensions. There was some doubt as to whether the 3 cells aggregated there really belonged to one nest or they were respectively made separately, since the direction of the cells could not smoothly be connected with the main tunnel at that time (Fig. 6). The prey belonged exclusively the curious wingless brownish longhorned grasshopper, *Eremus testaceus* Mats. et Shir., all being adult forms of both sexes. A very strange and characteristic habit is that the bodily orientation of the prey accumulated in the cell is uncertain. In cell 3 which was in the course of provisioning contained 5 prey of which 3 were head-in and 2 head-out; in cells 2 and 3 were stored respectively 8 and 7 prey, nearly half of which were laid head-out. Some of these lay dorsum-up, some venter-up and others side-up, involving every transitional state. The form of the egg, its method of attachment to the first prey is similar to the case of *S. argentatus*. The entrance to the burrow is sometimes closed, but usually left open.

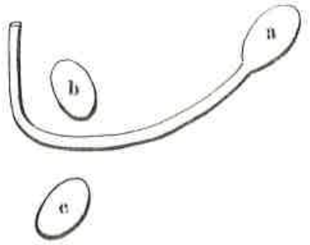


Fig. 6. A nest of *S. fukuianus*, seen from above.

2. OBSERVATIONS AT THE SECOND COLONY

I found a second nesting place of this species at about 10 km south of the first place (Fukui Pref.) at a path on a hill side running from north to south at about 50 m above the surrounding farm. The path was sparsely covered with deciduous trees and

* Tsuneki, K. 1957. Kontyu, **25**: 50–52.

exposed to the sunshine coming through the sparse canopy for several hours chiefly in the afternoon. On the path, 1.7 m in width, I could count 10 nests of this species scattered over the range of 15 m. Further, on a small flattened area at the path-side which appeared by demolishing the hill side a crowded colony consisting of 27 nests was discovered. The soil was clayey and considerably hard.

1. Carriage of the prey

The wasps each with a prey returned one after another to their nesting site. They came on the wing hanging the prey and rather dropped on to the ground near the nest. The prey belonged, without exception, to the same wingless species of Grillacridae, *Eremus testaceus*, as observed previously. Usually, after taking a rest a while they proceeded towards each own nest. During the resting time it was confirmed that the prey was held by the base of antennae with the mandibles of the wasp and when she walked forwards it was supported from the sides by the middle pair of the legs. Most of the prey were laid dorsum-up, but some ones venter-up, but always head forwards. They were straddled by the wasps and dragged forwards. At the side of the nest the wasp laid the prey alone and entered the nest empty handed and head first. It was repeatedly confirmed that this was the rule and the method of entering the nest with the prey directly from the preceding carriage that I observed in the first instance belonged to exception. Probably at that time the wasp would have dropped the prey in the tunnel soon after passing the entrance just as done by *Bembix niponica*.

The wasp spent a few minutes probably to clear the tunnel by removing the earth plug. During the time she came out backing once or twice to the entrance carrying the earth. Finally she appeared head first, grappled the antennae of the prey and pulled it backing into the larval chamber.

2. The nests and the contents

Three nests were dug open. Within the range of distribution of an aggregation of several larval cells were always discovered some old cells and cocoons. In nest 2 the new tunnel ran through an old cell. The facts seem to show that the newly born wasp has a habit of reutilizing the old tunnel through which it has come, for the first time, to the outer world.

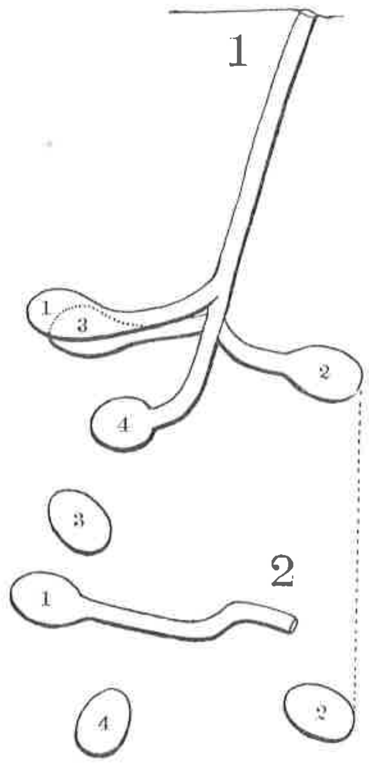


Fig. 7. The second nest of *S. fukuianus*, in the lateral and dorsal view.

The nests, though their branching feature could not be actually pursued, is considered still to belong to the compound branching type. Regarding this problem an explanation will be given in another section.

The prey found in the cells were restricted to the same species as observed outide the nest, so far examined, all being adult insects, mixing both sexes. Their bodily orientation in the cell was in all but 2 constant, namely, head-in, but utterly inconstant with respect to the dorso-ventral axis of the body, some dorsum-up, some venter-up and others side-up, though the last mentioned instances were greatest in proportion. This may partly due to the bodily posture of the insects when carried in, but mainly to their bodily structure. The two exceptional examples were found in cell 2 of nest 1 in which 4 prey were stored, of which the external two were laid with their head outwards.

The egg or the young larva was always found on the prey lying innermost, that is to say, on the prey stored first.

Nest 1 The structure was as given in Figure 7 and the contents in Table 6. The

Table 6. Three nests of *Sphex fukuianus* Tsuneki

Nest No.	Cell No.	Dimensions L×W	Depth to cell	prey ♀	prey ♂	Larval stage	Order of constr.	Remarks
1	1	30×18	13	2	3	Egg	4	
	2	25×22	14	4	0	L, 8	2	
	3	28×17	13	4	3	Egg	3	2 maggots
	4	28×20	16	3	2	Eaten	1	7 maggots
2	-	- -	18	-	-	-	-	
3	1	32×20	12	2	2	Egg	6	1 maggot
	2	30×22	13	1	-	Eaten	5	Ants
	3	28×20	13	1	3	L, 8	4	
	4	30×19	15	2	4	L, 10	3	
	5	35×18	14	-	-	Eaten	2	Many magg.
	6	38×20	15	1	3	L, 15	1	

Remarks. Depth, to the cell ceiling (cm). L, larva (mm).

main tunnel, nearly vertical, turns horizontal at the depth of 13 cm and after running for 4 cm connects with the larval cell. The horizontal portion was compactely stuffed with soil. The cells usually lie horizontal; however, cell 2 was slightly inclined. Between cells 1 and 4 there were two old cells, one being empty and the other containing a complete-formed cocoon with the corpse of the old prepupa in it.

Nest 2 The tunnel runs at a gentle inclination for the first several cm, then penetrates nearly vertically into the earth, piercing an old cell at the depth of 15 cm. Around the tunnel at about the same level (5 cm in depth) there were 3 old cells, one being empty, the other with a dried lump of the moulded prey and the 3rd with a cut cocoon filled with soil. The tunnel further goes in the earth for 3 cm and ends in an oblique inclination. No larval cell was discovered anywhere around the tunnel.

Nest 3 The structure of the nest was shown in Figure 8 and the contents in Table 6. Cell 2 was ravaged by a host of ants (*Lasius flavus*) and the egg had already been destroyed. Cell 3 was slightly inclined. Cell 5 was completely destroyed by the invation of a number of maggots of the parasitic fly. The number and the sex of the prey could not be counted. From the prey taken out of cell 1 appeared a maggot the next day.

3. Character of the nest

Judging by the pile of débris at the entrance the nests seem better to be treated as compound in structure, the aggregation of the cells having the main tunnel in common. However, the distribution of the cells and the directin of their longitudinal axes indicate that even so the portion of the tunnel used in common must be comparatively short. In general, in order to make a cluster of several cells situated in the same general direction the tunnel commonly utilized may be comparatively long. On the contrary, when the cells lying in the opposite direction are dug the portion commonly used may become sometimes the entrance only, since generally the tunnel near the entrance is inclined, though for a short distance, towards the cell just being dug or provisioned. However, the compact and thorough closure of the tunnels leading to the accomplished cells using the same kind of soil with the surroundings prevent us from pursuing the detailed feature of the nest. But, if the case is as above surmised, sometimes the nest of this species (for instance the first nest) comes to show a state of the nest construction very near to that of the close aggregation of several nests of the simple structure. The point will be of some interest in connection with the nest construction of the following species. (Vide addenda.)

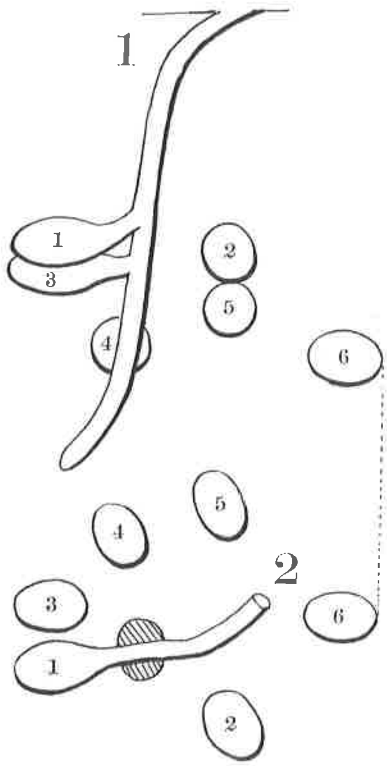


Fig. 8. Another nest of *S. fukuianus.*

Ⅳ. *SPHEX (SPHEX) HAEMORRHOIDALIS* FABRICIUS

The nesting habits of this species were observed in Korea. The first colony was found in Koryo, about 40 km northeast of Keijo (Seoul) and three others in the valley of Shoyozan, 40 km north of Keijo. Both places were well covered with forest and rich in the insect fauna, the oases to the investigators of nature in the bare mountains and flatland of Central and South Korea in those days.

1. OBSERVATION AT HOSENJI, KORYO

On July 9, 1941, I found at the ground of Hosenji temple, Koryo, several wasps of this red-legged black Sphex were flying low over the earth. Most of them were males, having the black legs. Apparently they were searching for the emerging females. Over the earth several old cocoons of Sphex, probably of this species, were scattered, telling me that this species also utilized the old nest for its own. They were not wet, despite the heavy rain of the preceding night. This showed that the cocoons were dug out of the nests that morning. On the ground several small holes were left open. But all of them were very shallow and very hard at the bottom. I thought that they were incompleted burrows abandoned after having been half dug. From time to time the female wasp appeared. They were, however, so violently chased and tackled by the contending males that they soon flew away. Occasionally, some females landed on the ground, examined the holes opening hither and thither. But they only looked in the holes one after another and never tried to dig them further. Probably the time is not as yet ripen to make them work actively.

A boy bonze of the temple told me that the wasp brought some green-coloured insects and buried them under the earth. But he did not know anything further about the habits of the wasp.

2. OBSERVATIONS AT SHOYOZAN

On July 27 of the same year, I found in the valley of Shoyozan another colony of this species, this time, too, led by the flying males. In this colony the numbers of the working females were counted up to 13. When the colony was intruded by the observer the wasps flew up to about a meter above the earth, hanging their long red legs and staring at the intruder, very slowly moving right and left with loud buzzing. If the observer remained still a little while, they flew down to each nest and resumed their stopped work. A number of rid cocoons were scattered on the ground and dzi-dzi sounds like those emitted by *Ammophila* were also uttered by the working wasps. Some nests were made at a side of the road, but most of them in the area outside it, sparsely covered with grasses. The wasps successively came back on the wing to the colony each with a prey, and departed to their hunting excursion. Another two colonies, each consisting of about 10–15 nests were also found on the road side of the same path. Therefore I could dig open the nests as many as I wanted, without the concientious pain of threatening their existence.

1. Activities of the wasp

A wasp without a prey, after flying hesitatingly in front me for about a minute, finally landed on the ground, a meter before me and proceeded towards her nest. When she was frightened by the moving shadow of the observer, she turned round at once to look at me, took a posture ready to flight. After a while, however, she turned round again and proceeded towards her nest which was left open a short distance away, with her wings twitching. At the hole, after a simple examination of the entrance, she entered it. The dzi-dzi sounds informing her digging work came from the burrow. Soon she came out with a burden of earth, backed for about 20 cm in the same posture and scraped away the earth through the underside of her abdomen. The same dgging work was continued further for some time. I thought that she was digging her nest. To my surprise, however, I found a green long-horned grasshopper laid near the entrance half covered with earth. Certainly the wasp had been removing the temporary closure of her nest. But I had not known such an elaborate temporary closure that needed an all-out effort to remove it. When the tunnel was cleared up, the wasp showed her anterior body at the entrance, caught the antennae of the prey with her mandibles and pulled it into the burrow. The manner was much the same as in other species of *Sphex* s. str.

The succeeding closing work was also very elaborate, so much so that I thought it was the final closure. But the later examination of the nest showed that it was only an temporary closure. The method: The wasp sweeps the earth backward through the underside of her abdomen towards the nest entrance. She then turns round and proceeds forwards, pushing the earth collected with the rough net-work formed with the front legs which are curled inwards. She enters the burrow, pushing the earth and presses it in place hardly with her mouth, emitting very loud dzi-dzi sounds. Soon she comes out head first and resumes the same series of behaviour again and again. But the wasp stops her closing work before the filling earth comes level with the surface. Therefore, the burrow entrance was left open, with the appearance of half dug and abandoned nest, as I saw on the ground of the Hosenji temple in Koryo.

The same strict mode of closing is also observed when the nest is closed for the first time, that is to say, when the larval cell is still empty. The fact shows that this behaviour has not been developed in direct connection with the condition of the larval cell.

2. The structure of the nest

Twenty-five nests of this species wese uncovered and examined. There is a certain fundamental type in the structure of their nests, but, of course, more or less vari-

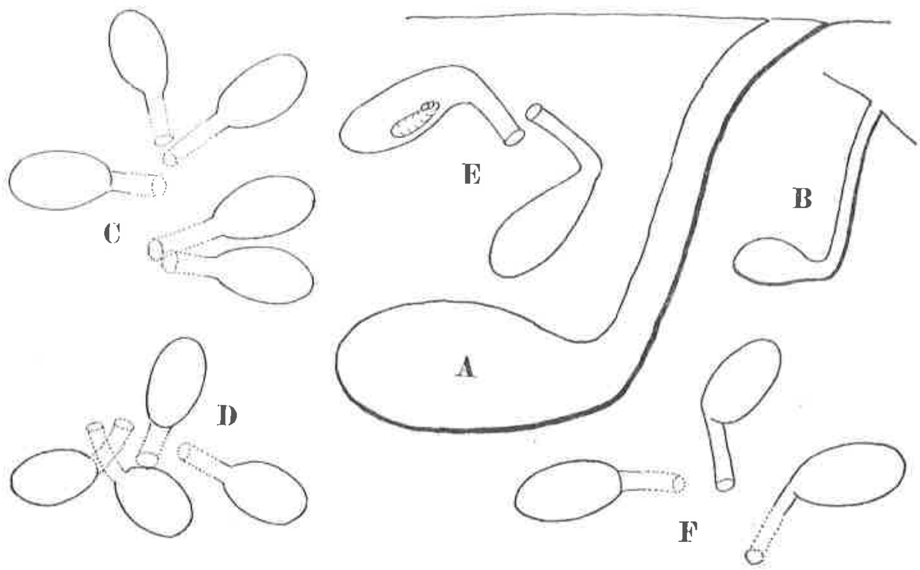


Fig. 9. Nests of *S. haemorrhoidalis*. A and B, in the lateral view; C, D, E and F, groups of nests seen from above.

ations are at times observed with respect to the inclination of the tunnel, the depth of the cell location and size and form of the cell, especially the size of the cell is fairly markedly varied.

In the typical nest the structure is as given in Figure 9, A. The tunnel is 10 mm or so in diameter; it goes for the first several centimeters obliquely in the earth, then penetrates with a steep inclination of about 70°–80° (sometimes 90°) with the earth surface for about 6–8 cm and again turns gradually horizontal and connects with the larval cell. The cell is comparatively large, subellipsoidal, usually with the dimensions 40×23×20 (h) mm, variation in length being 35–55, in width 17–28 and in height 15–25, but always the width is larger than height (Table 7). It is usually made horizontal, sometimes, however, slightly raised or declined inwards. Sometimes the brood-chamber is located only 3–5 or to the contrary 10–13 cm below the surface of the ground (depth of the ceiling). In the former case the inclination of the tunnel is very gentle and the tunnel itself is short, while in the latter *vice versa*. Not unfrequently the length axis of the brood-cell is suddenly turned to the right or the left at an angle of 70°–90° at the spot where the cell joins to the tunnel. The structure gives a suggestion that in the symmetrical position against the direction of the tunnel the other cell is located. So far examined carefully, however, no other cell could be discovered at the suggested place.

Table 7. Nests of *Sphex haemorrhoidalis* Fabricius

Nest group	Nest No.	Cell size L×W×H	Depth to cell	Prey ♀	Prey ♂	Prey Imago	Prey Nymph	Prey Total
1	1*	40×28×23	8.0	2	4	0	6	6
	2	48×25×22	7.0					?
2	3	47×25×23	5.0	3	3	2	4	6
	4*	45×25×20	3.0	3	1	–	4	4
	A	Old cell	5.3					
	B	Old cell	4.5					
	C	Old cell	6.0					
3	5*	– – –	5.5	1	2	1	2	3
	6	– – –	4.5					Rem.
	7	– – –	4.5					Rem.
	A	– – –	5.0					
4	8*	37×20×18	7.0	3	2	2	3	5
5	9*	43×25×22	8.0	–	1	–	1	1
6	10*	30×17×15	6.0	3	1	–	4	4
7	11*	45×25×22	6.5	–	–	–	–	0
8	12*	– – –	5.0	–	1	1	–	1
9	13*	– – –	7.0	–	1	–	1	1
10	14*	– – –	8.0	1	3	–	4	4
	15	– – –	6.5					Rem.
	16	– – –	5.0					Rem.
11	17*	40×25×22	7.5	3	1	1	3	4
12	18*	53×28×25	10.0	2	3	–	5	5
13	19*	45×25×20	13.0	–	1	–	1	1
14	20*	– – –	5.0	–	1	–	1	1
15	21*	40×22×18	3.0	1	–	–	1	1
16	22	Tunnel only						
17	23	Cell digging	5.5					

Remarks. Depth, to cell ceiling (cm). Rem., remains, including a cocoon. Old cell, including a cut cocoon.

The nest is considered to belong to the simple type, containing a single larval cell inside. Usually, however, several larval cells are made close together by one individual and the aggregation takes an apparent feature of the compound nest. In reality, however, I cannot perfectly deny the possibility of the common use of the entrance portion of the tunnel for two or more cells of an aggregation. However, if such is the case, each cell with the tunnel leading to it does not differ essentially from the separate nest. On the other hand, it is not necessarily the case that all the nests belonging to one individual are always made in aggregation. Because, as to the nests made late in the season, it is rather usual to find them isolated. On the contrary, early in the season, some wasps are considered to utilize the old cell in which they were borne. At least one of the sisters makes her own nest among those of her brothers and sisters, since, as given in the foregoing pages, we frequently find old cells near the one newly made.

3. Prey

The species, sex and the growth stage of the prey that I observed were given in Table 8. As for the species, almost all the prey observed early in the working period

Table 8. Prey of *Sphex haemorrhoidalis* Fabr.

Species	Imago	Nymph	♀	♂	Total
Conocephalus maculatus le Gouil.	2	9	5	6	11
Hexacentrus japonicus Karny	4	25	11	18	29
Phaneroptera nigroantennata B. v. W	0	4	2	2	4
Homorocoryphus lineosus Walker	1	2	0	3	3
Total	7	40	18	29	47

of the wasps (July and early in August) belonged to *Hexacentrus japonicus*, and as the time passed on other species were gradually mixed. Similarly they were all nymphs in the early season. But later imagoes are also observed mixed. The facts are merely due to the progress of their emergence and growth. As for choice, the wasps did not show any particular preference for any particular species, as observed in *S. argentatus*. Late in the season, therefore, several species of prey were mixed in the provision of a cell. The number per cell was 6 or more, judging by their method of provisioning given below.

O. Piel in his observation in Shanghai recorded as prey of this species *Homorocoryphus fuscipes* Redt., *Ducetia thymifolia* and other Phaneropterinae

The prey are placed in the cell head-in and mostly venter-up, sometimes, however, side-up. They are all alive and reacted for several days to the stimulus by moving antennae and palpi. Excretion, respiration and heart pulsation are also observed.

4. Progressive provisioning

Among the species of Sphecidae those which bring food to the larval cell even after the egg has hatched out — and, in the extreme case, supply food progressively as the larval development proceeds — are known only in the members of the Bembicine wasps. A species of Crabroninae (*Rhopalum latronum* Kohl) has been reported to form the only exception. It is therefore very strange and worthy of special attention that *Sphex haemorrhoidalis* shows the same type of the provisioning behaviour. This has been completely overlooked by the previous investigators of this species.

Table 9. Contents of the nests to which provisioning is going on.

Nest No.	Prey				Waspling (mm)
	Intact	Touched	Eaten	Total	
1	3	1	2	6	23
4	3	1	0	4	10
5	2	1	0	3	8
8	4	1	0	5	13
9	1	0	0	1	Egg
10	4	0	0	4	Egg
11	0	0	0	0	–
12	1	0	0	1	Egg
13	1	0	0	1	Egg
14	3	1	0	4	10
17	3	0	1	4	15
18	4	0	1	5	12
19	1	0	0	1	Egg
20	1	0	0	1	Egg
21	1	0	0	1	Egg

First, we will see the results of excavation of the nests to which the mother wasp brought a victim just before the excavation. Such nests were indicated by the numbers with an asterisk in Table 7. In the 7 nests in which the wasp's egg was found the number of the prey stored is, as a rule, but a single, only exceptionally 4 prey were accumulated in cell 10. On the other hand, 8 out of the 15 nests that were in the course of provisioning contained a larva respectively, from the young one soon after hatching to the one nearly full-grown. Remaining 7 contained the egg as above described. This informs us most eloquently that the progressive privisioning is the rule in this species and not of a fluke (Table 9).

To my regret, I did not carry out the continued observation on some marked wasps, as I did later on *Bembix*. Furthermore, detailed procedure of the provisioning remains unknown. However, the data obtained at that time give us some informations about the matter.

In the nests which contained a larva not long after hatching, we see that already 3 victims have been collected, while in those which contained a large larva we can not find more than 6 victims accumulated. On the other hand, in the nests containing a medium-sized larva 4–5 victim were provided. According to this the procedure of provisioning is presumed as follows:

The wasp, after laying the egg on the prey first carried in, waits for its hatching, and towards the time when it hatches out, she collects promptly during a comparatively short period of time 2 or 3 victims. Thereafter, she very slowly, probably once a day, brings a prey into the larval cell. When the larva approaches the full-grown stage she adds 1 or 2 prey further to the previous store and closes the cell and the tunnel finally. Whether or not the wasp tries an inspection visit regarding the egg hatching is unknown. But, judging from the elaborate method of the temporary closure it is presumed that the wasp does not do so as done by *Bembix*. But the interval of time will be measured instinctively through the internal mechanism.

On the other hand, the exceptional instance in which 4 prey had already been accumulated by the side of the egg is also interesting in showing that the wasp still occasionally takes the method close to the so-called mass provisioning.

5. Commensalismic maggots of the parasitic fly

The parasitic flies belonging to Tachynidae, such as *Miltogramma, Setulia, Araba,* and *Metopia,* are well-known enemies of the Sphecine wasps. The numberless instances as to the collapse of their nests through the encroachment of the flies' maggots well indicate how dreadful they are towards the wasps' life. However, in some species, the maggots do not always bring death to the host larva. They only share a part of food supplied by the mother wasp to her young. As far as the food is sufficient, therefore, they never touch their mouth to the body of the host grub. Such an instance is known among the species of our region in *Bembix* spp., the representatives that make progressive provisioning.

It seems quite implicit that the parasitic fly maggots found in the larval cells of *Sphex haemorrhoidalis* are just the commensals.

In cell 3 (Table 9) the waspling was nearly full-grown and still devouring the remains of food. In the interior of the chamber 3 maggots of the fly were also feeding on the remains. In cells 6 and 15, the wasplings were already in the cocoon and on the floor of the chamber were found 2 and 3 puparia scattered respectively.

6. The egg on the prey

The egg is in all the respects similar to that of *S. argentatus* and its manner of attaching is also much the same as in that species. In two instances it is 5.3×0.9 and 5.8×1.0 mm, slightly bent, yellowish in colour and with a lustre of wax. It is attached to the first prey laid upside-down, at the posterior to and slightly inside of one of the fore legs, with its anterior end, crossing obliquely the thorax and produced its posterior end from in front of the mid leg of the other side. In the case when the laterally compressed prey such as *Phaneroptera* is captured at first, it is laid on its flank and the egg is sometimes hung down from the attaching point directly downwards, without crossing the prey's thorax.

7. Growth process of the larva

I tried to rear the larvae each in a tube bottle, 18 mm in diameter, stuffed with a cotton layer at the bottom. At the nesting site the contents of each cell uncovered were shifted into the bottle and stuffed with a cotton plug at the mouth. Such bottles were transported in the rucksack to my house in Keijo and settled on a table. A considerable part of the eggs and the young larvae were dead during the course and I could observe only the following (cf. Table 9):

The larva in cell 1 It was already 23 mm in length in the posture with its head and thorax folded against its ventral surface. (The mother wasp still carrying food to its cell.) I added one *Hexacentrus* obtained from another nest in the glass chamber. The larva continued to eat it till a third day from the cellected date and spun the cocoon in the afternoon of that day.

The larva in cell 3 It was supposed that the nest of this larva had finally closed at least 2 days before, since the larva in the next nest of the aggregation was at that time about 1 day old. The larva began to spin the cocoon in the evening of the day of collection. This instance showed that the mother wasp stops her provisioning work 2 or 3 days before the full growth of her larva and closes the nest finally as in the case of *Bembix*. It is inferred that 1 or 2 victims are offered further to the larva prior to the final closure. This is also similar to the method of *Bembix*, though the amount of food is far smaller as compared with the latter.

The larva in cell 5 About 16 hours after hatching. It spent 2 days to eat the first victim to which it was attached, but died on a third day.

The larva in cell 8 About 1.5 days old. The next morning it ate up the first prey and attained about 15 mm in length (measured as above); on a third morning only a single victim was intact and the larva was 23 mm in length. In the evening of the day it began to spin the cocoon and on a fourth morning the cocoon has been completed.

The egg in cell 9 The egg was laid at 2:30 p.m. July 31. The next morning it hatched out. It spent 2 days to devour the first victim; during the next 24 hours it ate up 3 further victims that I gave and at 8 a.m. of the 6th day it was found to have spun the cocoon.

The egg in cell 10 The egg hatched in the next morning, 20 hours after being laid. The succeeding process was much the same as in the preceding instance.

Summary According to the results the egg period towards early in August in Keijo is about 17–20 hours. It needs about 48 hours to eat up the first victim on which it was laid. During the next 24–40 hours it devours all the store of food in the cell and begins to spin the cocoon. The larval period up to the cocoon formation is, therefore, about 3–3.5 days. Generally speaking (♀ and ♂), the egg hatches out on the 2nd day, the larva feeds up the provision before the middle of the 5th day and finishes the cocoon spinning by the morning of the 6th day at the latest.

8. Cocoon

The cocoon is very similar in form, structure (two layer structure) and coloration to that of *S. argentatus fumosus* and no particular explanation will be needed.

V. *SPHEX (PRIONYX) ALBISECTUS* LEPELETIER ET SERVILLE

The nesting biology of this species has already been well investigated in Europe by such authors as J. H. Fabre (1856, 1879), F. F. Kohl (1890), C. Ferton (1901, 1902) and L. Berland (1925). As to the East Asiatic representative no observation other than mine has been published. My study was made at Tiendang, Peking, during my military stay in 1938. At that time the ground of Tiendang involved vast wood between the outer and inner ramparts that protected the splendid architecture of the famous Tiendang. Through the wood there was a loop road of about 2 m in width, visited by few human beings and occupied by a host of various species of the hunting wasps and solitary bees. Making the most of my every possible free time I frequently visited the place and collected and observed the insects that were almost all new to me. Detailed accounts of my observations were given in Japanese in my book "A Naturalist at the Front" published in 1943.

1. THE FIRST OBSERVATION

1. Nest making behaviour

On June 27, 1938, I found a wasp of this Sphex burrowing on the side of the road. Her nest was dug close to the root of one of the tall grasses that bordered the road from the surrounding wood. It had already been deepened to about 20 mm. The entrance of the burrow was about 5 mm in diameter and a little too large as compared with the slender *Ammophila*-like feature of the wasp. The wasp repeatedly carried the soil out of the burrow. Her movement was very prompt and very active, without showing any warning attitude or hesitating manner as frequently done by some other hunting wasps. She runs to one side of the burrow, disappears into it like a lightening, comes out of it backing a moment later with a burden of soil, holding it between her mandibles and breast, goes backing for 10–15 cm to drop the burden. Sometimes she goes forwards across the entrance to throw away the soil. No pile of earth was made around the nest. As soon as the soil is thrown away the wasp hurriedly runs up to the entrance and plunges herself into the tunnel. The very diligent manner of her work is delightful to observe. However, from time to time she stops her digging hand, comes out empty-handed to the entrance and suddenly flys up vertically in the air to about 20 cm or so above the ground. Then she turns back quickly to her burrow to resume her work. Is this queer movement also done for the purpose of locality study? To be so, however, the movement seems too simple and too speedy. There might be hidden something other reason that was realized by the wasp only. Soon the burrow appeared to have dug up. The wasp ran about the place very quickly to search for the closing material. She picked up some grains of pebbles that were slightly larger than her head, carried them one after another to the entrance and accomplished the temporary closure of the nest. She then walked about over the ground for a while, but there was no appearance of studying the locality. She stops on a bit of fallen leaf of grass, bathed in the sun, rubbed her wings and antennae and flew away.

From the above observation I thought that the species closely resembled *Ammophila* in her nest making behaviour just as her style and coloration did.

2. Structure of the nest

A week later I revisited the place. The nest mark that I made remained as before. It showed indirectly the exact spot of the entrance of the nest. I began to dig 5 cm apart from it and succeeded to open from the side the brood-chamber of the wasp. The short tunnel was completely and very compactly stuffed with soil. The entrance of the chamber was situated 4 cm apart from right beneath the entrance of the nest and the ceiling of the brood-cell was only 5 cm in depth. To my regret the nest contents were already ravaged by the parasitic fly. From the remains I could confirm that the prey was one insect belonging to Locustidae. The chamber was rather large as compared with the small and slender style of the wasp, measuring 35 mm in length, 12 mm in width and elliptic in form.

2. THE SECOND OBSERVATION

1. Carriage and method of final closure

Just after examining the first nest I met with another wasp which was about to take in her victim to her nest which was dug some 20 m apart from the first nest. It was on the road, only 5 cm apart from the row of grasses standing like a hedge. The prey, a small short-horned grasshopper, was thrown aside on the ground and the wasp was clearing the closure of the entrance which was apparently 5.5–6.0 mm in diameter. The wasp approached the prey in a prompt movement, straddled it from the back, with her six legs stretched high and proceeded towards the entrance. One cm from the orifice she left the prey on the ground, entered the burrow head first, at once turned round in the tunnel and protruded her head from the entrance. She proceeded a little, caught the prey by the antennae and pulled it backing into the nest. After less than a minute she ran out of the nest and began to search about hurriedly for the closing material.

When she came across a pebble or a lump of earth of apparently favourable size, she picked it up without hesitation, but if it was too large or too small, she dropped it at once and began to search for another new material. When apparently a satisfactory pebble was selected she carried it into the burrow and returned at once. During a short while 6 pebbles were transported. She then began to sweep the fine dust like flour in the hole. It was thrown in backward through the underside of her abdomen. The movements were very smart. The next moment she entered the hole, stood on her head and pressed the material in place and hardened it with her head, emitting the dzi-dzi sounds loudly. Soon she came out, flew vertically up to about a meter and alighted on a twig of a grass. She rested there a very short while, brushing her antennae, wings and abdomen. But a few seconds later the wasp flew down and returned to her working place. Five pebbles were further carried in the burrow and again the dust was scraped in. She pressed them in place buzzing, with the tip of her abdomen projected from the entrance. Then she flew up to take a rest at the grass twig, a meter above the surface of the ground, and looked down from there. Soon she returned to her nest to resume the closing work. The same series of manoeuvre was several times repeated and the hole was shallowed gradually. The strange flying up to a twig of grass was also continued.

The nest was about to be completed and the wasp, as a rule, does not return to her nest already accomplished. Therefore, it seemed to me improper to take her behaviour as a sort of the orientation flight. It was of course not the warning behaviour against the enemy of the nest. Apparently it was rather an interlude to give a happy lism to her nimble mode of work.

The hole now became a mere impression on the road. The wasp brought together three lumps of earth, about as large as her head and arranged them upon the impression. But it appeared that the arrangement did not finally settle. The wasp rearranged them quite "*fastidiously*" again and again. Finally she scraped the dust in between the lumps and pressed them in place with the anterior surface of her head. During the course the lumps of earth which had so fastidiously been rearranged to form an equilateral triangle were broken into powder by her mandibles and evenly leveled and smoothed. The final closure of the nest thus finished. The wasp again flew up to the twig, a meter high, made her toilet and after a while flew down to the ground.

2. Orientation flight ?

She passed over the nest just accomplished, hurriedly ran about the neighbourhood and without any particular selecting appearance began to dig a new burrow at a spot only 30 cm apart from her preceding nest. Her subsequent movements were just the same as observed with the first wasp, except for a point that she flew up much higher in her intermittent flying up. In the former it was 20 cm or so in height, but in this wasp it reached about one meter and sometimes she alighted on the grass twig just as she did in her final closure of the nest. After digging up the burrow for which she spent about 20 min. she carried several pebbles in it to make a temporary stopper.

By the fact that the wasp made her second (?) nest close to the first, it seemed to me not unfavourable to consider that strange jumping up during the final closure and new nest digging a sort of the so-called orientation flight. But it might not directly be connected with a particular nest, but with the general survey of her nesting ground.

I capture the wasp to confirm her name and dug the two nest just observed.

3. The nest, placement of the prey and oviposition

I began with the first nest. The earth was not so hard and could be cut open without difficulty with my pen-knife. But it was rather difficult to distinguish the tunnel from the surrounding earth, since the stuffed particles were too fine, and too compactly pressed by the wasp. With care, however, it was clarified that the tunnel went in for the first 25 mm with the inclination of about 70°, then gradually turned gentle and after running for about 10 mm horizontally reached the brood-chamber. In the horizontal portion were piled up the pebbles first taken in. The chamber was as in the preceding instance, very large, with the floor somewhat elevated towards the interior. It was 35 mm long, about 10 mm wide and 7–8 mm high in the maximum values. The tunnel was about 6 mm in diameter all through the course (Fig. 10).

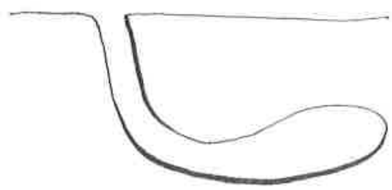


Fig. 10. A nest of *S. albisectus* observed in Peking.

The prey was placed head-in and side-up, singly. The egg of the wasp was laid on the membraneous area just above the base of the hind coxa. It crossed the base of the hind femur downwards, with its opposite end produced freely in the air. It was much the same in form with that of *S. argentatus*, but relatively shorter, measuring 2.3 mm in length and 0.6 mm in width and rather deep yellow in colour. The prey was alive but was reserved in alcohol. Later, it was identified by Dr. H. Furukawa with *Dasyhippus barbipes* Fisch. W. (Locustidae).

In the second nest the entrance was skillfully closed for 3 mm with pebbles and sand. The empty tunnel went down nearly vertically for 25 mm, thence it gradually turned horizontal in an adversed parabolic line and joined to the large brood-chamber.

(In Peking it appeared that the wasp of this species emerged once a year. Towards the middle of August the species could not be observed on the circular path of Tiendang.)

VI. *SPHEX (HARPACTOPUS) SUBFUSCATUS* DAHLBOM

In East Asia the habits of this species was recorded by O. Piel (1935). My observations were published in my two books in Japanese. The following is the essential from them.

1. AN OBSERVATION AT TIENDANG, PEKING

1. Carriage of the prey and taking it into the burrow

On August 13, 1938, at about noon, on the circular road of Tiendang I met with a wasp of this species carrying a large short-horned grasshopper, about twice as large as herself. The prey was laid dorsum-up and the wasp straddled it as done by other species. She grasped the antennae of the prey in her mouth and dragged it with great difficulty forwards. During the transportation the wasp laid aside the prey and went to her nest probably to inspect. It was repeated thrice in her carriage for the distance of 7 m to her nest. No particular care, however, was taken by the wasp at the time when she left the prey on the way. She did not take it on to the grass nor placed it on something such as a fallen leaf, a bit of wood chips ctc, but simply laid it on the ground.

The nest was left open on the side of the road. Every time in her visits the wasp entered the nest once. Finally she carried the prey to a side of the entrance of her burrow and dragged it into the brood-cell. The manner was much the same as in *S. albisectus*: Entered the nest head foremost, turned round in the burrow, protruded her anterior body out of the entrance, grasped the prey by the base of the antennae and pulled it backing into the burrow. After a while, the wasp appeared at the entrance tunnel, with her abdomen still kept in the tunnel and raked the earth around the entrance into the nest. Little by little she pulled her body out of the burrow and every time she closed the aperture with the earth raked in. Finally she was completely out of the nest, when she was caught in my net, to confirm her name.

2. The nest and the contents of it

I dug the nest in the evening. To my regret, the surface of the road was seriously disordered by the repeated turning of cars and the nest mark that I left had completely been lost. I searched for the nest at a likely spot judged by the surrounding objects and after a little enlarging the first excavation I succeeded in striking the tunnel of the burrow with my pen-knife. It entered the earth at an angle of 45° to the horizontal and ended after running for only 10 cm. Because of falling down of the earth it was uncertain to what range of the tunnel was closed by the wasp. The tunnel was 7–8 mm in diameter. The apical portion of it was not particularly enlarged into a formal brood-cell, but apparently only slightly broader than the entrance portion. There, however, the prey that I observed was laid obliquely on one side of her body, with head inwards. The egg of the wasp could not be discovered. Probably it was fallen off by the shock of the cars. The prey preserved was later identified by Dr. H. Furukawa with *Trilophidia annulatus mongolicus* Saussure.

2. THE SECOND OBSERVATION IN KOREA

1. Hunting, burrowing and carriage

One day, late in June, 1943, on the grassland at the entrance to the valley of Shoyozan, Korea, I found a wasp of this species walking among the grasses. The behaviour of the wasp showed me that she was doubtlessly in the course of hunting. I at once followed after her. It was about 3 o'clock p. m. The wasp sometimes crimbed the shrubs, sometimes carefully searched at the root of grasses, and patiently continued her search for the prey. After 33 min. pursuit I was rewarded by the drama of her hunting manoeuvre.

A grasshopper suddenly jumped up from a thicket and was at once swiftly chased by the wasp. The next moment she had already caught it a meter and a half away from me. I approached her carefully and could observe that the tip of her abdomen was directed to the underside of her prey, while she held it by the thorax with her legs, laying her crosswise against the length axis of the prey. I could not go nearer to her, to observe her behaviour in more detail, since her operation had quickly finished and she took a flee posture when I moved a step towards her. Apparently she stung the prey at least twice during the time. After rubbing her antennae and abdomen she began to carry her prey. However, she soon crimbed a grass, hung the insect between the blades and flew away. She landed on the ground about 8 m away from the spot and began to show the search behaviour for the burrowing place. Without a fastidious choice the wasp determined a spot and at once began to dig her nest. The manner was much like that of *S. maxillosus* observed in the Mongolian Steppe. During the digging work the wasp from time to time left her nest to examine her prey. Finally she carried it to the nest and stored it in it. The manner was only the repetition of that observed at Tiendang.

According to the observation it was made clear that this species has a habit of hunting the prey first and later digs the burrow to receive it. This is utterly unanimous with the habit of European and S. Chinese representatives.

2. Structure of the nest, prey and oviposition

I dug the nest at once. It obliquely entered the earth for 12 cm and ended without being particularly enlarged into a brood-cell (Fig. 11), just as was the case of the instance in Peking. Measurement showed that the tunnel at the entrance portion was 8 mm and at the cell portion 11 mm in diameter. The closure of the nest was rather rough, made of pebbles and earth, ranging for 4 cm.

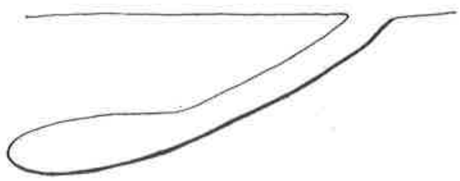


Fig. 11. A nest of *S. subfuscatus* observed in Korea.

The prey was laid head-in and flank-up (slightly obliquely) at the end of the burrow. The egg was attached to the prey in the same manner as in *S. albisectus*, namely, at the membraneous area just above the base of hind coxa, the egg body being placed across the basal portion of the hind femur, with the apex towards the ventral side of the prey. The prey was the same species of Locustidae as observed in Peking, *Trilophidia annulata* Thunb., nymph, ♀, a comparatively large insect, seemingly sufficient to rear a waspling.

The method of final closure was as simple as the temporary closure of most species of *Sphex* s. str. No particular pressing coud be observed from outside.

VII. *SPHEX (PALMODES) OCCITANICUS* LEPELETIER ET SERVILLE

To the western Hymenopterologists it will be of some interest what kind of the prey is caught by this species in East Asia, since no record has been published in western language up to now. A glimpse of the habits of the Chinese representative was reported by O. Piel, but he only recorded the nesting place. My observation was made in Shoyozan, 40 km north of Keijo, and was also quite fragmentary, but it involves an observation regarding the prey.

1. Carriage of the prey

On July 31, 1942, I was observing the habits of *Astata boops* Schlank which lived in very flourishing colonies on the earth under the roofs of the temples of Shoyozan, when I happened to see a large Sphex coming to me along the wall of a temple, dragging her prey. I hurried to her and knew that she had a red-banded abdomen. At a glance I thought that she might be a wasp of *Sphex maxillosus*. But the prey dragged by her was quite a different insect from those caught by the latter Sphex. It was a queer brownish Orthoptera, having a well plumped abdomen that was completely exposed, since it apparently lacked the wings to cover it. This led me to correct my glance identification.

The wasp straddled the prey from the back, capturing it by the antennae and proceeded forward with a great effort. She vigorously beated her wings to help her progress, since the burden carried by her appeared too heavy to carry with ease. She passed in front of the temple, 7 m in width, and turned along its corner. After proceeded for one meter further she approached the wall, and without showing the least hesitation began to crimb the stone wall that made the base of the white clayey wall of the temple. Her wings were more violently and more rapidly moved than before and she could vertically cross the stone surface of about 30 cm in height. Then she began to crimb up the white clayey wall upwards. The surface was smoother and it was very difficult to her to find favourable supports with her legs stretched over the prey. Without the aid of the rapidly moving wings she might be unable to crimb up the wall. With a great difficulty she at last reached a small hole opening on the wall at about half a meter above the surface of the earth and was about to enter, when she was caught together with her prey. The hole might lead the wasp under the floor of the temple where she might make her nest.

According to the literature this species has an inclination of crimbing a wall and makes her nest under the roof tile etc. In its general habits *occitanicus* (= Fabre's le Sphex languedocien) has a similar life pattern to *S. subfuscatus*. It hunts a prey prior to digging the nest and lays its egg to the side of the thorax, close to the base of the hind coxa.

2. The prey

The prey was a wing degenerated long-horned grasshopper, apparently somewhat similar to the Ephippigère, the commonest prey* of the European representative of this species, but belonging to the different genus, *Atlanticus ussuriensis* Uvarov (det. by H. Furukawa), It was also a female, having the abdomen filled with eggs. I measured the wasp and the prey. The former was 220 mg, while the latter 3020 mg, 13.7 times as heavy as the hunter.

VIII. *SPHEX (ISODONTIA) NIGELLUS* SMITH

The biology of this species was aleady published in fair detail by O. Piel (1933) in his observation made in the eastern coast of Central China. In Japan also several reports including my own have been published**. Among them some are far more detailed than that of Piel. But it is very regret that they were all in Japanese and remain as enigma to most of the wastern biologists. I have some data additional to those reported previously and as these contain nearly all of the cases known in Japan the following description will mainly be restricted to the observation of my own. (See also addenda)

1. THE NEST AND BEHAVIOUR RELATING TO IT

1. Nesting place

As well known the members of *Isodontia* are tube-renters, utilizing the ready-made hollows of proper size. The hollows most frequently utilized in Japan are those found in the cut ends of bamboos and reed-canes horizontally placed in hedges and fences. I collected a number of nests made in such materials sometimes artificially settled. I further observed instances made in the abandoned tunnel of some boring beetle larva. Occasionally, however, they utilize the vertically standing stems of dead plants. In two instances the wasps were observed nesting in the hollow of the

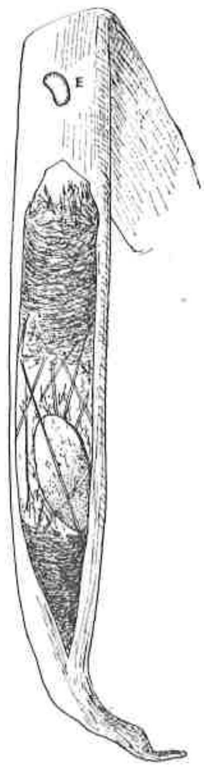


Fig. 12. A nest of *S. nigellus* made in the living leaf of *Allium fistulosum*

* Fabre considered that this Sphex exclusively captures the females of the genus *Ephippigera*. But according to Ferton he observed this species hunt a male of *Phasgonura viridissima* in Bonifacio.

** Masuda, H. (1930); Ikushima, Y. (1934, 35, the most detailed reports); Iwata, K. (1936); Baba, K. (1938); Tsuneki, K. (1931, 46); Ohta, A. (1959) and Okuno, H. (1959)

dried stems of *Macleya cordata* still standing, entering from the broken end on top. In one curious instance a nest was made in the hollow of a vivid leaf of *Allium fistulosum* which was folded down from the middle and the wasp utilized the drooping apical portion, entering the cavity from a small hole made by some other insect on upper portion.

2. **Structure of the nest**

The hollow tubes utilized by this species as their nesting place are from 7 to 15 mm in inside diameter, those of the medium-size (10 mm or so) being most preferred. The tube is markedly varied in length, from 6 to 20 cm. If the tube is much longer the wasp closes the interior and utilizes the external portion only of the proper length The number of the brood-cells made in a tube is, regardless of the tube length, mostly but a single. Sometimes, however, several cells (usually 2–4) partitioned with walls are linearly arranged (Table 10). The material used for partitioning and closing walls

Table 10. Nests of *Sphex* (*Isodontia*) *nigellus* Smith

Material of tube	Length of tube	Aver. W. of tube	Number of cell	Length of cell				Number of cocoon
				1	2	3	4	
Bamboo	205 mm	14 mm	4	45	37	38	35	4
〃	110	9	1	57*				2
〃	63	15	1	43				1
〃	240	14	2	57*	40			3
〃	175	13	2	33	31			2
〃	90	10	1	45				1
〃	175	12	2	52*	25			3
〃	150	12	1	45				1
〃	203	9	1	43				1
〃	173	12	2	43	40			2
〃	165	10	2	35	35			2
〃	130	13	1	45				1
〃	180	10	1	55				1
〃	170	10	3	28	32	39*		4
〃	155	12	2	58*	25			3
〃	107	8	1	45				1
Reed	174	9	3	32	22	27		3
〃	175	10	3	32	30	28		3
〃	147	8	3	30	28	30		3
〃	138	7	2	40	32			2
〃	67	7	1	52				1
〃	120	8	1	55				1
〃	158	8	1	53				1
〃	135	8	1	47				1
Macleya	220	12	1	45				1
〃	180	13	1	50				1
Polygonum	76	10	1	?				1
〃	120	9	1	45				1
Beetle hole	105	9	2	?	?			2
Allium	107	12	1	42				1

* ··· Including two cocoons.

is always fine straws, mostly dried halms and blades of wild grasses. These straws are very elaboratory crushed and torn off with the mandibles into cotton-like threads and circularly and very compactly stuffed, the appearance being a miniature nest of some Passerine bird. It is 1–2 cm in thickness when used for the cell partitioning walls and 3–5 cm for the final entrance closure. In the latter the material is gradually roughly treated towards the exterior and finally raw material — the intact fine straws — is utilized without modification (Fig. 13). The nest made in a vertically standing halm has a particular structure. When the bottom is too narrowly tapered, the space is first stuffed with straw-cotton (this is also the case in the horizontal tubes). Then, in order to support the upper wall, several fine intact halms of proper length are stood like the iron poles. At the bottom of the upper wall which is in contact with the standing straws the material is roughly circled to form a basal network, upon which the straw cotton threads are circularly woven and pressed into a slightly cup-shaped layer like a bird's nest.

Table 11. Number of cells in a tube

Number	1	2	3	4	5	Observer
Freqency	16	8	4	1	0	Tsuneki
〃	20	6	4	0	0	Ikushima
〃	20	5	0	0	0	Iwata

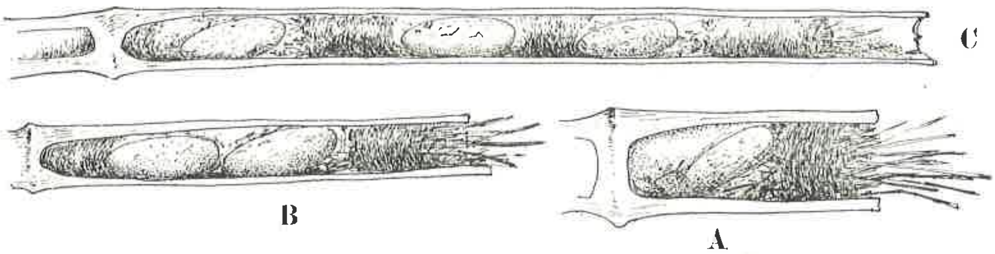


Fig. 13. Three types of nests of *S. nigellus*. A, the commonest simple nest made in the cut end of bamboo. B, two cocoons in a larval cell (rare). C, a linearly arranged multicellular nest in the hollow of a dried reed.

In the nest which is in the course of provisioning a temporary closure is made at the external portion. This is a rough wall of the same material, 20–30 mm in thickness and a slit can be made along the wall of the tube by loosening or pressing the material when the wasp enters the nest.

3. Nest building behaviour

In collecting the material the wasp makes a choice by flying from one dried halm to another. She perches on a halm, climbs upwards, with her flask-like abdomen slipped off the halm, reaches the top and thence flys off to go to another. If the material is satisfactory she twice and thrice gently grasps it between her mandibles and finally cuts it off at the level of her head. She then turns round on the halm, proceeds a little downwards and cuts the halm again. The halm falls down drawing a semicircle, with the wasp on it and finally falls off by the weight of the wasp. The halm thus cut off is usually 5 cm or so in length. The wasp grasps it with her mandibles by one end near the tip, holds it lengthwise under her body and flys away to her nest. The other end of the fine stick of the straw is usually protruded posteriorly from the apex of her abdomen. She enters the nest tube with the material thus held.

The movement of the wasp inside the nest-tube was observed with the nests made in the test-tubes or tube-bottles of glass, often with a paper half cylinder placed inside. This traditional method has also been utilized by some Japanese investigators (especially

Y. Ikushima) with good results. The wasp gnaws the straw progressively from end to end, pushing it little by little forwards. During the course the straw turns soft by receiving many injuries and tearings. The wasp bends and folds it along the wall of the tube and pushes and presses it with her head. As mentioned above, if the inner end of the tube is too narrow the wasp first stuffs material there. In tube-bottle, too, sometimes the innermost layer of the softened straw is made. She then makes a stopper of about 2 or 3 cm in thickness for the temporary closure. It is not so compactly stuffed a wall as the partitioning or final entrance closure, rather of a loose constitution. Usually the stopper for the temporary closure of the nest is placed 3–5 cm interior from the entrance.

2. THE PREY AND BEHAVIOUR RELATING TO IT

1. The prey

In my observations in Saitama and Fukui Prefs, the prey belonged mostly to *Conocephlus melas* (Tettigoniidae), the imago and the nymph being mixed, but occasionally nymphs of *Phaneroptera nigroantennata, Ducetia japonica, Heaxcentrus japonicus, Homorocoryphus lineosus* were mixed. According to other observers, *Gompsocleis burgeri, Oecanthus longicauda, Tettigonia orientalis, Holochlora japonica* and *Mecopoda nipponensis* (?) have been recorded, mostly being nymphs (especially as to the large species).

In most of the prey the antennae are cut off from near the base. They are laid head-in and venter-up in the horizontal nest, but in the vertical nest the direction of the head only constant, namely, head-in.

The number of the prey per cell is mostly 5–6, sometimes over 6 (7–8) and occasionlly only 3.

2. Provisioning behaviour

Two papers touching on this subject were pulished about 30 years ago by two Japanese observers, H. Masuda (1930) and Y. Ikushima (1934, 35), both using the glass tube. Observations of the latter entomologist is fairly detailed. My observation carried out several years ago could confirm their results generally.

The wasp comes back with a prey, hanging it by the antennae which are cut off by the wasp at about 3 mm from their bases. She enters the tube, leaves the prey in the entrance space of the nest, dorsum-up, and begins to loosens the stopper. She pulls it out a little, or presses a part aside and makes a slit along the glass wall and penetrates into it. At once she turns round in the chamber and returns through the slit, head foremost. She does not completely come out of the passage, however, always leaving her posterior body in it, catches the antennae of the prey between her mandibles and takes it backing in the chamber. At this moment the prey is always dorsum-up. The wasp then rolls her body round sideways so as to be upside-down, pulls in the prey further, first with the aid of the fore legs and then using the fore and middle legs. During the course the prey is also rolled and becomes embraced by the wasp from the back, head to tail. The wasp, venter-up, using her anterior four legs, moves the prey backwards into the chamber, leg over leg. Thus the prey was sent into the interior portion of the chamber, passing over the body of the wasp and placed upside-down. Then the wasp goes out of the chamber through the slit, turns round and emends the plug by pulling together the material and pushing and pressing it with her mandibles and head. After the work she turns round again, crawls to the entrance and flies away to her next hunting excursion. Later provisioning is comparatively promptly carried out, if favoured by the weather. During two or three hours she takes in all the victims necessary for the larva and closes the chamber very compactly and tightly with the straw-cotton. However, I have missed the chance to observe in the multicellular nest whether the wasp utilizes the temporary closure for this partition, pressing it more tightly, or she makes it independently, carrying the material from outside through the stopper. But to me it seems the former case is more probable.

3. THE PROJENY

1. Ovipositing behaviour

The egg of the wasp is laid on the prey first taken in, as is the rule in this genus. The method of carrying in the prey to the cell is the same as given above, but it is slightly changed on the way. The wasp lies at the innermost portion of the cell, instead of the entrance of the cell, venter-up, catches the prey with all her six legs, instead of anterior four legs, from the back, head to tail, turns her abdomen slightly aside and stretches it round the thorax of the prey. The tip of her abdomen thus reaches the mesosternum of the victim and the egg is laid. It comes out of her oviduct, caudal end first, and is glued to the insect at the moment of just leaving the body of the wasp with its cephalic end. The place and the manner of attachment is the same as in the species of the subgenus *Sphex*. The wasp creeps out from under the victim and goes out through the slit of the temporary stopper.

2. The egg, larva, cocoon and emergence

The egg is similar in character to that of *Sphex argentatus*, except for slightly smaller in size. The location on which it is laid is also similar, namely it is attached to the area posterior to and slightly inside of the base of one of the front legs. It crosses the mesosternum of the prey and projects the apical portion slightly beyond the opposite side. The egg period is about 20 hours and the larva takes 2–2.5 days for devouring the stored victims (in July — August) and on the 5th day, after resting for about 15–20 hours spins the cocoon. The cocoon has a thin semitransparent cellophane-like, slightly brownish outer layer, the so-called cocoon cover, and the cocoon itself quite roughly connects with it. The cocoon is cylindric, rounded on both ends and sometimes slightly tapering towards the caudal end. It is considerably varied in size, 25×7 —— 20×5 (mm). The larva hatched from the egg which is laid in July, after spinning the cocoon, emerges after about 3 weaks, that is to say, about 4 weeks after hatching from the ggg, while the projeny laid in late August and September passes the winter as a prepupa and emerges in next summer. Probably in the central and southern regions of Japan this species can repeat three generations a year. This is exceptional among the members of *Sphex* s. latr. in our region.

3. Two eggs found in one chamber

Masuda (1930) and Ikushima (1935) observed actually two eggs laid on each pedestal prey stored in one chamber, but they failed to perceive the important significance involved regarding the evolution in instinctive behaviour. I could not have the chance to observe actually the two eggs laid or two larvae eating in one chamber, but among the nests collected by my collaborators and myself we found 6 instances in which two cocoons were spun in one chamber. Moreover, the percentage of such instances is comparatively high (Table 10). Probably these instances were, by some reason or other, resulted from the omission of construction of the partitioning wall. It is presumed, therefore, that if other relations are similar to those of the normal chamber, that is to say, the victims carrying respectively an egg of the wasp are laid with a certain interval and the prey double the number of the usual cell (the fact was suggested by the description of Masuda), cannibalism between the larvae does not occur and the two larvae can coexist in the chamber. (See addenda)

If such habits as mentioned become constant and further develope we can expect a stage of aggregate rearing of several larvae in a large chamber which is furnished by the mother wasp with food sufficient for the growth of the group of larvae — the stage which has already been attained in our region by *Isodontia harmandi* Pérez.

IX. *SPHEX (ISODONTIA) HARMANDI* PÉREZ

This is an interesting species in that the wasp has a habit of rearing a number of the larvae collectively in one brood-chamber. Three reports, including mine, have been published up to now.

I first found the wasps of this species at a house near the summit of Mt. Mitsumine, about 80 km NNW of Tokyo in August, 1935. Under the eaves of a store house bundles of bamboos were piled up and numberless wasps having red hind femurs were nesting in their cut ends. There I could observe every section of the wasp's activity outside the nest. Later, I observed the same species carrying a partitioning material in Korea. But I could not find out their nesting place. Recently, since I came to Fukui Pref., I have been favoured by the common occurrence of this species in the montanic region. Every summer I have seen a number of their nests made in the hollows or abandoned tunnels of the Cerambicid beetles found in the piled up logs.

1. THE NEST AND BEHAVIOUR RELATING TO IT

1. Nesting place

The hollows having the diameter of 10–20 mm and the length of 10–20 cm found in the dead and dried trees or wood, or at the cut ends of bamboos placed horizontally are favourably utilized by the wasps of this species as their nesting place. In Fukui Pref. the abandoned tunnels of Cerambicid beetles found in the cut ends of the fire wood piled up in their habitat are most frequently utilized. The height from the earth surface has no apparent bearing on their nest selection. Therefore, the nests are distributed from 10 cm or less to about 3 m above the surface of the ground over the section of regularly piled up logs. However, if conditions are similar, the holes located higher appear preferred. In the case of the abandoned tunnels of beetles the curved or bent hollows are not selected by the wasp.

2. Selection of the nest and orientation flight

The wasp has a habit of reutilizing the old nest, especially when the cut ends of the bamboos piled up in the favourable place are annually utilized. She carries out the remains from inside of the tube and sweeps away the dust from the entrance.

When a certain tube or tunnel is selected, always the so-called orientation flight is performed. At first she tries a stationary flight in front of the nest entrance, with her head towards the orifice. Then she proceeds and alights at the orifice, sometimes enters the tube. Again she flies off, this time to somewhat a greater distance and makes the same hanging flight. Again she rashes to the entrance. Similar movements are repeatedly carried out, with the distance legthened greater and with the direction changed to the right and left, as the time proceeds. Finally she flies off. The orientation flight is markedly simplified when the new nest is made close to the previous.

3. Carriage of the material for the nest closure

As the nest closing material is used in the main the living green leaf-moss, but frequently barks of *Chamaecyparis* or *Cryptomeria* and rarely roots of grasses (probably artificially pulled out and dried) are used. The barks are usually applied to the material of the outermost closure, but at times they are gnawed into soft threads and firmly pressed into the inner layer of the closure. The mode of transportation of the material is practically the same as in the case of *S. nigellus* Sm., barks being protruded from the caudal end of the wasp and the mosses hung from between the mandibles.

4. Structure of the nest (vide addenda)

A large unicellular nest is the rule, rarely, however, there are bicellular nests. The closure of the nest is single, of considerable thickness, inwardly very compactly pressed and outwardly rough in the accomplished nest. In such a nest usually the outermost part of the closure is thrust out of the entrance and is very marked, but sometimes the closure is finished at some distance from the entrance. In the unaccomplished nest the tube is fairly compactly stuffed with the temporary closure.

Nineteen nests made in the cut ends of bamboos observed on Mt. Mitusmine, Saitama Pref., were sent to me by post and were investigated in detail. Most of them were accomplished ones and the data obtained were given in Table 12. In this table the thickness of the partitioning wall when two cells were present is an averaged approximate value, since the thickness is different in part. In the entrance closure the shift of the compact layer to the rough layer is sometimes very indistinct, and in the compact layer there is strictly an extremely compact portion. In the table such detailed difference was omitted. (Pls. IV and V)

Among the materials here tabulated nests 10 and 12 have distinctly two brood-cells respectively, while nest 7 only apparently so. In this nest the apparent cell 2 was probably brought about through the separation of the rough layer from the compact one by the shock during the transportation by post. On the other hand, nest 2 was an unaccomplished one and its outer layer is the temporary closure. This was made clear by the state of the provisioning in the cell. Actual appearance of the nests were given with some instances in Plate V.

Nests 13–19 were obtained in 1936 and examined in 1939 owing to the mobilization order except for nests 13–15. Therefore, the records were taken with the nests from which the wasps had emerged. Nests 20–22 were observed in Fukui Pref., all being made in the hollows of fire wood and all in the course of provisioning.

Table 12. Structure of the nests of *Sphex* (*Isodontia*) *harmandi* Pérez (mm)

Nest No.	Length of tube	Width of tube	Length of cell 1	Wall 1	Length of cell 2	Compact closure	Rough closure	Rest of tube
1	220	16	127	–	–	45	40	7
2	88	21	35[1)]	–	–	–	40[3)]	25
3	140	16	67	–	–	50	30	0
4	135	16	70	–	–	37	20	8
5	130	16	47	–	–	35	50	0
6	180	22	40	–	–	35	60	55
7	240	15	130	50	20[2)]	–	40	0
8	175	18	50	–	–	55	70	5
9	90	20	33	–	–	30	50	–23
10	165	17	30	10	65	25	30	5
11	175	23	60	–	–	65	40	10
12	235	18	80	10	55	50	45	– 5
13	210	20	70	20	60	35	40	–15
14	198	19	105[1)]	–	–	35	60[3)]	0
15	185	20	105[1)]	–	–	–	50[3)]	30
16	102	15	60[1)]	–	–	–	45[3)]	0
17	102	21	65[1)]	–	–	–	35[3)]	25
18	93	20	37[1)]	–	–	–	30[3)]	26
19	132	19	60[1)]	–	–	–	50[3)]	20

1) Not definitely determined space. 2) Appeared by the shock during transportation.
3) Temporary closure.

2. THE PREY AND BEHAVIOUR RELATING TO IT

1. Species, sex and growth stage

The prey hitherto observed by me belonged all to *Conocephalus* (=*Xiphidion*) spp. But, Iwata recorded *Xiphidiopsis suzukii* among the prey he observed.

The 12 nests that I observed first contained cocoons of the wasplings or dried victims uneaten. I collected with the utmost care the fragments of remains from all the brood-cells and arranged them per cell. Among the remains the head capsule, pronotum, genital appendages (♀, ♂) and the wing of imagoes were comparatively well reserved, of which the pronotum and the wing were most useful to distinguish the difference between the imago and the nymph, and the genital appendages the sex of the victim. From these as well as the number of the crania and dried intact insects the total number of the victims was presumed. Of course, the number is the possible lowest value. The results were given in Table 13.

Generally speaking, it seems that females are somewhat preferred by the wasps to males, and nymphs decidedly to imagoes. But there were also exceptions.

Table 13. Prey and waspling in the nests examined of *Sphex harmandi*

Nest No.	Prey								Egg	Larva	Cocoon	Parasite
	I. l.	I. d.	Rem.	♀	♂	Ima.	Nym.	Total				
1	–	–	54	53	1	0	54	54	–	–	6	2
2	–	14	–	11	4	0	14	14*	–	–	–	
3	–	–	41	37	4	0	41	41	–	–	8	
4	–	3	31	30	4	0	34	34	–	–	4	
5	–	2	28	19	11	24	6	30	–	–	4	
6	–	5	29	27	7	–	34	34	–	–	3	4
7	–	6	56	51	11	0	62	62	–	–	6	
8	–	45	–	38	7	0	45	45	–	–	–	5
9	–	1	29	29	1	2	28	30	–	–	5	
10a	–	4	18	7	15	0	22	22	–	–	2	
10b	–	41	–	19	22	33	8	41	–	–	–	
11	–	59	–	38	21	2	57	59	–	–	–	11
12a	–	–	50	43	7	3	47	50	–	–	6	
12b	–	9	39	33	15	0	48	48	–	–	1	3
13a	–	–	–	–	–	–	–	–	–	–	8	
13b	Many	–	–	–	–	–	–	–	–	4	6–8	
14	–	–	–	–	–	–	–	–	–	–	11	
15	Many	–	–	–	–	–	–	–	5	–	(5)	
16	–	–	–	–	–	–	–	–	–	–	4	
17	–	–	–	–	–	–	–	–	–	–	6	
18	–	–	–	–	–	–	–	–	–	–	5	
19	–	–	–	–	–	–	–	–	–	–	4	
20	26	–	–	–	–	–	–	26*	11	(11)	(1)	
21	3	–	–	–	–	–	–	3*	3	3	–	
22	6	–	–	–	–	–	–	6*	5	5	1	

Abbreviation : I. l, Intact living prey; I. d, Intact dried prey; Rem., Remains; Ima, Imago; Nym., Nymph.

* In the course of provisioning.

2. Placement of the prey (see also addenda)

In some instances (e.g. nests 10, 11) greater part of the eggs of the wasp did not hatch (probably by being sucked by the maggots of the parasitic fly) and a number of the prey remained as they had been stuffed by the wasp (Pl. VI, Fig. 2). Such instances inform us the method of storing the victim by the wasp. They are obliquely laid, one piled obliquely on top of the preceding. In the natural state, they are laid probably venter-up.

According to the observation outside the nest, the wasp carrying the prey enters the nest, lays it at the entrance porch and loosens the temporary closure to make a passage. She penetrates into the closures head first and then sticks her head out of the passage, catches the prey by the antennae and pulls it in the chamber. At this moment the prey is always dorsum-up. Therefore, probably by the same method as in *S. nigellus* the prey must be turned over in the chamber. But it is quite uncertain as to her subsequent behaviour whether she follows the same method as in *S. nigellus*, or simply carries it by the forward progress, since in the chamber much broader than that of *nigellus* the latter method seems also possible.

3. The number of the prey per larva

The number of the prey per larva is difficult to ascertain, since it is very difficult to obtain such nests as were soon after accomplished. In the nests just provisioning the prey do not attain full in number, while in those containing large larvae or cocoons it is doubtful whether their number strictly coincides with the number of the eggs laid, because cannibalism occurs not unfrequently among the grown larvae. Of the instances listed in Table 12 nests 4, 5 and 7 in which some dried intact victims are left in the chamber without the parasitic fly pupalia may show the approximate value, because the fact shows that the food store was ample and cannibalim did not occur accordingly. According to these nests the number of the prey shared to one larva is in nests 4 and 5 7–8 and in nest 7 about 10. Later process showed that the wasplings in the former two were all males and those in the latter all females. We may conclude from the facts that the prey offered is 7–8 in males and about 10 in females, of course, in the case sufficiently supplied. The results of the observations by Iida (1934) were approximately the same as above, though he did not deal with the sex of the adult wasps emerged.

3. REARING MULTIPLE LARVAE IN A BROOD-CHAMBER

The method of rearing the larvae is characteristic of the species. It lays several to some ten eggs in a brood-chamber, each on a respective prey, and later collects a number of the additional prey in it. The larvae grow in aggregation and finally spin the cocoons which lean upon each other and are wrapped with a common cocoon cover.

1. Oviposition

The morphological and colorific characters, together with the manner of deposition, of the egg is similar to those of *nigellus* Sm. It has been believed that all the eggs in one nest are laid successively to each pedestal victim at the first phase of provisioning and later the additional prey only are collected, the relation being representable by the behaviour formula as $(HTSO)^n(HTS)^m$. (H, hunting; T, transportation; S, storing; O, oviposition) Because in the nests at the early stage of provisioning always an egg is laid on all the prey found in it and in those at the later stage the egg-carrying prey are collectively placed at the interior portion of the chamber.

According to my recent observations, however, it seems that this conclusion must partly be corrected.

In the case when the egg are 5 or 6 in number, they will be laid successively at first. But when they attain 10 or so in number it appears that after 5 or 6 eggs are laid a prey or two without the egg are inserted between the ovipositions.

On July 29, 1957, I cut open a nest of this species at Koike, Fukui Pref. The chamber was made in the hollow of wood. It was 40×20 mm in dimensions and partitioned with a temporary moss plug of 28×20 mm. In the chamber 26 insects of *Conocephalus melas* was accumulated and the mother wasp was still carrying the prey. Eleven eggs were found attached to one larva respectively. Their position : Five eggs on five insects placed innermost, others on each pedestal prey which were scattered broadly in the chamber. Between the prey carrying the egg were laid one or two insects without the egg, the outermost of the egg-bearing prey being placed near the entrance. At that time the wasp was stuffing victims in the empty space above the layer of the prey thus arranged.

In two other instances the eggs were 3 and 5 in number respectively and there was no insect without the egg, except the outermost one in the 2nd instance.

2. The number of eggs laid in one chamber

It is also difficult to grasp the exact number of eggs laid in one chamber. The reasons for this are three : (1) Difficulty in collecting the nests in the proper condition, especially because of the nests of this spcies are found in the district located beyond the possibility of daily observation. (2) The eggs in the provisioning nest are likely to be destroyed by the parasitic fly maggots. (3) The number of the cocoons does not always represent the number of the eggs laid, because of the cannibalism between the larvae and the damage through the parasites.

On the other hand, the number of the cocoons never surpasses the number of the eggs in a chamber. Therefore, a comparatively large number of the cocoons shows that at least as many numbers of the eggs were laid as the cocoons. According to Table 12, there are instances of 8, 10 and 11 cocoons in a chamber. Further, in the reliable instances (Nos. 4, 5 and 7) for which explanation was given earlier the number of the cocoons is 4, 4 and 6 respectively. These may represent the instances of comparatively small number of the eggs. Furthermore, I actually observed an instance of 11 larvae eating in a chamber. In the records given by other investigators there is no instance of over 10 eggs. We may therefore conclude that the eggs laid in one chamber vary from 4 to about 11 in number.

3. Cannibalism between the larvae

It has been believed that cannibalism does not occur among the larvae of this species, as far as food is adequately supplied. Certainly this is a great progress in the larval habits, since in other species, if the larvae placed in one chamber happen to meet with each other cannibalism always occurs even if the surplus of food is stored by the side of them. The larvae of *harmandi* are born close together. They come into contact with each other when the prey on which they were laid have been eaten up by each larva. Despite the fact they do not try to eat the near-bye brothers or sisters, but they always eat the Orthopterous insects only, which the mother wasp stored for them. This is shown by the cluster of cocoons found in the nests collected after the season.

If the trend of not to eat the companions, as in many species of parssitic insects which send multiple offsprings to the body or cell of the host animals, has become the infallible nature by regulating the amount of food, and the size of the resulted adult wasps accordingly, cannibalism will never occur in this species and it will be said that the gregarious rearing of the larvae has attained the complete stage.

In reality, however, the habits of the larvae have not as yet reach such a stage in this species, and by the very reason it is interesting in the evolutional significance.

When the amount of food is inadequate connibalism does occur between the larvae. In nest No. 13, the second chamber contained 6 cocoons and 4 grown larvae when I examined it soon after collection. However, when I reexamined it 3 years after (when I came back from the war) it contained only 8 empty cocoons. Two larvae must have died through the cannibalism. The fact was more decidedly observed in a nest obtained in Koike. It had 11 eggs laid, each attached to one prey and the total number of victims including the egg-pedestals was 26, and the mother wasp was still collecting the additional grasshoppers. Two days later (Sept. 1) when I returned to my laboratory after climing, walking, riding and sometimes running with the bottle in which the contents of the nest were shifted, I found that all the eggs had hatched and the larvae were eating the respective pedestal insect. Among them there was a marked difference in growth, the outermost larva being soon after hatching and about half as large as the interior larvae. The next day at 10, the growth of the larvae was markedly proceeded and the size difference among them became more striking. At 19, greater part of the victims had already been cut into pieces and the number of the wasplings was reduced to 8, probably as a result of cannibalism. The size of the larvae became more uniformalized, since the smaller ones were devoured up. The next day (Sept. 3) at 9, the larvae were further reduced to 5 in number. They were mostly 15 mm or so in length and eating the remains of the victims. One of them, however, had been driven the tips of the mandibles into its throat by another larva and was about to be devoured. It was calmly eaten thereafter by the larva without showing any struggle nor resistance. I put in the tube 5 decapitated and dismembered large crickets (*Grillulus mitratus* Sauss.). At 16 the remaining larvae were only 4 in number of which 3 occupying the interior of the cell were large, measuring about 25 mm in length, and 1 lying at the outer portion of the cell was comparatively small, about 20 mm in length, each eating the crickets. On Sept. 5, at 9, at the innermost portion was an accomplished cocoon, by the side of it was a full grown larva, but it was dead. Near the entrance portion also a large full-grown larva was present, but it was about to die and the slightly smaller larva had completely disappeared. Whether the death of the two full-grown larvae was caused by the cannibalism* or not I can not say definitely, but it is certain that out of 11 eggs supplied with 26 victims only one cocoon (if went good 3 cocoons) was obtained as a final outcome.

According to other observers, in nearly all instances the cocoons obtained are smaller in number than the eggs observed, except for some wherein surplus of food was provided.

However, it must be stressed that cannibalism is not the rule in this species. This is distinctly shown by the number of the cocoons spun in one chamber (Table 12). Rather it can generally be said that under the normal state in nature cannibalism is an exception.

4. THE COCOON, EMERGENCE OF THE ADULT WASPS AND SEX DISTRIBUTION

1. Cocoon

As perceived from the photograph (Pl. VI, Fig. 3) the cocoons are usually spun in a mass, leaning to one another. The outermost layer is a thin semitransparent pale

* Such probability is large, since in many rearing trials with various species of the Sphecine wasps it is very frequent that the larva which ate the flesh of the same species dies before spinning the cocoon.

brownish silk membrane which is not tightly attached to the cocoon itself, the so-called cocoon-cover. It appears that the cocoon-cover envelops the group of cocoons as a sheet of silk. In reality, however, each cocoon is separately covered by the layer, only on the surface they are glued to one another into a sheet. The cocoon itself is subcylindric, slightly tapered towards the caudal end and sometimes suddenly narrowed behind the middle (Pl. Ⅵ, Fig. 3). In colour it is slightly purplish dark brown with a thin ashy white silk layer on the surface and towards the middle comparatively broadly whitish.

Table 14. Measurement of cocoons of *Sphex harmandi* Pérez (mm)

Nest No.	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	(Sex)
1								–	2	1	–	1	–	1	–	–	1	-	♀
3					–	1	1	4	2	–									♂
4							–	1	2	–	1	–							♂
5							–	1	1	2	–								♂
6	1	–	–	–	–	–	1	–											♂
7							–	3	–	1	2	–							♀
9					–	2	1	1	1	–									♂
10a						–	1	1	–										♂
12a			–	1	–	–	–	–	–	–	1	–	–	1	–	3	–		♀
12b							–	1	–										♂

I measured all the cocoons in the first 12 nests (Table 14) and compared the results with the sex of the emerging adult wasps. It was shown in Table 15. The direction of the cephalic end of the cocoons was also recorded in detail, but it was quite inconstant.

2. Emergence of the adult wasps

Early in summer of the next year, from the 12 nests preserved in my room the adult wasps appeared successively. Prior to their emergence I placed the cocoons each in a separate bottle and gathered them per nest. They were numbered according to the order of their emergnece. The date of emergence of the adult wasps from one and the same nest is not always the same. The intervals between the first and the last days of emergence were given in Table 15, and the relation between the order of emergence and length of the body of the adult wasps in Table 16. It was made out that no definite relation was present between them.

3. Liberation from the closed chamber

It seems of interest to observe how the wasps emerged in the same larval chamber perforate the compact and tightly stuffed tampon to liberate themselves to the outer world. Further, to make clear whether or not a cooperation takes place in this case seems not less interesting. In order to observe the behaviour of the wasps I moved the contents of the nests into the glass-tubes of the same diameter. First I placed the group of cocoons in the inside, then the compact layer of the tampon was pushed in by the aid of a stick, keeping the very firm states as in the natural condition and finally the rough layer was added. The space of the larval chamber was kept as large as in the natural nest.

When a wasp emerges it first cuts off the cepahlic portion of the cocoon roundly from within, then it perforates the cocoon cover and comes out in the glass chamber.

It then takes a rest for a considerably long time (usually about a day), during which other wasps come out of the cocoons. There was no quarrel among them, at the same time there was no familiar attitude shown towards other individuals. They were only mutually tolerated.

In this case it is apparently strange that the bright daylight filling around them gives rise no confusion to the wasps. This is not because that they cannot perceive the luminous stimulus as yet, since they can respond promptly if such a stimulus is artificially given to them. The apparent indifference to the light of the emerged wasps in the tube bottle is only due to the fact that they do not as yet reach the status in the development of instinct in which the light works as stimulus to them. In the natural condition the emerged wasps are in the dark of the chamber. Accordingly it is considered that the behaviour with regard to the light has not been developed in them at this stage of ontogenetic instinctive development. In other word, they can respond to the light physiologically, but they cannot respond instinctively. At any rate, the wasps remain calm; they do not run about or fly against the glass wall as done by the wasps captured in the open field. The next work imposed upon them in the order of development of their instinct is to cut through the tampon of the chamber. The stimulus without connection with the behaviour requested at that moment has nothing to do with them.

After about a day or so of resting the wasp acquires vigour. One of them that has reached this stage begins to perforate the tampon compactly pressed against the glass wall. It stretches its mid and hind legs firmly against the glass wall, drives its mandibles into the hard plug, little by little gnaws it into pieces and scrapes them backwards with the front pair of legs. It then pulls a string of dried moss and loosens the tissue of the tampon, inserts its head into the shallow excavation and presses the loosened material sideways. The compact layer of the plug is very hard and shows a strong resistance against the picks of its mandibles. It continues gnawing, pulling and pressing of the tampon and little by little the hollow becomes deep. When it is deep enough to push its anterior body into it the wasp begins to roll her body round and round in it, as if drilling with its body.

During the time all other wasps remain quite calm in the chamber. Some of them go to the rear of the working wasp from time to time, but as soon as they know that other wasp is still working they turn back at once to wait in the chamber calmly. In most cases the vigour of a single wasp is sufficient to dig a tunnel through the tampon. In some cases another wasp enters the hollow at the moment when the working wasp cames out of it and replaces and continues her work. The first wasp then retreats without contending the digging work with the second.

When a passage is accomplished through the compact layer the digging work has finished, since the wasp can force its way through the rough layer, without preparing a particular passage. When the wasp engaged in the digging work goes through the tunnel others follow it one after another.

Of the several nests that I observed only one had two passages through the tampon.

In this instance two female wasps dug independently a pass way through the closure and one of them was much more delayed to go out of the chamber than any other wasps who calmly waited for the opening of a passage.

4. Distribution of the sexes

As already given in Table 14, the adult wasps emerged from one and the same brood-chamber always belong to the same sex. When two chambers are made in a nest the sex of the two groups is independently constant. The reason for this is not clear. It seems not so favourable as in usual case of other species in order to uniformalize the adult insects, because in this species the difference of the body length between the different sexes is not always larger than that between the individuals of the same sex (Table 16). At most it may be somewhat favourable to concentrate the dates of emergence of the adult wasps (Table 15). But such seems not an important matter towards the wasp.

Table 15. The first and last dates of emergence of the adult wasps per nest

Nest No.	The 1st emergence	The last emergence	Interval (day)	Sex
1	7. VII	8. VII	1	♀6
3	1. VII	4. VII	3	♂8
4	30. VI	2. VII	2	♂4
5	1. VII	2. VII	1	♂4
6	1. VII	1. VII	0	♂3
7	7. VII	9. VII	2	♀6
9	30. VI	2. VII	2	♂5
10a	30. VI	30. VI	0	♂2
12	1. VII	7. VII	6	♂7

Table 16. Length of body of the adult wasps emerged from the nests (mm)

Nest No. \ Emergence order	1	2	3	4	5	6	7	8	Maximum difference
1	21.5	19.7	17.8	?	24.5	22.0			6.7
3	17.8	19.5	18.2	18.4	17.2	18.0	19.0	17.5	2.3
4	18.7	20.7	19.5	?					2.0
5	?	?	?						
6	21.5	18.2	15.3						5.2
7	17.0	19.3	23.0	20.5	24.5	21.0			7.5
9	19.2	17.8	15.2	20.0	?				4.8
10	17.5	18.0							0.5
12	17.0	26.0	24.0	23.8					7.0

X. *SPHEX (ISODONTIA) MAIDLI* YASUMATSU

This species is the same in making the uni-cellular nest in the hollow of the log and in rearing a single larva in one cell as *S. nigellus* Sm. But it is the same in the habit of using the moss for the material to close the nest as *S. harmandi* Pérez.

On Aug. 15, 1956, while collecting small wasps nesting in the hollows of logs piled up along the roadside at Ichinose, at the foot of Mt. Haku, I became aware of two wasps of this species entering among the logs with some greenish material. They came from time to time with the similar substance and carried it in the hollows of logs. On capturing one of them it was made clear that they had been collecting green mosses, probably as material for closing the tunnels of their nests. I released the wasp to make her continue the nest building activities.

The next day the owner of the logs cut off for me an end of one of the logs that included the wasp's nest. The other nest could not be pulled out of the pile. After carrying about the block of wood for two days in the mountain, I came back home and at once examined the nest. Rather elaborate task of sawing and cutting of the hard wood revealed that the nest was constructed in the abandoned beetle hole and it consisted of a single brood-cell and was in the course of the permanent closure. Unfortunately, however, it had already been parasitized by a host of a Tachynid fly. The larva of the wasp as well as the prey collected for it had almost completely been devoured up by the maggots.

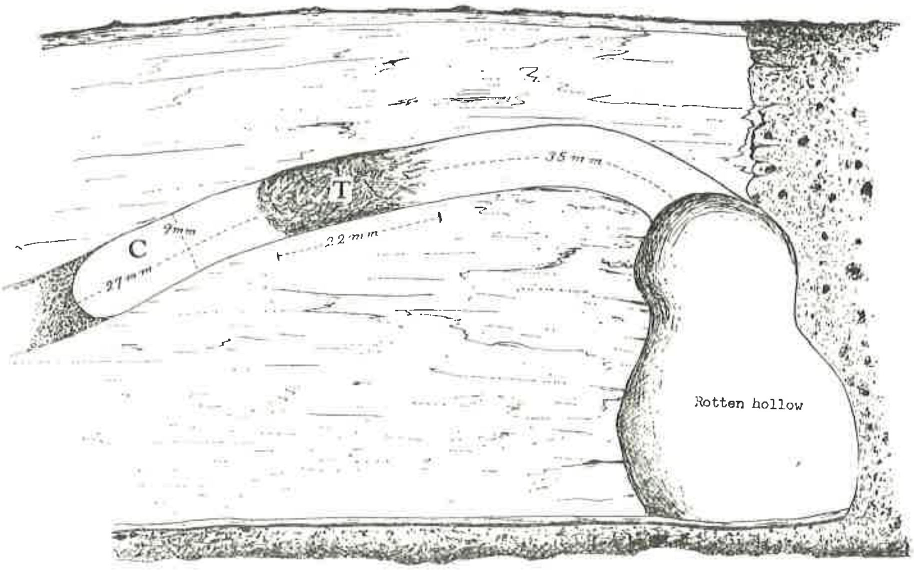


Fig. 14. A nest of *S. maidli* made in a beetle tunnel of a log. C, the cell; T, tampon of the moss.

The structure of the nest was shown in Figure 14.

Careful collection of remains of the prey in the cell, however, gave me 1 male and 2 female caudal parts, 6 pronotums, 6 crania, 11 hind legs, 19 fore- and mid legs and 19 egg of a certain species of grasshopper. In addition, one nearly intact nymphal male prey was found half buried from beneath the tampon at the entrance which, together with the remains of the pronotums showed that the victims doubtlessly belonged to some species of the genus *Conocephalus*. Judging by the result, the prey might consist of 7 insects, including 5 ♀♀ (probably 1 adult and 4 nymphs) and 2 females (both nymphs). Parasitic maggots when counted showed that they reached as many as 191 in number, all being 3–5 mm in length. It seems possible that they must be laid by more than one flies at several times.

The packing material at the gallery consisted of a species of the lively moss, *Erythrodontium leptothallum* (C. M.) Nog. (Dr. S. Kamuro det.). The tampon was not so compact as usually met with in the case of the permanent closure of *S. harmandi*. It might, therefore, be a temporal closure, or at the beginning of the final closure.

Judging from the fact that the wasp was collecting the moss a couple of days before, the matter is considered to be at the begining of the final closure. The amount of food assembled in the cell is also well accords with the normal diet of a single larva. Still further, the space taken as brood-cell is considered proper to a single larva.

However, in order to give the final conclusion further studies are still requested. (Vide addenda)

II. COMPARATIVE CONSIDERATION ON THE EVOLUTION IN BEHAVIOUR

In dealing with the evolutional grades and the mutual relationships among the members of the genus *Sphex* (s. latr.) it will be necessary to give some considerations on the possible criteria with respect to evolution in behaviour.

1. Criteria of evolution in behaviour

First, we can take up the *substratum* on which the nest is made. In a sense it can be said *habitat* of the wasp. Second, we must pay attention to the *structure of the nest*. Third, the *time of the nest construction*, namely, the relation between the nest construction and hunting of the prey. It is the matter relating to whether the burrow is dug prior to hunting of the prey or succeeding to it. Fourth, the *method of oviposition*. It concerns with the position and manner of the egg of the wasp is laid. Fifth, the *taxonomic position of the prey*; sixth, *the number of the prey given to one larva*; seventh, some *particular behavioural characters*. In the following attempt will be made to classify the species dealt with in the present paper upon the bases of the above listed items.

2. General survey basing on the indices

From the view point of the nesting substratum the members of *Sphex* s. latr. can be divided into two groups, the burrowing group and the lenting group (or tube lenting group), the latter being, of course, more advanced. In the representatives of eastern Asia the species of the subgenera *Sphex* s. str., *Palmodes*, *Prionyx* (= *Parasphex*) and *Harpactopus* (= *Priononyx*) belong to the first group and the species of the subgenus *Isodontia* to the second.

Of the nest structure, the compound type is more advanced than the simple type and of the time of burrowing the nest, pre-burrowing in retation to prey hunting is considered more progressed than post-burrowing.

According to the above mentioned three criteria we can arrange the species dealt with in the present paper from the more advanced to the less advanced as follows:

(*nigellus* · *harmandi* · *maidli*) — (*argentatus* · *flammitrichus* · *maxillosus* — *fukuianus* — *haemorrhoidalis* — *albisectus* — *subfuscatus* · *occitanicus*)

On the other hand, in order to make clear the relationships between the burrowing group and the lenting group, and also among each of the subgenera of the burrowing group it is most useful to compare them from the view point of oviposition as well as the kind and number of the prey.

As for the type of oviposition the members of the subgenera *Sphex* s. str. and *Isodontia* are perfectly the same, while those of other subgenera are quite different. The former belong to the sterno-ovipositing type and the latter pleuro-ovipositing type*. In view of the number of the prey offered to one larva the former can be classified to the multi-victim type, while the latter uni-victim type. Multi-victim type is believed more advanced than the uni-victim type (cf. W. M. Wheeler, 1922, 23). The fact, together with the information from the nest structure, leads us to make the following classification:

(*Isodontia* — *Sphex* s. str.) — (*Prionyx* — *Harpactopus* · *Palmodes*)

With respect to the kind of the prey we can divide them into two or three groups: Hunters of the longhorned grasshopper and hunters of the shorthorned grasshopper, or hunters of Tettigoniidae, hunters of Gryllacridae and hunters of Locustidae:

(*Isodontia* — *Sphex* s. str. — *Palmodes*) — (*Prionyx* — *Harpactopus*)

(*Isodontia* — *argentatus* · *flammitrichus* · *maxillosus* — *haemorrhoidalis*) — (*fukuianus*) — (*Prionyx* — *Harpactopus*)

3. Comparative consideration on various grouping

The distance between the burrowing and lenting groups is certainly great, and the lenting group is, as far as dealt with in the present paper, well united. But the burrowing group is, on the contrary, lacks unity. It involves various heterogeneous groups, the distance between some of which is considered much greater than the distance between some of them and the lenting group. This division is, therefore, similar to the division of Vertebrata and Invertebrata of the animal kingdom.

On the other hand, the division based on the method of oviposition seems more fundamental, since this has multiple connections with other characters, namely, number of the prey, kind of the prey (except for *Palmodes*), the time of burrowing (except for *Prionyx*) and the depth of the nest. The exceptions belong rather to the particular characters which have not direct bearing on the main track of evolution. According to this criterion *Sphex* s. str. lies closer to *Isodontia* rather than to the pleuro-ovipositing group.

The criterion of the nest structure seems of more use in dealing with the close relationships between species of the same subgenus than in attempting the general survey, though sometimes it can give a parallel support.

The same can be said with respect to the kind of the prey.

4. Relationships within *Isodontia*

Regarding the nest and the prey the three species are considered rather equivalent to one another. Only the nest-closing material separates them in two : *nigellus*—*harmandi* · *maidli*. As to *maidli* the study is insufficient, but if it is as earlier concluded, it is less advanced than *harmandi* which performed a particular development in that it rears multiple larvae aggregatively in one cell. Moreover, it shows a trend of making the multicellular nest. On the other hand, *nigellus* also shows an inclination of building

* In the strict sense, the place does not belong to the pleuron. But for convenience' sake the term was used.

ing the multicellular nest and the tendency seems stronger than in *harmandi*. But it has some connection with some species of *Palmodes* in utilizing the grass halms as nest closing material. The relation between the three species may be: (*harmandi* — *maidli* · *nigellus*. In the present status *harmandi* occupies the highest position and the other two are at nearly the same level.

5. **Relationships within *Sphex* s. str.**

From the structure of the nest *argentatus fumosus* must be ranked highest, since its nest is provided with the side holes ; *flammitrichus* and *maxillosus* are at nearly the same level, but if the characters on the depth of the nest and paticularity of the prey are taken into account *flammitrichus* may be slightly higher. Generally speaking, *flammitrichus* is most close to *argentatus*, while *maxillosus* is considered standing against the two.

There is no doubt as to the fact that *fukuians* and *haemorrhoidalis* are less advanced than the three species above treated from the view point of the nest structure. But, both species are interesting in showing two aspects in the evolutional process of the nest structure. The branched compound nest of *fukuianus* is structurally very close to the group of the aggregated simple unicellular nests of *haemorrhoidalis*. But the latter has a particularity in the method of the temporary closure. Apart from the nest structure, both species have developed a special character respectively, *fukuianus* in the kind of the prey (Gryllacridae) and *haemorrhoidalis* in the method of feeding the young (progressive feeding). In the present status *haemorrhoidalis* should be regarded as occupying the highest behavioural position of all the species of *Sphex* s. l., although it still retains a primitive character in the structure of the nest.

6. **Relationships among the pleuro-ovipositing species**

The species belonging to this group are, as a rule, hunters of Locustidae and burrowers of the simple shallow unicellular nest; their nests are made after capturing the prey and the prey is always single in number. The typical species of this group is represented by *Harpactopus subfuscatus*. Its method of closing the nest is also quite rough and simple. It seems certain that this species represents the most primitive stage in the biological characters among the members of *Sphex* s. latr. As to the comparative biology of the representatives of this subgenus of America an excellent paper was published by H. E. Evans (1958).

Prionyx albisectus, on the other hand, is more advanced in that it makes the nest prior to capturing the prey and closes it temporarily. *Palmodes occitanicus* is slightly deviated in that it hunts peculiar species* belonging to Tettigoniidae, but it is very primitive in that its method of burrowing is simplest and quite rough. Certainly this species is not advanced from the view point of general behavioural characters. However, it is considered to represent a position very close to the branching point of the group

* Fabre describes that the prey of this species are restricted to species of *Ephippigera* (Tettigoniidae). Ferton, however, recorded in his observation in Corsica that this species also hunted *Phasgonura viridissima* (Tettigoniidae). In my observation it was *Atlanticus ussuriensis* (Tettigoniidae).

of *Isodontia*, of which explanation will be given in the next section.

7. *Palmodes* and its relationships to *Isodontia*

Palmodes occitanicus has a slight connection with *Sphex-Isodontia* group in the character that it captures a longhorned grasshopper, though the prey belong mainly to some peculiar wingless form. Moreover, its burrowing work is very simple, sometimes half utilizing a hollow under some shelter, such as the rock, house floor and roofing tiles. Frequently it crimbs up the wall to make the nest high above the earth. All these characters have some bearing on the habits of the hole-lenting *Isodontia* species. But it still retains the post-burrowing and pleuro-ovipositing habits, the fundamental characters of the primitive gronp of the genus *Sphex* (s. latr.).

In relation to the connection of *Palmodes* with *Isodontia* a very interesting and

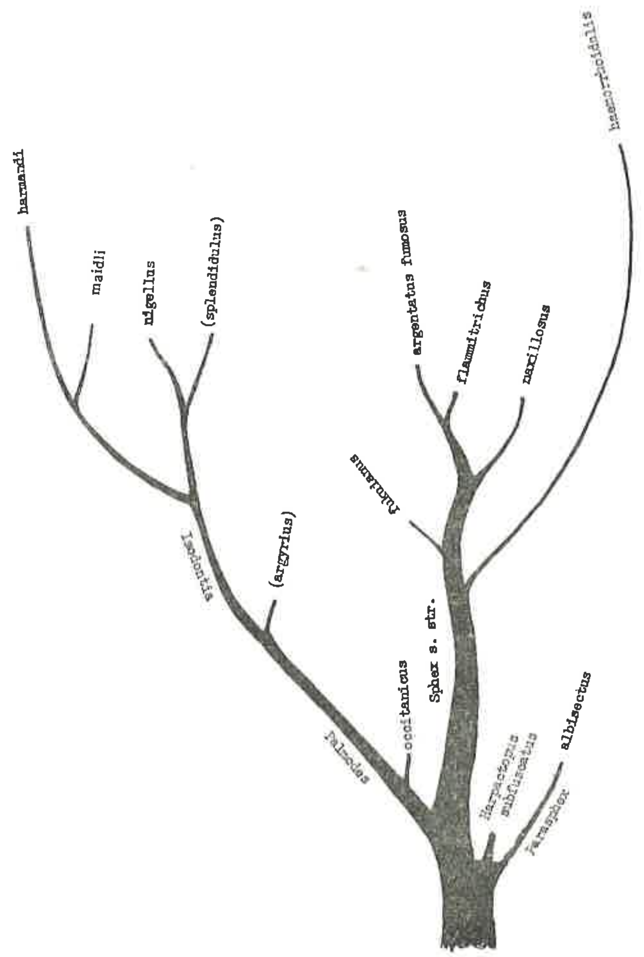


Fig. 15. The dendrogram of *Sphex* occurring in East Asia viewed from their nesting biology. (*Parasphex* Smith is now replaced by *Prionyx* V. d. Linden.)

important instance was afforded by *Palmodes argyrius* observed and discussed by L. Berland (1958). This French species utilizes a pre-existing hole as its nesting site, uses grass halms for inner and outer stopper of its nest and stores several long-horned grasshoppers as food for the young. As far as such matters go. its habits are quite identical with those of some species of *Isodontia* (for instance *nigellus*, *splendidulus*), but the space used for the nest is not the vegetable tubes found in mid air, but the hollow between stones of the stone wall, that is to say, it still keeps the earth as its nesting substratum. Furthermore, its manner of egg-laying belongs to the pleuro-ovipositing type. In so far as these matters are concerned the species undoubtedly belongs to the primitive group.

Judging from the accounts given above *P. argyrius* is closest to the members of *Isodontia* and *P. occitanicus* remains in a more primitive state of *argyrius* and at the same time closest to other members of pleuro-ovipositing group. Hence, it may be said that the species is situated close to, if not at, the branching point of the two main groups divided here rather conveniently by the manner of oviposition.

CONCLUSION

We cannot directly connect the species occurring in our region at present with one another from the biological standpoint in a phylogenetic tree, since they represent only some twigs of the separate branches of the stem-group and the southern stock including a number of main branches and twigs mostly remains uninvestigated with respect to their biology. But we may be allowed to arrange them in a tentative dendrogram to show the relationships among them from the point of view of the nesting biology. It was given in Figure 16.

Literature

Baba, K. 1938. コクロアナバチの巣の記録. Ent. World (Tokyo), 6 (55) : 32–36.

Berland, L. 1925. Notes sur les Hyménoptères fouisseurs de France, V. Observations biologiques. Ann. Soc. ent. France, 1925, 39–51.

——— 1925. Faune de France. 10. Hyménoptères Vespiformes. I. ref. pp. 36–40.

——— 1926. Notes sur les Hyménoptères de France. X. Observation biologique sur *Sphex occitanicus*. Ann. Soc. ent. France, 95 : 173–178.

——— 1958. Observations sur le comportement du *Sphex argyrius*. Bull. Soc. ent. France, 63 : 66–73.

Claude-Joseph, F. 1928. Recherches biologique sur les prédateurs du Chili. Ann. Sci. Nat., Zool., 10. Ser. 1928, 10 : 67–207 (ref. p. 183–).

Evans, H. E. 1958. Studies on the nesting behaviour of digger wasps of the Tribe Sphecini. Part 1: Genus *Priononyx* Dahlbom. Ann. Ent. Soc. America, 51 (2) : 177–186.

Fabre, J. H. 1856. Etudes sur l'instinct et les metamorphoses des Sphégiens. Ann. Sci. nat. Zool. 4e Ser., 6 : 137–183.

——— 1879. Souvenirs entomologiques. Ref. 81–115, 136–164.

Ferton, C. 1901. Notes détachées sur l'instinct des Hyménoptères mellifères et ravisseurs. Ann. Soc. ent. France, 70, ref. p. 108.

——— 1902. Ibid. (2e Ser.). Ibid., 71, ref. 504–512.

——— 1905. Ibid. (3ᵉ Ser.). Ibid., 74, ref. 64-65.
——— 1909. Ibid. (5ᵉ Ser.). Ibid., 78, ref. 142.
——— 1910. Ibid. (6ᵉ Ser.). Ibid., 79, ref. 177.
——— 1911. Ibid. (7ᵉ Ser.). Ibid., 80, ref. 366, 388.
——— 1921. Ibid. (9ᵉ Ser.). Ibid., 89, ref. 350.

Fujimatsu, K. 1937. クロアナバチ *Sphex umbrosus* Christ の生活史. 特にその幼虫期及び蛹期について。Kontyu, 11 (5) : 347-356.

Grandi, G. 1928. Contributo alla conoscenza biologica e morfologica degli Imenotteri melliferi et predatori. VI. Boll. Lab. Ent. R. Ist. Sup. Agr. Bologna, 1 : 3-30. (ref. p.12).

——— 1961. Studi di un entomologo sugli Imenotteri superiori. Boll. Ist. Ent. Univ. Bologna, 25 : 1-659 (ref. 144-147).

Iida, K. 1934. アルマンモモアカアナバチの生態。Mushi, 7 (2) : 101-108.

Ikushima, Y. 1934. コクロアナバチの造巣観察。Trans. Kansai Ent. Soc., 5 : 55-60.

——— 1935. 続コクロアナバチの観察。Ibid., 6 : 55-59.

Ishii, T. 1934. コクロアナバチの巣。Kuntyu, 8 (4・5・6) : 286.

Iwata, K. 1936. アナバチの習性。Kontyu, 10 (4) : 163-187.

——— 1942. Comparative studies on the habits of solitary wasps. Tenthredo, 4 (1-2) : 1-146.

Kano, T. 1934. クロアナバチの観察小記。自然研究, No. 7, pp. 18-20.

Kawamura, M. 1953. *Sphex nigellus* コクロアナバチの異常巣について。げんせい, 2 (1-2) : 45-46.

Kohl, F.F. 1890. Die Hymenopterengruppe der Sphecinen. I. Ann. naturh. Hofmus. Wien, 5 (2), ref. pp. 119-133.

Marchal, P. 1893. Notes sur la nidification de divers Sphégiens. Ann. Soc. ent. France., Bull., 1893, p. 68.

——— 1893. Sur les nidifications du *Sphex splendidulus* et du *Chalicodoma perezi*. Zool. expér. 1893 : 29.

Masuda, H. 1930. ツツアナバチ *Sphex muticus* Kohl の習性に関する研究。動雑, 41: 174-189.

Nicolas, H. 1893. *Sphex splendidulus*. C.R. Soc. Biol., 9. 5 : 826-828.

Peckham, G.W. et E.G. 1898. On the Instinct and Habits of the Solitary Wasps. Wisconsin Geol. Nat. Hist. Surv. Bull. 2, 245 pp.

Picard, F. 1925. Note sur la biologie des *Sphex maxillosus* F. et *flavipennis* F. Bull. Soc. ent. France, 1925, 24-26.

Piel, O. 1933. Recherches biologiques sur les Hyménoptères du Yang-tse (Chine). *Sphex (Isodontia) nigellus* F. Smith. Ann. Soc. ent. France, 102 : 109-154.

——— 1935. Recherches biologiques sur les Hyménoptères du bas Yang-tse (Chine). Etude sur les Sphégides. Ibid., 104 : 273-306.

Rau, P. et N. 1918. Wasp Studies Afield. Princeton Univ. Press. 372 pp.

Sonan, J. 1927. 台湾産蜂類数種の学名及び観察。Trans. Nat. Hist. Soc. Formosa, 17 (89) : 131.

Torikata, T. 1931. 蜂類2種の生態観察。Mushi, 4 (1), ref. pp. 1-5.

Tsuneki, K. 1931. Studies on the habits of the Japanese hunting wasps. II. Trans. Tokyo Nat. Hist. Soc., 39 : 89-95. (In Jap.)

——— 1937. The life of *Sphex umbrosus* Chr. Koyukai-shi of Utsunomiya Daini-Kojo, 1937 : 1-13. (In Jap.)

——— 1942. A Naturalist at the Front. Osaka. (In Jap.) 424 pp. ref. 70-86, 260-273.

——— 1946. The Japanese Hunting Wasps, Their Ecology and Psychology (Sapporo). (In Jap.). 254 pp, ref. 66-141.

——— 1946. Biological observations on hunting wasps. I. *Sphex (Sphex) haemorrhoidalis*

Fabricius. Seibutsu, 1 (1) : 46–49. (In Jap.)

——— 1946. Ibid. II. *Sphex occitanicus, Tachytes etruscus* and *Lyroda japanica*. Ibid., 1 (3) : 164–167. (In Jap.)

——— 1957. Biology of *Sphex* (s. str.) *fukuianus* Tsuneki. Kontyu, 25 (2) : 50–52.

——— 1957. Biology of *Sphex* (*Isodontia*) *maidli* Yasumatsu. Akitu, 6 : 35–36.

Tsuneki, K., Ohta, A et Okuno, H. Nests of *Sphex* (*Isodontia*) *nigellus* Smith. Life Study (Fukui), 3 (1) : 3–6.

Wheeler, W.M. 1922. Social life among the insects. Sci. Mon., 15 (4) : 320–337.

——— 1923. Social Life Among the Insects. New York. 375 pp.

Williams, F.X. 1919. Philippine Wasp Studies. II. Bull. Exp. St. Hawai. S.P.A., Ent. Ser., 14, ref. 124–128.

Yasumatsu, K. et Okabe, K. *Sphex harmandi* Pérez 雑記。Mushi, 8 (2) : 117.

Addenda

Since the manuscript went to press considerable data have been collected to be added to the present paper :

(1) **(*Sphex*) *flammitrichus*.** A just finished 14-celled nest was excavated in Tsuruga. It contained 4 cells ravaged by the fly. The prey : All *Holochlora japonica* 2–4 in a cell. The cells located in a semicircle with the entrance at the centre, distance from the entrance 40–60 cm and the depth below the surface 25–39 cm.

(2) **(*Sphex*) *fukuianus*.** Examined one finished 9-celled and one unfinished 5-celled nest made in the rocky ground not completely weathered. Hard ground made it confirm that the branch-tunnels are given off directly from the main tunnel at different heights. The entrance to the nest is always left open, the branch-tunnel alone closed. Cells located 7–20, and 15–25 cm below the earth surface. Prey the same.

(3) **(*Isodontia*) *nigellus*.** Examined 27 nests, 4 in the beetle burrows in logs and 23 in the bamboo tubes artificially settled, including 9 1-cellular, 8 2-c., 8 3-c. and 2 4-c. nests. Therefore, the multicellular nest seems rather rule in this species, if conditions favour for it. In 5 cells 2 eggs or 2 young larvae discovered with double the amount of prey, a state transitional to *I. harmandi*. 3–4 larvae reared experimentally in a glass cell showed no cannibalim among them, if food was sufficiently furnished, as in *harmandi*. The prey mostly *Conocephalus melas* de Haan, frequently *Hexacentrus japonicus*, sometimes *Conocephalus gladiatus* Red. and *Ducetia japonica* Thunb., mostly nymph, the number per one larva 2–9.

(4) **(*Isodontia*) *harmandi*.** Examined 71 nests (of various stages of provisioning) made in bamboo tubes artificially placed; 4 2-chambered and 17 just finished nests included, 8 of the latter ravaged by the fly. The number of eggs found in a chamber *including additional prey*: 2 (3 instances), 3 (3), 4 (5), 5 (10), 6 (16), 7 (4), 8 (3), 9 (4), and 12 (1). The prey necessary for one larva under laboratory rearing normally proceeded (except shown in the Table): 4 (1), 5 (5), 6 (6), 7 (4), 8 (2), 9 (2) and 10 (1). Cannibalism among larvae likely to occur when the successive provisiong is impeded by

the bad weather and the larval growth becomes uneven. In the wide tube the floor is raised by placing moss-mat, and the prey are put in several rows and in two layers, always head-in, venter-up and with body oblique. The chamber is always filled with the prey up to the ceiling. The prey mainly *Conocephalus melas* (mainly nymph), partly *Xiphidiopsis suzukii* M. et S. On the temporary closure, usually 25–40 mm thick, a passage in the form of a furrow is always left at the inner half. In the finished nest the place is also stuffed with prey. The eggs are successively laid on the first 4–5 prey, but later with some intervals, sometimes 1 or 2 eggs are laid on the prey at the outer portion. Exceptionally in a chamber 8 eggs were found on the first 8 prey. When the nest contents are disturbed the wasp soon abandons it.

Table 17. Number of contents

Prey	Egg	C.R	PPE	PPC
42	6	5	7	8
27	5	4	5	7
20	4	4	5	5
27	5	5	5	5
37	6(4)	4	6	9
8	2(1)	1	4	7*
26	6	5	4	5
45	5	5	9	9
59	6	6	10	10

C. R : Cocoon resulted.
PPE : Prey per 1 egg.
PPC : Prey per 1 cocoon.
Numeral in ( ) : Living egg at the start.

(5) (***Isodontia***) ***maidli***. A tricellular nest of linear structure was made in a bamboo tube, 182×13 mm in dimensions. When examined each cell included a cocoon, similar in character to that of ***nigellus***, only slightly paler in colour. The cells were 36, 30 and 28 mm in length and the partition walls 17, 17 and 47 (final entrance closure) mm in thickness, made of moss. The prey ***Conqcephalus melas***; 5, 5 and 4 from inner to outer cell, including ♀ (mainly) and ♂, and nymph (mainly) and imago.

Explanation of the Plates

Pl. I. *Sphex argentatus fumosus* Mocsáry carrying a prey

Pl. II. The prey taken out of a brood-cell of *S. argentatus*, one of them carrying the egg of the wasp. (Slightly enlarged)
Cocoons of the same species, under laboratory rearing. (Ditto)

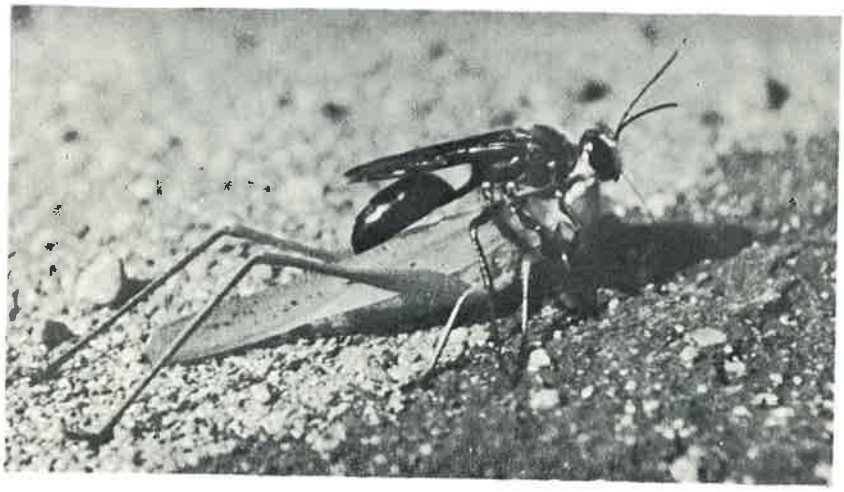
Pl. III. Rearing the larvae of *S. haemorrhoidalis* Fabricius.
S. occitanicus Lepeletier et Serville and its prey, *Atlanticus ussuriensis* Uvarov.

Pl. IV. The neste (with cocoons) of *S. harmandi* Pérez.

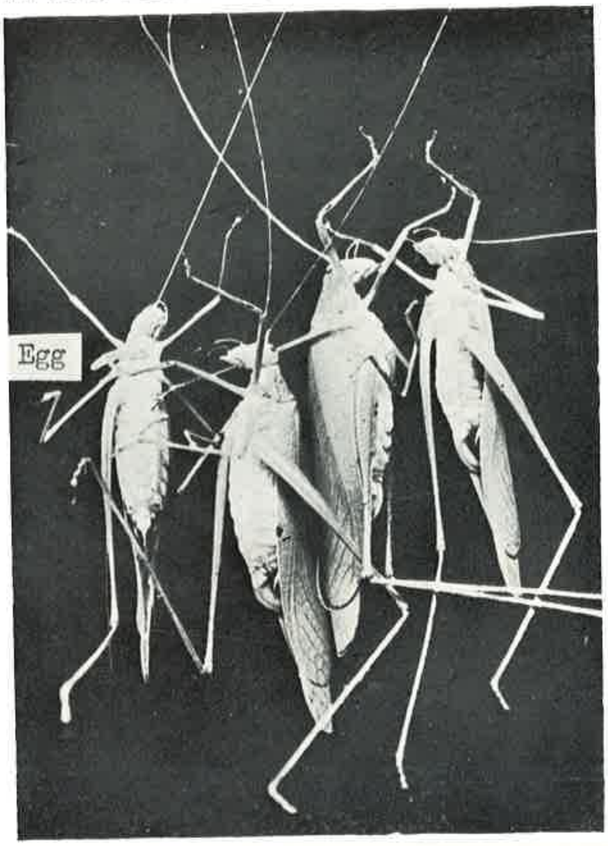
Pl. V. Ibid.

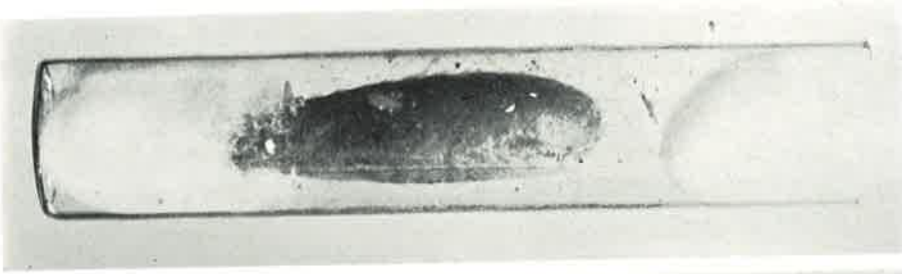
Pl. VI. Ibid. Stuffed prey. A cocoon, cocoon cover and a group of cocoons of S. *harmendi* Pérez.

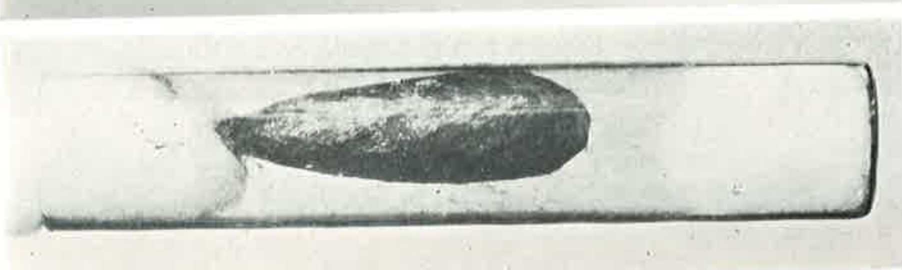
(All the photographs by the author.)



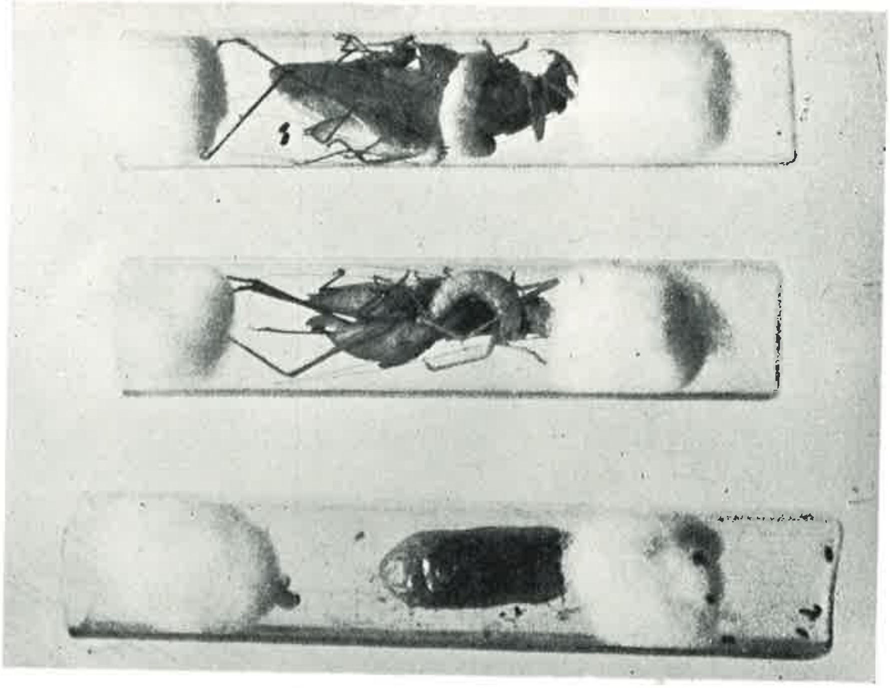
K. Tsuneki: Nesting Biology of Sphex in E. Asia

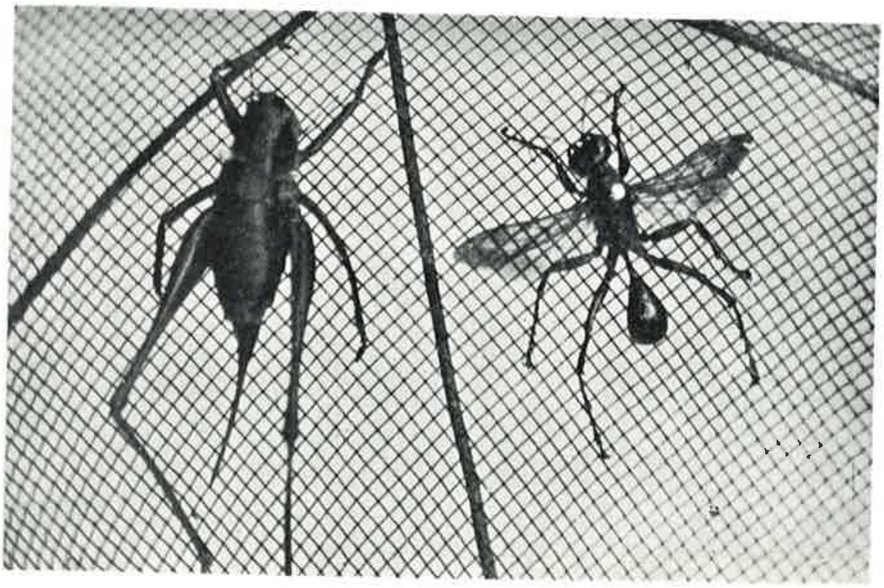






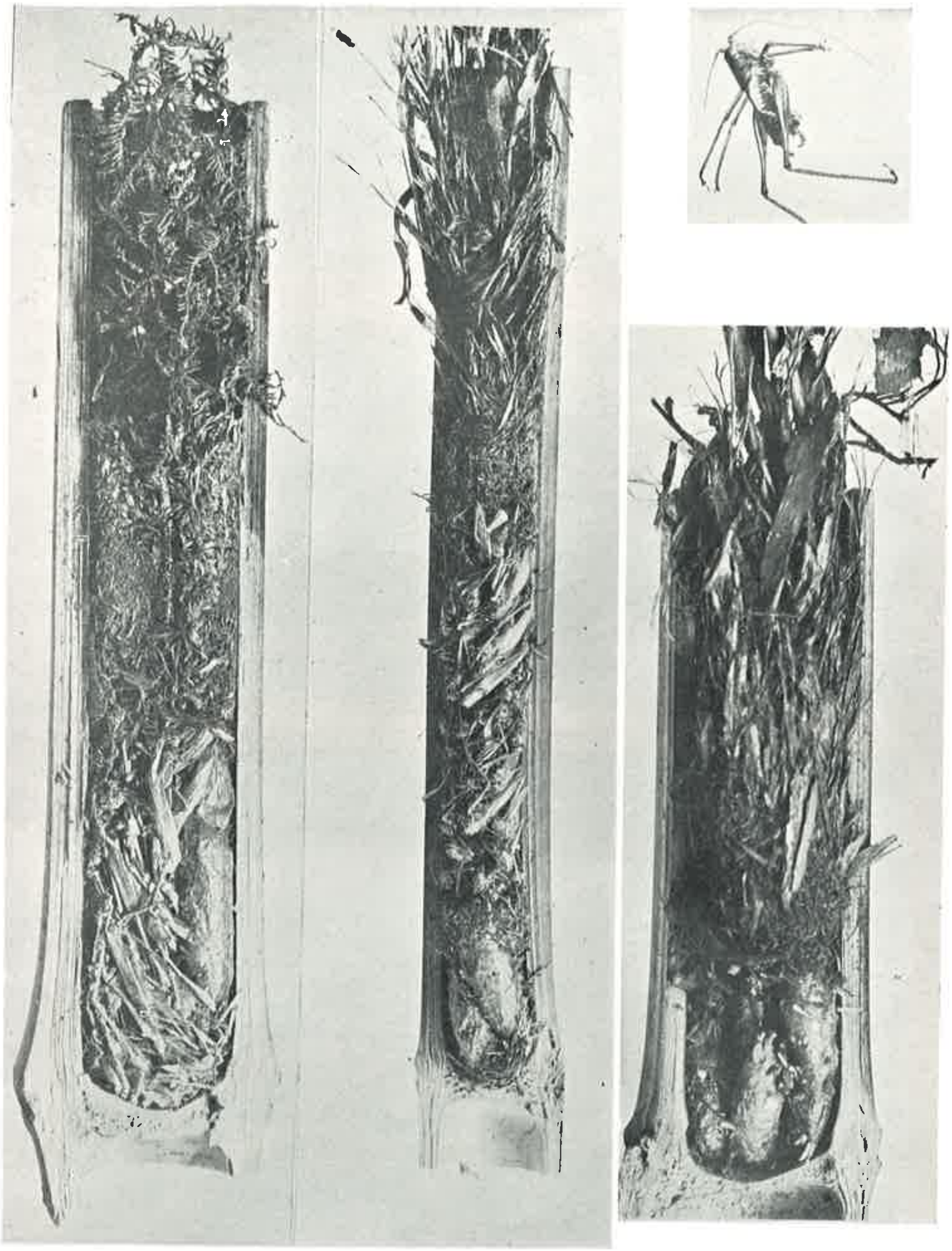
K. Tsuneki: Nesting Biology of Sphex in E. Asia





K. Tsuneki: Nesting Biology of Sphex in E. Asia

K. Tsuneki: Nesting Biology of Sphex in E. Asia



K. Tsuneki: Nesting Biology of Sphex in E. Asia

K. Tsuneki: Nesting Biology of Sphex in E. Asia