To Mr. W. J. Pulawski
With the Compliments of
K. Tsuneki

Ethological Studies on *Bembix niponica* Smith, with Emphasis on the Psychobiological Analysis of Behaviour inside the Nest

(Hymenoptera, Sphecidae)

I. Biological Part

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(With IV Plates and 22 Figures in the Text)

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FUKUI, JAPAN

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(Hymenoptera, Sphecidae)*

I. Biological Part

by Katsuji TSUNEKI
(Biological Laboratory, Fukui University)

CONTENTS OF THE PRESENT PART

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I. INTRODUCTION

The wasps belonging to the genus *Bembix* Fabricius represent a group of the Fossorial Hymenoptera that catch other insects as food for their larvae. All the members of this genus live in sandy districts, forming generally aggregate colonies. Hence they are called subsocial wasps. Each of the mother wasps, however, has her own nest which is burrowed shallowly in sand and has a blood-chamber at the end of a comparatively short tunnel. As a rule, in one nest is reared only one larva. The mother wasps make only several of such a nest during their lifetime. The reason for this is that the wasps, unlike the majority of other hunting wasps, take particular care for their youngs. They do not collect the whole provision necessary for the development of the larva promptly and massively during a short period of time, but bring the victims progressively day by day as long as the larva remains in its feeding state. Doubtless the state indicates one of the connecting chains between the non-social and the social lives in the Aculeate Hymenoptera. Therefore, the life of the wasps has attracted attentions of many scientific observers since the time of Latreille (1809), and a mass of knowledge concerning their biology has been accumulated.

About 300 species of *Bembix* have been described up to the present from the main continents of the world (probably including many synonyms and many species of other genera in the present-day meaning of Taxonomy). Among them about 30 species have been observed in relation to their biology in different detail. The majority of the species are hunters of Dipterous insects, but a few of them are known to hunt Orthoptera, or Hemiptera, or Lepidoptera or Odonata. Judging by the kind of the insects caught by the wasps (for instance Hemiptera), it seems clear that some of them must belong to some species of other genera in the recent systematics.

A species of *Bembix** widely occurs in Japan which is known under the name of *B. niponica* Smith, 1873. Two other species were also described from this country —— *B. miserabilis* (!) Parker and *B. fumida* Parker (1929). But the former is quite doubtful in validity; probably it is nothing but a synonym of *B. niponica* Sm. As for the latter it is also a doubtful matter whether or not such a species occurs in this country.

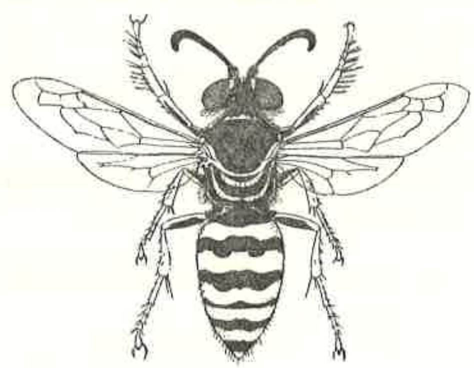

Fig. 1. *Bembix niponica* Smith

B. niponica has also been the subject of papers of several interested observers in Japan, such as T. Torigata (1930), K. Iwata (1936), K. Baba (1937), K. Yasumatsu (1939) and myself (1936 and 1948). Therefore, their habits are fairly closely investigated in a general way. According

* Some taxonomists split the genus *Bembix* into two, namely *Bembix* (s. str.) Fabricius and *Epibembex* Minkiewicz. According to this opinion, our *niponica* is to be belonged to *Epibembex*.

to the investigations of these observers, this species seems to be very nearly related in habits to the European species, *B. rostrata* Linné, just as it is in their morphological characters.

The present author made acquaintance of the wasp of this species for the first time in Chiba, near Tokyo, in 1931, when he was engaged in his military service. At that time he had been so fascinated by the Fabre's *Souvenirs Entomologiques* that he devoted all his possible hours to the study of the insect. But how severe that feudalistic restraint! He struggled with all the difficulties surrounded him and could accumulate the general knowledge concerning this species. The most interesting observations he made during this period (1931 - 32) were those on the compound type of the nest structure and those on the very suggestive "simultaneous caring for two larvae at a time". Later, in 1934 - 36 he had a chance of further observations upon the wasp in the suburbs of Utsunomiya, near Nikko, and carried out some supplementary investigations on the cocoon-spinning of the larva. In 1937 he was called away to the Chino-Japanese Conflict and passed about three years in battle in North China and Inner Mongolia. During the time he could observe in his leisure hours the habits of *B. picticollis* Morawitz and *B. weberi* Handlirsch in the Mongolian Steppe. The accounts on the life of these Bembicine wasps, together with those concerning scores of other Chinese and Mongolian solitary wasps and bees were given in his book, "A Naturalist amid the Battlefield" (Osaka, 1942 in Japanese). During the periods 1941 - 43, he stayed in Korean Peninsula and made some biological studies on a race of the Japanese *Bembix* having a somewhat different hue. But it was during the several years (1943 - 52) in Sapporo, that he truly devoted ample hours allowed to him to the detailed study of the ethology of this interesting wasp. Because the study conducted up to that time on this species of *Bembix*, as well as on any of the species of the world of this genus, seemed to him to be far from being called "*thoroughgoing*".

Indeed, it is rather strange to say, when we think of the fact that the habits of species of *Bembix* are so well known not only to the biologists, but also to any body who has some interest in the life of the insect, that not a single study has thoroughly been carried out by any one upon any of the species. No one has ever attempted to pursuit the activities of a single wasp continuously for several days in order to know the true aspects of the so-called "progressive provisionment". No one has ever observed the behaviour of the wasp inside the nest. Observations made for several hours on the wasp's activities outside the nest, knowledge acquired from the states of the nests dug open, informations obtained from the breeding of the larva in the laboratory and patching up the records thus collected by imagination! That is all. Especially as for the interesting problem on the mental ability of these subsocial wasps no investigation has ever been attempted from the viewpoint of comparative psychology, excepting for the problem regarding the return to the nest.

Therefore, at the commencement of his investigation in the suburbs of Sapporo it was the first aim to fill the blank pages left untouched pertaining the biology of this genus. At the same time he intended, for the second aim, to analyze, as far as possible, the behaviour of the wasp from the psychobiological point of view. In order to achieve the first aim he followed the activities of a great number of wasps which were numbered by means of marking continuously during a season and observed especially the behaviour of them in their subterranean chambers. To make clear the psychic ability of the wasps, he induced them to act in the glass-tubes having a variety of patterns and attempted various sorts of experiments upon them. The investigations were carried out during the most difficult periods of our country caused by the defeat in the War, and besides, the field was situated 5 miles away from his laboratory, without any conveyance but a half broken bicycle. These conditions became serious obstacles for the continuous study and sometimes compelled him to throw some details in the observations. In those days man had to search for food before to search for the secret of a wasp.

In the present treatise the results of his observations obtained so far (chiefly up to 1949) regarding the general biology of this species will first be dealt with, and later the behaviour of the wasp analyzed from the point of view of animal psychology will be described and discussed.

Before proceeding further the author expresses his sincere gratitude to Professor Tohru Uchida, Hokkaido University, for his kindness rendered during the course of this study in Sapporo.

II. GENERAL BIOLOGY

1. Emergence and the period of activity

According to the observations made in Chiba (about 35.7° in *lat.*), the emergence of *Bembix niponica* Sm. seems to occur late in June in the male and early in July in the female. Of course the male early disappears and the female alone continues to work up to the middle of August and then gradually passes out of sight. Towards early in September the wasps were rarely seen working in their nesting site. While in the suburbs of Sapporo (about *43°* in *lat.*), the male appears late in July and the female early in August. The activities of the female are continued toward the end of September, until the wasp is destroyed by the coming cold. According to J. B. Parker (1917), *B. spinolae* of North America makes its appearance twice a year. But it is not the case in our species.

2. Mating and courtship

The male wasps, as soon as they emerge and come out of their underground chambers, wait for the appearance of the female wasps, hovering low over the ground or alighting on the surface of the sand plain. Some of them, several in number, make a crowd within a certain limited area and busily walk about, buzzing from time to time and trying hither and thither to scratch the earth. When a shallow hole is made by the observer, they cluster there and try to penetrate, contending to be the foremost. In such cases, however, they do not dig out the earth with a will.

They appear to be attracted by something invisible calling them. Their behaviour is much like that of the excited crowd of male moths gathering about a certain spot where a female has been a short time before. The behaviour seems to be aroused by the diffusing smell of the female wasp which is still under the earth. Mating usually occurs immediately after the female comes out of her underground chamber, but it also takes place, rather rarely, during the period of her work. But it is uncertain whether the latter case occurs upon a individual already fertilized, or upon a virgin wasp. Usually, however, the male that chases every female coming within his sight and pounces upon it is coldly refused by the working female. The fact seems to suggest that the female wasp is fertilized, as a rule, once for all in her life time.

Apparently the mating is practised rather by force by the excited male, which swoops suddenly down upon a female while she is resting on the ground and captures her from the back with his mandibles and legs. At that moment a brief but fierce resistance of the female is usually observed. Then copulation takes place. It finishes quickly within a few seconds. The so-called marriage flight, accompanying one above the other, as seen in some solitary wasps (for instance in *Ammophila*), does not succeed or precede the performance. But I once had a chance of observing an interesting behaviour of a male wasp shown, probably, prior to the copulation. It took place as follows :

A male came flying to a female digging her tunnel and as usual darted at her when she appeared out of her burrow with a load of dirt. She flew up in a surprising manner, but did not swiftly flee away, as usually done by the working female when she refuses the male, but flew about up and down in a leisurely manner at a height of about 30 – 50 cm above the ground. Very slowly she moved, drawing large and small waves in the air as if making a dancing flight. The male followed her, keeping a distance of about 20 cm between her and himself, dancing or not dancing in accordance with her flight. At last the pair came to a shrub and the female alighted on a twig, the male followed her on the next lower twig. At that moment a very interesting and strange action of the male was commenced. He stretched his body and touched her with the tip of his antennae by the sides of her abdomen and began to rub there. Then the rubbing was turned into the tapping and the rate of the movement was gradually increased. This queer tapping of the male with his antennae continued, with a few interruptians, for about two minutes. While the female remained motionless. At last she crimbed up to the top of the shrub, followed by the male and they flew up again in the air and went away dancing in a couple across a sand hill.

3. Nesting place and its succession

Bembix niponica, as other members of the genus do, prefers the sandy ground, well dried up on the surface but reserving a favourable humidity below, for the foundation of their colony. Thus, out of the eight nesting places (each having several colonies) observed by me, six were found on the fine-sand plain. One of the rest was on the sandy ground mixing, however, a little earth. Only one was selected on the well trodden, hard soil. Out of the six sand plains, two were the alluvian of a river, two were located on the beach of the sea, one was a half vegetated sand dune and the last was a small mound of sand amid a dry river bed where there was a danger to be under water, had the river once flooded. According to the records of four other investigators of this species, the colonies of their wasps were all settled on sand plain. The surface of the nesting site may be either horizontal or inclined. As a rule, however, a gentle slope is beloved of this species and the tunnel is burrowed against the inclination. But towards the end of their activities, when the cold climate approaches, they gather to nest in the upper portion of some steep slopes or some sand cliffs, where the ground is well beated by the sun, and form a very crowded colony. This phenomenon could be observed every year in all the Bembix-colonies in the suburbs of Sapporo, and the same fact was also observed by my in the Inner Mongolian Steppe with regard to *B. picticollis* and *B. weberi*. Perhaps this will be the common habits among the members of *Bembix* living in the regions of comparatively high latitudes.

Their habits of forming a colony, the so-called subsocial nature, seems to be due, in the main, to their homing instinct in reference to the native place. But it is not always a proper thing to call them subsocial, if it is only based upon such a mere gregarious habits. Because, similar colony-formation due to the habits of return to the birth place is not a rare phenomenon in the world of non-social aculeate Hymenoptera. Apart from a mere gregarious habits, however, *Bembix* (*niponica* at least) should be called subsocial, because (1) among the members of the same colony a certain degree of familiarity can be observed (this is not alwalys the case among the colony members in other genera); (2) the relationships between the mother wasp and her young is (in this species) very much like that of the ant, as will be mentioned later in detail.

Besides the seasonal succession of the nesting site which seemed to depend mainly upon the change of temperature, the annual succession of the nesting site was also observed in some colonies of *Bembix* in the suburbs of Sapporo. This seemed to be resulted by the invation of the plant. Some of the colonies of *Bembix* were settled respectively in a basin. These basins were dug open in the vegetated sand dunes in order to build hiding places for airplains near the end of the War. In 1946 when I resumed the investigation the basins had been abandoned and the bottom of one of them formed a clear sand plain and about two scores of the wasps were working flourishingly. But the next year the plant began to invade. At first *Miscanthus sinensis*, *Zoysia pungens* stretched their root system from the circumference of the area. *Artemisia bulgaris* formed hither and thither small patches of green amid the wholly grey ground. The domain of *Bembix*, however, hardly received any interferance from these intruders as yet. In 1948, the invasion from the surrounding vegetation became fairly striking. Several large tufts of *Miscanthus* and the tall community (!) of *Artemisia* threw large black shadows over the grey sand plain. The bottom of the basin was already sparsely occupied by the seedlings of various species of Graminae. *Bembix* had to avoid these vegetations for the nesting site. But there is still a large clear area near the northern cliff and on the north-eastern slope. There the population of the *Bembix* colony was fairly dense. Moreover, they made their nests also among the sparse vegetations at the bottom plain, although the number of the wasps nesting there was very small. The next year the wasp's colony was restricted to the northern small area and the number of the working females was markedly eliminated.

In 1951 when I visited the place in the midst of the *Bembix*-season, only a few wasps remained burrowing among the Graminae plants and no trace of the flourishing colony could be observed. At that time, nearly all the basins that were good grounds several years before for my investigation were densely covered with vegetation and had returned to their original pasture. At that time, *Bembix* shifted their nesting sites to the scattered areas where the ground was comparatively sparsely covered with plants and burrowed among the grass. But the main colonies were found at the roadside where in this sandy district the ground was rather broadly cleared. However, the place was not always safe for colonization and the inhabitants were being disturbed from time to time by the passing vehicles and cattles. As the ground was narrow and long, nowhere could a large population such as found before be met with. The population had dispersed.

4. Burrowing of the nest

Apart from the first nest she makes, *Bembix* burrows her nest more frepuently in the afternoon. Ths is due to the fact that the last provisionment for her larva of the previous nest is more frequently performed in the forenoon and the wasp usually digs the next burrow at once. In burrowing the nest, *Bembix niponica* does not make, prior to her digging, such elavorate imspection of the nesting site as sounding the ground with the antennae apparently with great care, as often carried out by many other hunting wasps that nest in the earth. *Bembix* begins rather capiously to dig hither and thither. After a few scratches of sand or after burrowing in several centimeters, however, the place is very frequently abandoned, in most cases without any apparent reason for the abandonment. Therefore, it takes sometimes more than half an hour and no less than a dozen fruitless trials are repeated before the right place is finally settled. These abandoned holes and tunnels are always found numerously in every colony of the wasp (Pl. I, Fig. 1).

In digging, front pair of legs alone is used when the ground is composed of fine grains of sand, but in case the ground is more or less clayish and somewhat hard, the mandibles also take part of the burrowing. The wasp doubled up her front pair of legs inwards, so as to form a rake of long spines of her tarsal joints, wherewith she sweeps the dirt behind her through the underside of her abdomen. As the legs of *Bembix* are comparatively short, it is incapable for her to held her body high above the ground while she is digging, as easily done by the members of the Pompilidae. In the normal posture when sitting on the earth, the body of *Bembix* is held somewhat obliquely against the surface, lifting the head high and lowering the abdomen, with the apical portion always kept in contact with the earth. Therefore, when she throws the dirt behind her, the abdomen must be lifted. However, her body is rather heavy and clumsy, so that she is unable to do so without lowering the anterior body. Thus the up-and-down movements of her anterior and posterior bodies are repeated alternately every one sweep. During the time, the body of the wasp is held straight on the inverted V-shaped support formed by the mid and hind legs on both sides, so that the attitude of her burrowing gives her a very stiff aspect, making her look as if she were a small automatic seasaw. The seasaw-like movements of the wasp is, however, carried out fairly quickly, so that the dirt, each in a small lump, comes out behind in rapid stream, flying to a distance of 10 - 15 cm. However, as the speed of the digging is not so high as in Pompilid wasp, each lump of sand is, when carefully observed, clearly distinguishable in the stream. When the burrow becomes deep, the dirt displaced at the bottom is carried to the entrance by a particular method. First the wasp sweeps the sand behind as usual with the front pair of legs. Then she pushes it backward with the hind pair of legs. At the same time, her abdomen is bend ventrally and pushes the dirt with the tip of its dorsal surface. The manoeuvre is repeated with her backing progress and the sand is gradually shifted near the entrance. After several time of such transportations, however, the tunnel comes to be plugged with sand for a considerable distance. Then the wasp appears, head first, through the stoppage and sweeps the accumulated sand from without. In case the ground is pebbly, the wasp grasps the pebble that happens to be in her tunnel with the mandibles and drags it out backward. These pebbles are usually transported far away (50 - 150 cm) from the entrance to be cast off.

In general, this species burrows the tunnel without stopping on the way, but rarely she does, and closes the entrance temporarily to go out. But soon she comes back and resumes her activities at once. The time required for burrowing a nest is about 15 - 35 minutes; but it is, of course, variable according to the conditions of the ground. When the burrow is completely dug up, the wasp closes the entrance and goes out for a foraging excursion, However, in the strict sense, the nest is not completely built up at this time, because it does not contain as yet an enlarged pocket, the brood-chamber, at its end. Notwithstanding, when the tunnel is burrowed up, the wasp stops her work and comes out head first, gathers some dirt and closes the entrance. After temporarily closing the entrance, the wasp, before departure, sets about the work to even the surface in front of the nest, scattering and sweeping the dirts that have been thrown out of the tunnel. But this part of the work is soon ceased in our species, leaving alone the heap of the dirt in front of the nest which is useful to the observer as well as to some of the enemies to find the nest, and the wasp begins at once to take the orientation flight. In this respect *niponica* is very characteristic. Most of the species investigated heretofore are said that after preparing the nest they turn their attention to scattering all the dirt that have been heaped in front of the nest, sweeping the ground so clean and so elaborately until no sign of their work remains there. The brood-cell is made after the first victim is taken in, at least in this species. The details regarding this point will be mentioned later.

The male, too, burrows the tunnel to pass the night or to get a shelter for the bad weather. Although he prefers to utilize the ready-made holes of others such as the abandoned tunnels of the females, if no favourable place can be found near-bye, he begins at once to burrow the tunnel in the same fashion as the female. In general, the tunnel thus made temporarily by the male are shallow and simple. They are closed with the dirt pushed out behind while the owners remain within. The closure of the entrance is carried out in the same manner as done by the female. He pushes backward the sand displaced inside by the tip of his abdomen. The female having no nest as yet digs the like tunnel as the shelter in case of the shower or toward the evening. The behaviour of digging and closing of these shelters can easily be observed, if one rears a wasp in a glass pot half filled with sand.

5. Orientation flight

As soon as the nest-burrowing is over and the entrance to the nest is closed, the wasp begins to make a special sort of flight known as the orientation flight, which may be useful for the study of the locality. One of the typical instances was observed on the 9th September, 1947, at about 3 o'clock in the afternoon. The nest was situated in the middle of a gentle slope having the area of about 5 × 10 m. and facing the west. The north and the east of the slope were bordered by a small cliff respectively. The wasp, showing anterior half of her body out of the burrow, scratched in some dirt first from in front and then from the surrounging walls of the entrance, loosening it with her mandibles. Having closed the door-way, she proceeded forward a few steps, turned round at once and faced the nest. Then after a few times of automatic sweepings, she flew up and hovered over the ground very slowly at a height of 30 – 40 cm above the surface and within a circle of about 50 cm in radius, with the nest as centre, humming loudly but intermittently and moving up and down. During the course of hovering, she visited most frequently the site of her nest. After a while the wasp landed before the nest, facing the entrance, but at once turned around and threw a few scratches of sand backward on to the entrance. Again she rose on the wing and after circling about a while, once more alighted in front of her nest and made the similar simple sweeping as before. At once she flew up and the same manoeuvre of circling and landing was repeated still several times. But on and after the third time, the circles were gradually enlarged and at last turned into an irregular ellipse of about 4 – 5 m. in the long axis, the form of which was nearly in accordance with the natural space of the slope. While performing these circling and sinuating flights within this limitted area, the wasp came from time to time just in front of the nest and there she held her body motionless in the air at a height of 20 – 40 cm above the ground, just as the *Bombilius* fly usually does. At that moment her face was always directed toward the nest entrance, as if she was trying to remember the relative postion of the landmarks that came in sight at that position against the nest. A few moments later the wasp started to resume the hovering and circling as before. On and on the flying range was extended and the flying speed was increased and at last the wasp became to return to her nest only in the course of her 8-shaped flying passage then taken, in stead of stopping over and in front of her nest. This part of the manoeuvre gave the observer an impression that the wasp was learning her homing course from every direction. After a few minutes she alighted on the ground 2 m. away from the nest and took a rest for a short time. Then she came flying to her nest and, after repeating once more that motionless flight, gazing the entrance, suddenly rushed away over the northern hill. The next moment, however, the wasp came back in front of the nest and made that stationary flight again, but instantly she flew far away towards the south. A few second later, she came back again in front of the nest. The same manoeuvre was still twice repeated. At last, for the fifth time, the wasp flew far away in reality and this time did not return. During the course, the departures of the wasp were made either directly from in front of the nest, or from the end of her circling around the nest, but all her return flights were carried her directly in front of her nest.

Similar behaviour of *Bembix* was always observed when a new nest was dug somewhat far (more than 10 m.) from the previous one, or when it was made in a different slope. But when it was burrowed in the same slope or only few meters away from the previous nest, such an elaborate orientation flight as mentioned here could not be observed. It was markedly simplified. The wasp took, as a rule, only a few gazing flights in front of her nest, or made brief circlings around her new nest, before she finally flew away. Judging from these informations this sort of flight is considered to be of use for the wasp to remember the landmarks around the nest which will serve as visual cues in her homing journey.

6. Structure of the nest

I have opened no less than 200 nests of this species and found that they can be classified into two types in structure. One of them is the simple type, including only a single brood-cell inside, while the other is the compound type bearing branched galleries and more than two brood-cells in a nest. In the latter type the cells are always made one at each end of the branch-tunnels and in no case are they formed linearly, having one brood-cell before the other at the end of the same tunnel, as has been reported by J. B. Parker on *B. nubilipennis* Gresson of North America.

(**a**) *The simple type.* The tunnel is usually 20 - 35 cm in length (Table 1), circular, or slightly flattened circular in form in the cross section and about 10 - 12 mm in diameter. Usually it retains the same broadness throughout, but sometimes it becomes narrow near the brood-cell. It penetrates obliquely in the ground at a gentle angle (about 15° - 20°) to the surface and end horizontally into an enlarged pocket, the brood-chamber. Rarely, after proceeding for about 5 - 10 cm from the

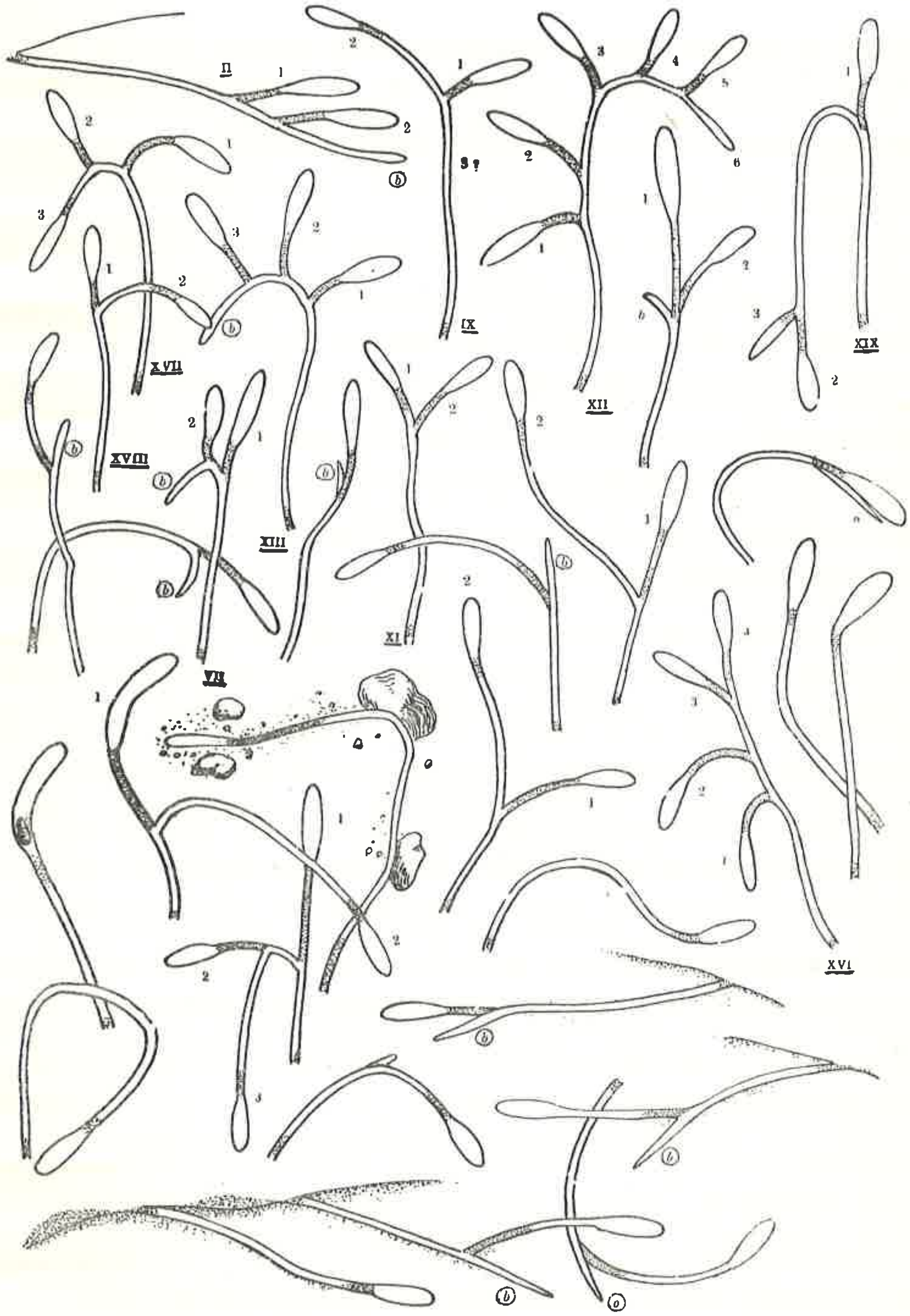

Fig. 2. Structure of the nests of *Bembix niponica* Smith.
Instances marked with Roman numerals are the nests observed in the suburbs of Chiba. b ··· the accessory branch.

entrance, it becomes somewhat steeply sloped, but usually it recovers soon the original inclination. In such a case, sometimes the tunnel rather turns slightly

Table 1. The length of the tunnel of the nest.

Length	– 15	– 20	– 25	– 30	– 35	– 40	– 45	– 50	– 55 (cm)	–	Total
Frequency	1	9	29	35	26	6	2	2	0	0	84
%	2	8	27	32	24	5	2	2	0		

upwards near the end, for about 5 – 10 cm in front of the brood-cell. Seen from above, the tunnel runs sometimes straight, sometimes in a curve. In the latter case, it is undecided whether it turns to the right or to the left. The curvature is also quite variable in degree and in the extreme case it draws a half circle and ends in the opposite direction, sometimes even reaching beyond the entrance. In case the nest is burrowed in the stony ground, the tunnel is forced to curve or to turn at irregular angles to the right and to the left, or sometimes up and down, in order to avoid the obstacles. Thus, the general aspect of the tunnel comes to be more complex than the one found in the sandy locality.

The brood-cell is usually a slightly flattened ellipsoid in shape. At first, it is 30 – 50 mm long, 15 – 18 mm wide and 13 – 15 mm high. But later, toward the end of the growth of the larva, it becomes, in general, 60 – 100 mm, rarely even 150 mm in length. Furthermore, in the cells containing a cocoon, the cavity is, as a rule, much more enlarged both in width (18 – 22 mm) and in height (15 – 17 mm). The increase in length is effected by the special mode of provisionment of the mother wasp and the increase in largeness is probably due to the activity of the larva before cocoon-spinning, of which explanation will be given later on. At times, the brood-cell is scarcely enlarged than the tunnel, especially at the beginning of the larval development. In such a case, however, the wasp enlarges the chamber during the course of her provisioning activities. The brood-cell is used to lie in horizontal, 6 – 15 cm below the level of the ground. However, in case, the nest is burrowed against the inclination of the ground and penetrates straight, it comes to lie 20 cm or more below the surface. Sometimes it lies slightly inclined and rarely it curves in itself. The curved cell is often found in the nest in which either a larva of the later stage of the development or a cocoon is present.

The tunnel is always closed just in front of the cell with the compact packing of sand for about 1 – 3 cm. Sometimes, however, the closure is made several centimetres before the brood-cell, especially when the tunnel is provided with the accessory branch stated below. This partition-wall is made, as a rule, more thickly than usual when the wasp does not frequently visit the chamber, e. g. at the time when she is waiting for the hatching of the egg or when it is before dark. Besides this wall, the tunnel is always closed at the entrance for about 1 cm with the loose dirt of sand, while the wasp goes out of the nest or while she is resting inside. In the former case, however, during the time when the wasp busily goes in and out in her provisioning work the orifice of the nest is sometimes left half opened, or the work of closure is entirely omitted.

The most interesting structure of the nest of this species is that the tunnel is provided with a specially made short accessory branch just in front of the partition wall of the brood-chamber. In most instances it runs in obliquely downward for about 4 - 9 cm and ends in tapering apically. This accessory branch is, however, not always present. Moreover, later, as development of the larva proceeds, it is frequently filled with sand and becomes indistinct. When one digs open a nest of this species from the entrance along the tunnel, if he finds the burrow taper at the end and penetrate somewhat more steeply downward as if it were an incomplete or abandoned nest, the apical, tapering part is the accessory branch itself. In such a case, the entrance to the true tunnel leading to the brood-cell is usually concealed by a closure of sand at a distance of 4 - 7 cm in front of the bottom of this accessory tunnel. The concealed, true tunnel goes horizontally either straight or in a curve. Sometimes it turns slightly upward. In these cases the empty space left beween the stoppage of sand (originally the partition wall of the brood-cell just in front of it) and the larval cell is usually several centimetres, but sometimes attains as long as 10 - 18 cm. When these empty space is very long, a new partition wall is again constructed just before the larval cell. Sometimes the accessory branch forms the apical portion of the straight tunnel and the main tunnel turns to the right or to the left, 4 - 7 cm in front of the end of the branch. In this case the investigator is most likely perceived to take the nest as an incomplete one. In other instances the accessory branch itself is made obliquely sidewise from in front of the stoppage of the main tunnel, that is to say the partition wall of the brood-cell. In these instances the branch is very often extended later to form the gallery of the second cell of the compound nest. What is the significance of this curious cavity is a thema of a later paragraph.

(**b**) *The compound type.* The percentage occupied by the compound type among the nests belonging to a colony of this species varies from district to disrict it locates. In a colony observed in the neighbourhood of the city Chiba, the majority of the nests contained more than two brood-cells within, while the nests examined in the suburbs of the city Utsunomiya belonged all to the simple type. According to other investigators of this species, the nests observed in Fukuoka, Osaka and Niigata Prefectures were all of the simple type alone, excepting for some observed at Gogahama, Niigata Pref. by J. Nozawa. Among the great number of the nests opened by myself in the suburbs of Sapporo, Hokkaido, the greater part belonged to the simple type, only less than 4 percent being of the compound type (Table 2). Of the compound type of the nests, those observed in Chiba seem to show the well-developed structure, while those found in Hokkaido are considered to indicate more primitive states.

Table 2. The structure of the nest.

District	Year	Type of structure		Accessory branch	
		Simple	Compound	Present	Absent
Chiba	1931–32	8[1]	11	5	14
Utsunomiya	1936	5	0	2	3
Sapporo	1946	45	3	27	21[2]
Sapporo	1947	29	3	17	15[2]
Sapporo	1948	52	1	25	28[2]
Sapporo	1949	15	3	8	10
Sapporo	1950	8	0	5	3
Sapporo	1951	26	1	19	8
Tatal		188	22	108	102

1) All but one contain the larva within. Therefore it is possible that these nests are at the beginning of the compound type.
2) Including some uncertain instances.

In the most usual form of the compound structure, the main tunnel curves laterally from the end of the entrance gallery which runs in straight for 20 – 30 cm. Several cells, 2 – 6 in number including the end cell, are arranged somewhat radiately on the outside of this curved portion of the gallery. Each cell is connected with the main tunnel by a short branch, 3 – 5 in length, which is perfectly closed after the provisioning of the cell is finished. Judging by the conditions in the imcomplete nests, the procedure of the construction of these compound nests is supposed as follows :

The first cell is made at the end of the entrance gallery, usually somewhat obliquely to the right or the left. While this cell is being provisioned, an accessory branch is dug laterally on the opposited side to the lst cell. When the first cell is perfectly provisioned and permanently closed, or occasionally in the course of its provisioning work, the accessory branch is extended and turned again toward the same side as the first cell to be enlarged into the second cell. A second accessory branch is burrowed anew and later extended and turned into the third cell. The following cells are made in the same manner. Thus, in the course of the construction of the compound nest, the accessory branches are successively burrowed and are in turn changed into a part of the main tunnel.

The above is the usual form and the process of the construction of the compound nest. The followings may be the variations of it: In the first place there is a form whereof the main tunnel is not curved at the end, but penetrates straight. Accordingly the cells are arranged at one side of the main tunnel, that is to say, each cell is made obliquely sidewise and the accessory branch is always burrowed in the extention of the main tunnel. In the second place, there is a form which is similar in pattern to the previous case, but some of the later cells are constructed in front of the previous cell. In this case, the main tunnel is very much lengthened after the first cell is completed, and comes to have enough space to make several cells between this and the end cell. The third form is somewhat different, wherein the second cell is burrowed below and slightly beyond the first cell, and the third cell still below and beyond the second cell. Perhaps in this form the next cell will be made by the extention of the accessory branch that is burrowed steeply downward just in front of the partition wall of the previous cell. In this form, however, not a single instance has been found in which more than 3 cells are included. Perhaps the mother wasp may take care of the cells not to lie too deep.

The compound type found in Hokkaido was similar in the general scale, but seems to be more irregular not only in the divergency of the directions of the branches. but also in the length of the tunnels. Furthermore, in all the nests of this type examined there, the cells included in one nest were always less than 3 in number. Three instances have been shown in Figure 2. In the compound nests, it occurred sometimes in relation to the second cell that the end of the branch was enlarged into a perfect chamber prior to the receipt of the first prey. This is especially often observed towards the end of the season when the growth of the larva becomes very slow.

c) *Nests of the same individual* It is an interesting problem whether the different nests made successively by the same wasp have the similar structural distinctions or not. I was able to follow the activities of some of my marked wasps during their work of 2 or 3 nests. The ground was composed of fine grains of sand,

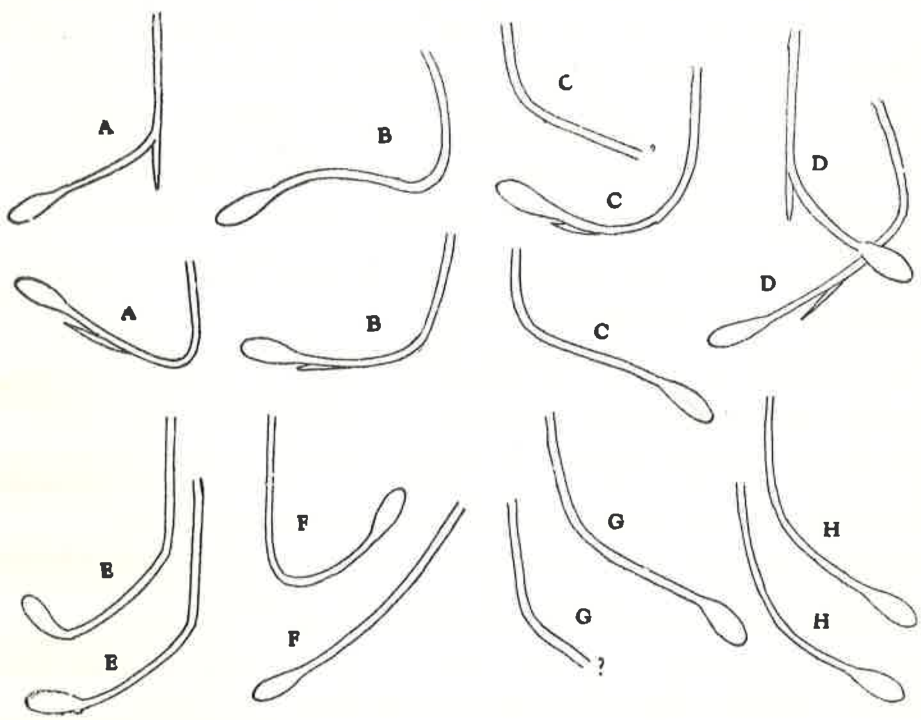

Fig. 3. The form of the nests made by the same individual of the wasp. (Shown by the same letter)

lacking any pebble or stone to hinder their free burrowing activities. So the nests constructed had to show the natural trend of their nest construction. The results of my observations were as shown in Figure 3. Judging from the figure it seems that *Bembix niponica* has a tendency to dig the tunnels of similar form successively in her nesting activities.

7. Food of the larva

Bembix niponica Sm., as in the majority of the members of the genus, hunts the Dipterous insects as food for the larva. According to the results of my observations details regarding their prey are as follows :

a) *Species of the prey and their frequency.* The materials actually examined by me concerning the subject are as shown in Table 3. Besides my results, four more species are reported by other investigators, namely, *Ptecticus tenebrifer* Walker, *Promachus yesonicus* Bigot, *Ommatius chinensis* Fabricius and *Lathyrophthalmus viridis* Coquillet. On the whole, they belong to 11 Families*, including more than 57 species. This number will, of course, be increased as studies progress on the biology of *Bembix* as well as on the taxonomy of the prey in Japan. At any rate, it can be perceived from the table that the specialization of the prey has not so grown up in this species as to restrict them to some particular species. Accordingly, the list of the prey and the relative number of each species are variable according to the Diptera-fauna of the district where the observation was made. At the same time, however, we can not deny the fact that something like preference develops in this species within a certain bound. For instance, in my observation at Chiba, *Stratiomyis japonica* v. d. Wulp was overwhelmingly numerous, whereas in the investigations at Sapporo, *Eristalis cerealis* Fabricius was exceedingly dominant. In both cases it can not necessarily be said that these species are particularly abundant (in proportion to the percentage occupied among the prey) in the neibourhood of the colonies observed.

On the other hand, such cosmopolitan flies as *Lucilia* spp. *Sarcophaga* spp. seem to be numerously captured everywhere.

b) *The quantity of food for one larva.* This can practically roughly be measured from the species of the prey and the number of each species. Because each species represents a certain destined size, excepting a few parasitic ones. Here, therefore, mention will be made as to the number of the prey. The number of the prey as a whole varies, of course, according to the specific constitution of them. In *Bembix*, however, somewhat strange to say, it varies also according to the climatic conditions — chiefly the weather — during the course of the provisioning activities of the wasp. When the bad weather intervenes in the course of the activities of the wasp while the larva is in its final instar, the victims collected in the cell show a tendency to increase in number.

* Syrphidae, Anthomyiidae, Rhagionidae, Stratiomyiidae, Tabanidae, Muscidae, Sarcophagidae, Dexiidae, Tachinidae, Asilidae and Pipunculidae.

Table 3. List of species of the prey and their frequency.

Derivation	Working cell					Old cell	Total
District	Chi.	Uts.	Sap.	Sap.	Sap.	Sapporo	
Species / Year of obs.	1931–32	1936	1946–47	1948	1949	1946–49	
Eristalomyia tenax Linné	1	2	9	35	6	13	65
Eristalis cerealis Fabricius	–	1	268	215	90	144	718
Eristalis nigricans Matsumura	–	–	–	2	1	–	3
Rhingia laevigatus Loew	–	–	–	1	3	–	4
Eristalinus sepulchralis Linné	–	–	21	40	32	6	99
Volucella jeddona Bigot	–	–	1	–	–	1	2
Syrphus corollae Fabricius	–	–	2	–	–	1	3
Syrphus ribesii Linné	–	–	1	–	2	–	3
Syrphus balteatus de Geer	–	3	2	–	–	–	5
Pipizella bigulonis Matsumura	–	–	3	–	–	–	3
Olbiosyrphus sapporensis Matsumura	–	–	2	–	1	1	4
Megaspis zonata Fabricius	–	–	–	2	–	–	2
Eumerus strigatus Fallén	–	–	1	2	–	–	3
Helophilus virgatus Coquillett	–	–	–	1	–	–	1
Chrysotoxum japonicum Matsumura	–	–	5	8	4	2	19
Chrysotoxum grande Matsumura	–	–	1	–	–	–	1
Takaomyia johannis Hervè-Bazin	–	–	–	1	–	–	1
Chrysotoxum festivum Linné	–	–	1	1	–	–	2
Syrphidae 2 spp.	–	–	–	4	–	1	5
Anthomyiidae spp.	–	–	1	17	–	–	18
Rhagio tringarius Linné	–	–	1	–	–	–	1
Rhagionidae 2 spp.	–	–	1	2	–	–	3
Villa limbatus Coquillett	–	–	20	47	3	13	83
Stratiomyia japonica Van der Wulp	254	–	–	8	1	–	263
Eulariaga ratus Welker	–	17	–	–	–	–	17
Sargus niphonensis Bigot	–	–	1	–	–	3	4
Tabanus mandarinus Schiner	–	3	48	21	20	51	143
Tabanus chrysurus Loew	–	–	1	–	–	–	1
Tabanus rufidens Bigot	–	–	3	–	–	–	3
Tabanus sapporensis Shiraki	–	–	2	–	–	–	2
Tabanus trigonus Coquillett	–	–	1	–	–	–	1
Tabanus distinguendus Verrell	–	–	2	–	–	–	2
Ochrops bivittatus Matsumura	–	–	4	2	2	–	8
Ochrops fulvus Meigen	–	–	49	19	14	17	99
Therioplectus taradinus Linné	–	–	4	–	–	4	8
Therioplectus tropicus Panzer	–	–	1	–	–	–	1
Chrysozona tristis Bigot	–	–	10	14	1	1	21
Heterochrysops mlokosiewiczi Bigot	–	–	1	1	–	–	2
Chrysops suavis Loew	–	–	–	3	5	–	8
Tabanidae sp.	3	–	–	–	–	–	3
Lucilia caesar and spp.	34	16	88	104	11	31	284
Musca domestica Linné	–	–	3	4	1	–	8
Ophyra leucostigma Wiedermann	–	2	–	2	–	–	4
Calliphora erythrocepala Meigen	–	–	4	12	–	6	22
Calliphora spp.	–	–	2	1	3	3	9
Muscidae spp.	–	–	8	21	–	5	34
Sarcophaga carnaria Linné	12	12	59	70	5	–	158
Sarcophgidae spp.	–	2	54	23	–	83	162
Theloria leucozona Fallén	–	–	3	–	–	–	3
Dexidae spp.	–	–	2	4	–	–	6
Gymnochaeta elegans Matsumnra	–	–	–	8	–	1	9
Echynomyia mikado Kirby	–	–	–	–	1	–	1
Tachinidae spp.	–	–	8	10	–	5	23
Neoitamus angusticornis Loew	–	–	–	1	–	–	1
Pipunculidae sp.	–	–	–	1	3	–	4

District —— Chi., Chiba; Uts., Utsunomiya; Sa., Sapporo.

Table 4. List of the number of victms found in the cell that contained a cocoon.

Cell No. \ Prey	*Stratiomyia japonica*	*Eularia garatus*	*Therioplectus tarandinus*	*Tabanus mandarinus*	*Ochrops fulvus*	*Chrysozona tristies*	*Eristalomyia tenax*	*Eristalis cerealis*	*Eristalinus sepulchralis*	*Volucella jeddona*	*Syrphus corollae*	*Olbiosyrphus sapporensis*	*Chrysotoxum* spp.	Other Syrphidae	*Villa limbatus*	*Sargus niphonensis*	*Lucilia* spp.	*Calliphora* spp.	Muscidae	Sarcophagidae	Tachynidae	Total
1	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13
2	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17
3	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
4	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18
5	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15
6	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
7	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
8	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	16
9	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	12
10	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9
11	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15
12	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18
13	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
14	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	16
15	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	2	7	-	16
16	-	-	-	1	-	-	-	5	-	-	-	-	-	-	-	-	-	2	-	2	-	10
17	-	-	-	-	-	-	-	8	-	-	-	-	1	-	-	1	-	3	-	1	-	14
18	-	-	-	2	-	-	-	4	-	-	-	-	-	-	-	-	-	1	-	3	-	10
19	-	-	-	-	-	-	-	13	-	-	-	-	1	1	1	-	-	-	-	-	-	16
20	-	-	-	2	1	-	-	3	-	1	-	-	-	-	-	2	1	-	-	4	-	14
21	-	-	-	6	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	7	-	14
22	-	-	-	3	1	-	-	6	-	-	-	-	-	-	-	-	1	-	-	10	-	21
23	-	-	-	8	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	6	-	17
24	-	-	-	4	2	-	-	13	-	-	-	-	3	-	-	-	-	-	-	3	-	25
25	-	-	1	2	1	-	-	11	-	-	-	-	-	-	-	-	-	-	-	-	-	16
26	-	-	-	2	1	-	-	13	-	-	-	-	-	-	-	-	1	-	-	1	-	18
27	-	-	-	2	-	-	-	7	-	-	1	1	-	-	-	-	5	-	-	1	-	17
28	-	-	-	-	3	-	1	9	-	-	-	-	-	-	3	-	8	-	1	4	1	30
29	-	-	1	1	-	-	-	9	-	1	-	-	-	-	-	-	1	-	-	-	-	13
30	-	-	1	-	2	-	-	12	-	-	-	-	-	-	2	-	1	-	-	2	-	20
31	-	-	1	3	-	1	-	1	1	-	-	-	-	-	2	-	3	-	-	3	4	19
32	-	-	-	-	-	-	-	12	-	-	-	-	-	-	1	-	-	-	-	-	-	13
33	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	3	-	-	16	-	22
34	-	-	-	4	-	-	5	3	-	2	-	-	-	-	-	-	1	-	-	-	-	15
35	-	-	-	3	-	-	1	5	-	-	-	-	-	-	-	-	1	-	4	2	1	13

It seems that in such a case the wasp is compelled to stop the provisioning activities and the scanty food provided in the larval cell is likely to be devoured *completely* by the larva, and the lack of food in the brood-chamber, when it is perceived by the mother wasp (this is really occurred under experiment), drives her on the first fine day to accumulate too much food for the larva. Besides the above-mentioned two reasons (size of the prey and the weather), some unknown environmental or psychological factor or factors sometimes stimulate the wasp to collect food in excess. This is indicated by the fact that several intact flies are frequently left on the floor of the cell after the encasement of the larva.

Thus the number of the prey, even when the relation to the size of them is quite obvious, does not always indicate the exact quantity of food necessary for the development of a larva. Moreover, in the species of *Bembix* in which food is progressively gathered from day to day, there is technical difficulties regarding how to count the actual number of the victims taken in one cell. Fabre took a half-grown larva of *B. rostrata* L. from a nest and lavishly fed it thereafter. He attempted to estimate the number of the victims given to a larva by the mother wasp under natural conditions by summing up the number of remains of flies found in the cell and that of the victims (the house fly) which he gave to the larva until the time of its full maturity. The result obtained was 82. According to the investigation of the Peckhams in the same line, a larva of *B. spinolae* Lep. a fairly smaller species than *rostrata*, ate 42 house flies and 1 big horse fly, *Tabanus* sp. Similarly the Raus showed that the larval *B. nubilipennis* ate more than 78 *Musca*. It seems to me, however, that the results obtained by such means will never indicate the real number of the prey in the natural conditions. Because, the larvae of *Bembix*, when fed with excess of food, would eat beyond the necessity, or rather would eat a bit of everything. This relation can easily be ascertained by feeding a larva which has

Table 5. List of the numper of victims found in the cells that have just been permanently closed.

Victims \ Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	–
Eristalis cerealis L.	–	–	–	–	–	1	1	3	5	3	13	3	6	1	–
Other Syrphidae	–	–	–	–	–	5	–	1	1	–	4	1	4	6	–
Tabanidae	–	–	–	–	–	3	10	3	1	10	1	–	1	1	–
Sarcophagidae	–	–	5	–	–	5	6	1	1	8	4	3	1	–	–
Muscidae	–	–	24	–	–	13	–	3	–	5	5	2	10	–	–
Tachynidae	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–
Villa limbarus Coq.	–	–	–	–	–	–	–	–	1	–	–	–	2	–	–
Anthomyidae	–	–	–	–	–	–	–	–	–	6	2	–	–	–	–
Stratiomyia japonica V.d.W.	11	12	4	10	18	–	–	–	–	–	–	–	–	–	–
Other flies	–	–	–	–	–	2	–	–	–	1	1	–	–	–	–
Total	11	12	33	10	18	29	17	11	9	33	34	9	24	8	0

been taken out of an accomplished nest with more than as much food as was found in the nest.

In order to know the actual number of the prey stored in one larval cell, I attempted to count it from the remains of food left in the chamber. The larva of *Bembix* usually does not eat the head and the hard sclerites of the thorax of the prey (a habit which is very lavish in comparison with the species having a habit of mass provisionment). Therefore, as a rule these portions of the body remain in the cell. I took out carefully these remains from the cells in which the cocoon was found or for which the tunnel was permanently closed*. In both cases the material was carefully examined numerically as well as taxonomically**. In the latter case, it was summed up with the number of non-eaten flies. The results of my investigations are as shown in Tables 4 and 5 and in Figure 4.

According to the above results, the number of the prey of *B. niponica* Sm. varies from 7 to 34 under the natural conditions. Although there is a case in which the mother *Bembix* takes some of the remains out of the brood-cell and throws them away, such a case occurs rarely, so that these material will represent the actual food quantily of our species. But the variation of food quantity roughly shown by the number of prey seems to be beyond the normal extent of variation of food quantity in the fossorial Hymentoptera. The fact does not necessarily depend upon the variation of the size of the victims accumulated, since it is also the case when a single species of the fly, less variable in size, is hunted as prey (e. g. *Stratiomyia japonica* in the observations in Chiba). But as it is a general rule in this species also that the smaller the prey, the greater the number, we must convert them to a convenient unit, in order to make a more exact comparison. Since it is practically impossible to measure them by weight, if they were averaged roughly to the case of middle large flies (like *Eristalis cerealis*),

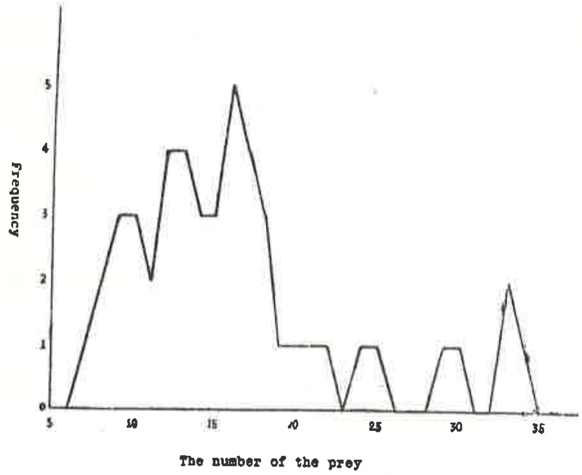

Fig. 4. Number of the prey stored in one cell (Obtained from the remains of food of the accomplished nests)

* The amount of food in the members of *Bembix* hitherto recorded are mostly based on the number of victims and their remains found in the larval cell which is still in the course of provisioning.

** A special care was taken as to the small and soft flies. Because, sometimes when the supply of food is scanty the larva is likely to devour such small victims nearly completely. Even in such a case, however, the postscutellum at least is always left in the cell.

the number becomes about 9 – 25. The variation is still strikingly large.

On the other hand, in spite of such a marked variation of food quantity supplied to the larval wasps, the size of the adult wasps does not show the corresponding variation. But this contradictory fact can easily be accounted for by the mode of eating of the larval wasps. They devour the victims completely when food is scarce, but quite imcompletely, rather partly, when it is very rich. Anyhow, the marked variation of food quantity like this can hardly be met with in other fossorial wasps that have the habits of mass provisionment. That is to say, the variation of food quantity in *Bembix* is dependent in the main upon the habits of progressive provisionment, or more exactly, upon the various conditions that occur during the long course of the progressive provisionment. This fact will be proved by some experiments later described.

8. States of the victim

As for this problem there have been published two different opinions by the previous authors. Fabre and Wesenberg-Lund insist respectively that the prey of *Bembix* are crushed at the thorax with the mandibles of the wasp and are completely dead and quickly dry up. Other investigators such as Lepeletier (1841), Marchal (1893), the Peckams (1898), Ferton (1897 and 1910), the Raus (1918), Parker (1917) and Nielsen (1945) are unanimous in admitting that the victims of *Bembix* they observed are stung by the wasp, but are kept in mere paralysis. Lepeletier first reported the living state of the victims of *Bembix*. He said that the flies he examined lived for 10 days after taking out of the nest of *B. rostrata*. According to Marchal, the prey are immobile at first; they begin, however, to respond to the contact stimulus by moving the mouth parts or the legs after 2 or 3 days. At least in the Japanese species things are in fair accordance with the opinion of the latter group of the investigators.

a) *The living victims* Among a great number of flies that I have examined, not a single example has ever been found which was crushed at the thorax or which was already dead at the time when the wasp brought it to her nest. All of them show signs of life by extending and contracting the proboscis and genitalia, by quivering the antennae and legs, by showing the breathing movements on the abdomen, as well as by excreting faeces. In addition to the above account, the visceral movement can easily be observed in Syrphidae through the ventral integument of the abdomen. Sometimes in Muscidae, a quick pulsation on the rounded membrane at the inner apical portion of the hind femurs is also observed. The degree of vivacity of these movements is variable according not only to the individual example, but also to the group of the insects. In general these signs of life are most remarkable in Syrphidae, whereas much less so in Muscidae, Sarcophagidae and Anthomyiidae, and hardly apparent in Stratiomyiidae. But in all the examples of these Families, if carefully examined when they are taken out of the nest, at least the respilatory movement is always observable upon the ventral plates of the abdomen. On the other hand, I have frequently observed, when I opened the nest, flies that were making humming sound, or that could walk about with some difficulty. Moreover, during the course of my continuous observations in Sapporo, 12 *Eristalomyia tenax* L. and 1 *Villa limbata* Coq. were able to escape from between the legs of *Bembix* at the very entrance to the wasps' nests.

In the following table (Table 6) some of the results of my observations concerning the movements of the victims which were taken out of a nest will be given. Symbols used in the table are as follows : A ··· movements of the Antennae, B ··· respilatory movements of the Belly, C ··· movements of the Caudal portion of the abdomen, D ··· Died, E ··· Excretion, H ··· movements of the Head, L ··· movements of the Legs, M ··· movements of the Mouthparts, V ··· Visceral movements. The annexed numerals show the degree of the vivacity of the movements : 1) Very distinct without giving any stimulus, 2) less striking than 1, 3) very faint, or responsive only to the stimutus. D ?) uncertain death, with body as yet being soft, D) perfect death.

Table 6. States of the victim. (collected on the 4th, Sept.).

No.	Species of victims	Sept. 4, at 4. p.m.	Sept. 5, at 11 a.m.	Sept. 6, at 9 a.m.	Sept. 7, at 9 a.m	Sept. 8, at 11. a.m.
1	*Eristalomyia tenax*, ♀	B_2M_2	$A_3B_2EM_2V_2$	$A_3B_2E\ M_2V_2$	$B_3E\ M_3$	D?
2	*Eristalis cerealis*, ♀	$A_2B_1H_3L_2M_2V_1$	$A_2B_1EH_3L_2M_2V_1$	$A_2B_1L_2M_2V_2$	B_3M_2	D
3	〃 〃 ♀	$B_2M_2V_1$	$B_2E\ M_2V_1$	$B_2E\ M_2V_1$	$B_2E\ M_2V_2$	D
4	〃 〃 ♀	$B_2M_2V_1$	$B_2EM_2V_2$	$B_2E\ M_3V_2$	B_2M_3	D
5	〃 〃 ♂	D?	D	–	–	–
6	〃 〃 ♀	D	–	–	–	–
7	*Lucilia caesar*, ♀	B_3M_3	A_1B_3E	B_3M_2	D	–
8	〃 〃 ♀	B_3	B_3C_2	B_3C_3E	D	–
9	〃 〃 ♀	B_3	$B_3E\ M_2$	D?	D	–
10	〃 〃 ♀	$B_3M_3V_2$	B_3M_2	B_3M_2	D?	D?
11	*Sarcophaga carnaria*, ♀	B_2	D?	D	–	–
12	〃 〃 ♀	B_2	B_3E	D?	D	–
13	〃 〃 ♀	B_2	$B_3C_3V_3$	B_3C_3	B_3C_3	D
14	〃 〃 ♀	B_2	B_3	B_3	D?	D
15	Muscidae gen. sp, ♀	B_1V_2	B_3	B_3	D?	D
16	〃 〃 ♀	D?	D?	D?	D	–
17	*Tabanus mandarinus*, ♀	B_1L_2	B_1E	B_1C_2	D?	D
18	*Chrysozona tristis*, ♀	D?	D			

Remarks. Nos. 5, 6 and 18 were left for a while on the sun-baked ground after the collection.

As to the condition of the prey at the time when it is carried in the nest, things are as mentioned above. Indeed, most of the prey retain the same vivid condition till it is devoured by the larva. But there is a single exception against this general rule. That is the fly which is used for the pedestal of the wasp's egg. It is either perfectly killed or received some operation and very weakened (*vide* Addendum). At the time of hatching of the egg, always it does not show any sign of life. The detailed accounts regarding this problem will later be treated.

b) *Longevity of the victim after being captured.* In order to ascertain this problem I have made a series of observations upon the material which was taken out of the nests on the same day. The results are as shown in Table 7. The material

Table 7. Longevity of the victim.

No. of Exp. \ Longevity (day)	1	2	3	4	5	6	7	8	9	10	Number of insects used
1	?	2[1]	2	10	1	-	-	-	-	-	15
2	0	2	1	2	3	1	1	-	-	-	10
3	1[2]	2[2]	1	5	7	2	-	-	-	-	18
4	0	2	1	4	6	1	-	-	-	-	14
5	0	0	2	1	3	6	1	1	-	-	14
6	0	1	1	4	3	5	1	1	1	-	17
Total	1	9	8	26	23	15	3	2	1	0	88

1) The flies were caught two days before the collection.
2) The flies were left on the sun-baked ground for a while

treated in each observation, however, might contain ones that were hunted a few days before. So that, as shown in the table, some flies were found already dead when I examined them after bringing to the laboratory. These flies were laid on their backs on a sheet of paraffin paper per one and covered with a Petri-dish. They were again covered with a sheet of black paper and were preserved at the dark corner of the room. Most of them normally excreted during the first several days

Table 8. Longevity of each species of the victim

Species \ Longevity (day)	1	2	3	4	5	6	7	8	9	10	Number of insects used
Eristalomyia tenax	-	-	-	-	1	1	1	-	-	-	3
Eristalis cerealis	1	3	2	12	10	2	-	-	-	-	30
Lucilia caesar	-	-	-	3	-	2	-	-	-	-	5
Sarcophaga carnaria	-	-	2	3	5	1	-	-	-	-	11
Muscidae gen. sp.	-	-	-	1	1	-	-	-	-	-	2
Tabanus mandarinus	-	-	-	1	3	6	-	2	1	-	13
Ochrops fulvus	-	-	2	3	2	3	-	-	-	-	10
Ochrops bivittatus	-	3	1	-	-	-	-	-	-	-	4
Chrysotoxum japonicum	-	1	1	2	-	-	-	-	-	-	4
Chrysotoxum grande	-	1	-	-	-	-	-	-	-	-	1
Chrysozona tristis	-	1	-	-	-	-	-	-	-	-	1
Tachynidae gen. sp.	-	-	-	1	-	-	-	-	-	-	1
Helophilus virgatus	-	-	-	-	1	-	-	-	-	-	1
Chrysops suavis	-	-	-	-	-	-	1	-	-	-	1
Syrphus ribesii	-	-	-	-	-	-	1	-	-	-	1
Total	1	9	8	26	23	15	3	2	1	0	88

and their death seemed to be due merely to the starvation. Table 8 shows the longevity of each species of the victims of the same material.

9. Hunting

As described in the foregoing pages, the Japanese *Bembix* does not kill the victims she hunts by crushing the thorax with her mandibles, but only stingst hem into permanent paralysis. I have not as yet a good fortune to observe the hunting activity of the wasp at the actual spot of her hunting ground. But I have had several opportunities of observing her hunting behaviour in the neighbourhood of her nesting place. One of which may represent a natural mode of their hunting :

On Sept. 18, 1947, at 2.30 p m. a wasp came back from her foraging excursion with a prey (*Elistalomyia tenax*) and landed 1 m. in front of my sitting place. She then changed slowly her orientation against the prey so that she might be crosswise to the length axis of the flower fly Then she bent her abdomen and stung the victim on the thorax beneath in the centre. Having looked such a scene, I gathered my attention and knew that the fly was caught by the wasp from the back. The next moment the hunter turned the victim around and made it upside-down. At that time the victim which had not been perfectly paralyzed violently quivered the wings. The wasp appeared to be frightened. She grasped the fly tightly, rolling it between her legs and again bent her abdomen. But as the ground was a fairly steep slope, they rolled down in a mass for about 1 metre and a half. But as soon as they stopped the wasp turned the victim once more upside-down, grasped it with the mid legs and flew off to her nest that was 7 m. away from the place.

In some of my observations a wasp was induced artificially to sting an already paralyzed fly of another individual. The method is quite different from what attempted by P. Marchal (1893) on *B. rostrata* L. It was carried out as follows: I select a nest which is just about to be burrowed up. I crouch near the entrance of the nest with a paralyzed fly between my fingers and wait for the moment when the wasp comes backing out with her last load of sand. She emerges and proceeds backward a few step further to sweep off the dirt in front of the entrance. At that moment I drop the fly on to the ground between the wasp and the entrance. In most cases the wasp, when she proceeds forward to enter the nest, finds the fly and grasps it. She then flys up, but stops in the air usually at a height of about 1.5 – 2 m. above the surface of the ground, turns the victim around between her legs so as to hold it crosswise and quickly inserts her sting. Her action is so quick that I have been unable as yet to make sure the exact point of stinging. But judging from the posture of the hunter and the victim, it will be certain that the fly is stung from beneath the thorax.

All the other observations were made at the time when an inadequately paralyzed fly fled from between the legs of the wasp at the entrance of her nest. As a matter of fact I have observed such an phenomenon rather by chance. But it seems to me that such is not always a rare accident, since I once had an opportunity of meeting with such a phenomenon more than dozen times during the course of several days' observation. The victims observed were all *Eristalomyia tenax* L., with a single exception of *Villa limbata* Coq. Probably these stout flies alone will be able to resist against the poison of the wasp.

The fly which is crasped with the mid legs of the wasp under her body suddenly beats violently its wings either at the time when the wasp is opening the entrance closure or during her slow flight before landing at above her nest entrance. The wasp looses her hold in a frightened manner and the victim swiftly flies away. The wasp, of course, follows her escaped game in full speed. But out of 12 instances which I have observed 7 were the cases in which the victim could surely run away*, though they would probably soon after at some place or other drop to the ground to fall into a permanent paralysis. In the remaining 5 instances the wasp could fetch up with the fugitive and stung it again. The manoeuvre was as follows :

(1) Aug. 26, 1948, 9.27 a.m. A wasp (No. 138) carrying a flower fly showed a landing posture above the entrance of her nest, but probably owing to the sudden struggle of the victim, she changed her intention and flew away over the nest. About 10 m. away from the nest, however, she alighted on the ground. So I went stealthily there at once and observed with attention the behaviour of the wasp at a distance of 70 cm from her. She stung the fly repeatedly and I could confirm that the following 3 methods of operation were used by her : a) The wasp catches the fly from the back, curves her abdomen from a side of the victim to the underside of the thorax and dirts her sting on the anterior portion of the area. b) The wasp overturns herself upside-down, grasping the victim from its back and holding it crosswise on her breast. She then circles her abdomen around the fly and stings it on the anterior portion of the thorax, probably on the throat. c) The wasp holds the prey by the abdomen with her six legs from a side, stretches her abdomen towards the underside of the thorax of the fly and stings it on the anterior portion.

(2) The same day as above, at 9.43 a.m.

(3) The same day, at 2.10 p.m. In both cases, the wasp (No. 136 and 141), after capturing the run-away in her pursuit, went far away from the recapturing place and came back after several minutes with the same fly. Probably, the sting is carried out at a distance from the nest. These instances seem to indicate that sometimes the wasp transports her prey some distance before giving it her sting.

(4) The same day as above, at 10. 30 a.m. A wasp (No. 139) stung the fugitive quite in the same mannar as described in a) of the first instance. The stinging point, however, appeared to be the throat of the victim.

(5) Sept. 6, 1949, at 10. 31 a. m. The behaviour of the wasp (No. 155) was the same as given in a) of the first instance. But the stung point appeared to be the throat of the fly.

Judging by these observations it seems that the hunting of this species is performed under the natural condition as follows :

* In one instance, the wasp captured the fugitive in her pursuit and at once came back without giving a sting. But the fly which was dragged in the tunnel and laid aside as usual while the wasp was opening the closure of the brood-cell recovered suddenly its vivacity and flew out of the nest. This time it succeeded in running away, in spite of the violent pursuit of the hunter.

The wasp, when she finds a favourable insect on the flower or on the animal skin or on the ground etc., swoops down upon it and grasps it from its back. Then she swiftly flys up in the air and gives a dirt of her sting either while she is on the wing, or after transporting it some distance and alighting on the ground. In the manipulation of the prey, the wasp circles her body around the thorax of the victim and dirts the sting beneath in the anterior portion of it. Judging from the swiftness of the first sting, it seems rather improbable that exactly the same special point is always selected for the operation. It will be evident, however, from the mechanical certainty of the uniform attidude of the wasp that the anterior portion of the underside of the thorax of the victim is suffered the sting of the hunter. But whether it is on the throat or between the first pair of legs etc. will be determined according to the condition of the moment, that is to say, according to the relative position of the two insects, to the hardness of the sclerite of the prey, to the size of the fly, etc.

It will be necessary to note here that even if the sting of the wasp is inserted in the throat of the fly, the poison will be injected not upon the cephalic ganglion, but upon the thoracic ganglion. The reason will readily be understood, when we take into account that the tip of the abdomen of the wasp curved ventrally is always directed toward the thorax of the fly. It may also be worthy to mention here that the accident, "escape of the stung victim", occurs not only late in the day, but also early in the morning, that is to say, the imperfect paralysis of the victim does not depend upon the comsumption of the secretion of the poison gland on the part of the wasp, but upon the weakness of the poison itself. This conclusion will be supported by the fact that the sting of the wasp can not cause any marked lasting pain to us.

10. Carrying-in of the prey

When a wasp comes back with a prey and alights on the ground in front of the entrance to her nest, the victim is held upside-down with the mid legs of the wasp under her abdomen. While she opens the entrance closure the fly is held as before, but at the moment when the entrance has been cleared and the wasp is about to enter, it is pushed backwards beyond her abdomen. The wasp holds it by the neck or by the anterior portion of the thorax with her hind pair of legs alone and proceeds in the tunnel, dragging the fly behind her. This behaviour has been observed in all the species of *Bembix* hitherto investigated, but in reality, such is merely the first scene of the work of taking in of the prey. When she reaches the second tampon of sand at the entrance to the brood-cell, or, in most cases, before arriving at that place, she lays the fly aside in the tunnel and begins to open the chamber. As soon as the closure is cleared, the wasp enters the brood-chamber empty-handed and examined the larva (*vide* "Behaviour inside the nest"). Then she comes back to the fly left in the tunnel. There she grasps it by the neck or by the anterior portion of the thorax between her mandibles and pulls it backward into the chamber. After the work finishes, she closes again the entrance of the brood-cell and then that of the nest and starts on the next foraging excursion.

11. Oviposition

a) *Manner of attachment of the egg.* In this species, as in the majority of the allied species, the egg is laid on the first prey just after it has been carried in. The method of oviposition is also similar to the allied species, that is to say: The fly which is destined to be the pedestal for the wasp's egg is placed on its back on the floor of the cell, with one of the wings dislocated and half opened, and with the fore and mid legs twisted. The egg of the wasp is attached, not only to the base of the dislocated wing with its caudal end, but also to the mesopleuron with the lateral surface of the lower portion and stands upright. It is 5.0 – 6.0 mm in length, slightly curved and slightly tapering upwards, bearing the width of 1.2 – 1.5 mm near the basal extremity and about 0.8 – 1.0 mm near the apex.

Sometimes the egg shows more or less variation in its state of attachment. In some cases it is not glued either of the supports mentioned above, and in other case it does not stand vertically, but inclines in some direction. In addition to these variations the direction of the curvature of the egg is also inconstant. In most cases the egg is laid to be curved towards the body of the fly, but sometimes it is not so done. The matter has some significance in relation not only to the mode of feeding of the larval wasp, but also to the special problem concerning the provisioning habits of the mother wasp. Because the curvature of the egg indicates the direction of the body (the back and the venter) of the hatching larva, accordingly the direction of its mouthparts. The inside of the curvature is destined to become the ventral side of the larva and to be provided with the mouthparts. Therefore, if the egg does not curve towards the body of the pedestal fly, the hatching larva can not fall down upon it. This means that in such a case the young larva must eat, first, other victim than the pedestal fly.

b) *Manipulation given to the egg-bearing fly.* The egg-bearing or pedestal fly is perfectly killed or nearly perfectly killed. It is placed either in the middle of the brood-cell or slightly more bottomwards. I have never observed the instance wherein it is placed near the entrance. Ferton found in his observation on *B. oculata* (1889 and 1902) and *integra* (1910) that "La patt médiane de la mouch, du côté où est fixé l'oeuf, est egalement luxée, le tibia est ramené vers la tête de la mouche, et le tarse est recourbé sous aile". I have specially examined 10 instances of the egg-supporting flies on this respect and found that all of them received more or less manipulation on their legs. The states of each instance are as follows :

1) *Eristalis cerealis.* The first instar larva was on its sinister side. The sinister front leg of the fly was luxated at the base and stretched nearly straight anteriorly. The sinister mid leg was also dislocated and a little twisted at the basal articulation, with the femur directed latero-posteriorly and the tibia bent anteriorly. The leg, thus bent in a V-shape, was laid as if embracing the wasp's egg from behind. But it was not placed on the half-opened wing so as to prevent its return to the natural position. Remaining legs were all normally

bent and drawn to the body.

2) Dexiidae gen. sp. with the first instar larva at its sinister side. The manipulation of the fly was quite similar to the previous instance.

3) *Sarcophaga carnara*, already rotten, with\the first instar larva on its dexter side. The bexter mid leg was dislocated and half twisted at the base. It was disposed as in the above instances, but this time the tarsus was laid on the half-opened wing. Rest of the legs were normally bent and drawn to the body of the fly.

4) *Lucilia caesar.* The egg was absent, but no doubt the *Lucilia* was the egg-supporting pedestal. Because its sinister wing was dislocated and half-opened. The mid leg of the same side was distorted at the base and the femur was directed oblipuely forward and the tarsus was almost stretched straight. Reminder of the legs were normally drawn to the body of the fly.

5) *Sarcophaga carnaria.* The egg was on its sinister side. The front leg of the same side was dislocated and slightly twisted at the trochanter articulation. Its femur and tibia were stretched forwards. The mid leg of the same side was also dislocated and distorted at the base. It was stretched straight obliquely backwards and the tip of the tarsus was placed on the posterior margin of the wing (Pl. VI, A and A') The instance seems to indicate the similar condition observed by Ferton.

6) *Eristalis cerealis* ♂. With the egg on the sinister side. The mid leg alone of the egg-side was dislocated and distorted at the base. The leg was bent in a widely opened V-shape (with the tibia ditected forwards) and held horizontally against the surface of the floor, as if embracing the standing egg from behind. Remaining legs were all normally bent Pl. VI B).

7) *Sarcophaga* sp. Manipulation was observed on the mid leg alone of the egg-side, and its state was similar in the preceding instance. In this instance the dislocated wing has returned nearly to its normal position (Pl. VI, C).

8) *Theloria* sp. The egg was at its sinister side. The sinister front leg is stretched forward in a V-shape. The mid leg of the same side is stretched obliquely backwards. It is luxated at the femur-tibial joint and the tip of the leg is placed on the posterior margin of the half-opened wing of the same side, just as described by C. Ferton (Pl. VI, D and D').

9) *Eristallinus sepulchralis* L. The egg was on the dexter side. The mid leg of the egg-side is luxated at the basal joint and pressed slightly dorsad. The femur-tibial joint is opened in a V-shape and is placed nearly horizontally as if to support the egg from behind (Pl. VI, E and E').

10) *Eucilia caesar* L., very small specimen. The egg was on the sinister side. This pedestal was so small that it could not support the weight of the egg. It tuned over, resulting that the top of the egg was in touch with the sand floor of the cell. The mid leg of the egg-side of the fly is stretched and luxated at the femur-tibial joint and pressing with its tip the surface of the half-opened wing of the same side. The mid leg of the other side seems also to be more or less manipulated. Its tibia is held horizontally and directing forwards. Other legs is normally drawn to the body (Pl. VI, F and F'). Beside these manipulations, the abdominal tergite of this fly had been hollowed, but I could not think that the hollow was induced by the intentional crush of the wasp.

In addition to the above observations, a photograph of an egg-supporting fly which was obtained at Utsunomiya supplies an instance of the similar manipulation operated on the leg (Pl. VI, G).

Judging from these observations, it is evident that our species has the similar habits in this respect to the European *B. rostrata* and *integra.* As to which side of the wings and legs is selected to be dislocated, no certain rule could be discovered. But it was certain that the wing and leg of the same side is dislocated. This fact, when we think of that the operation must be made prior to the oviposition and, beside, in the dark, will be worthy of special notice, since it shows an instance of the foreseeing adaptability of the instinctive behaviour.

12. Larva

a) *Number of the instar.* According to the field observation it seems to me that *B. niponica* shows four instars in the larval life, that is to say, the larva sheds its skin three times during the course of its growth. This supposition differs by one instar from the results of the investigations made by Koehler (1923), Berthohoff (1924) and Prell (1924) on the honeybee. So that, in order to obtain the morphological basis for my consideration, I have collected a number of larvae of the different stage of development and measured on each of the material the width of the head. The results gave my cosideration a strong support, showing that there were 4 distinctly separated classes among them (Pl. VII, A). These 4 classes, as given in Table 9,

Table 9. Dimension of the larva of each instar

Portion / Instar	Length of body	Width of body	Width of head (mm)
1	5.5 - 6.5	1.6 - 1.9	1.00 - 1.02
2	7.0 - 9.0	1.9 - 2.5	1.28 - 1.30
3	9.0 - 12.0	2.5 - 3.2	1.62 - 1.68
4	13.0 - 23.0	3.2 - 5.8	1.92 - 1.94

indicate that the width of the cranium of the larva increases in each instar at the rate of mathematical progression. But this result striked me as a very strange affair, so I doubted myself if some instar, prodably the first or the last one, might escape my eyes. Accordingly I collected the material anew which included two of the first instar larvae that were just in the course of moulting the egg-shell and many of the final instar that were dormant in their cocoons. The results of the measurement on these larvae of the two classes of the developmental degree showed that their crania were quite as large as those of the first and the last instar larvae respectivelyof my previous investigation. Judging by the above results, there is no doubt that the larva of *B. niponica* Sm. carries out 3 moults before its final instar is reached*.

* Later, when I was investigating the Diplopterous wasp, I knew that R, du Buysson (Monographie des Guêpe ou Vespa (Part 1), Ann. Soc. entom. France, 72) already in 1903 observed 4 instars in the larval development of the social wasp. In the field of the Fossorial wasps, however, no definite observation regarding this problem has been contributed so far. An analogical inference basad upon the study of Anthophilous Hymenoptera which must be a quite improper one seems to be prevailing in the field of Fossores (cf. H. Bischoff : Biologie der Hymenopteren, Berlin, 1927).

b) *Growth*. Growth of the larva depends in the main upon the climatic conditions, especially upon the temperature. According to my observation at Sapporo, in August when the air temperature is 20° – 32° C and the earth temperature at the depth of 10 cm below the surface of the ground is about 16° – 23° C, the progress of the larval development is smooth and regular. It requires only a week or so from the oviposition till the encasement. Field observations indicate that the time required for the hatching of the egg and for each instar may be as shown in Table 10.

Table 10. Duration of each instar

Stage or instar	Egg	The 1st instar	The 2nd instar	The 3rd instar	The 4th instar
Time (hour)	44 – 53	10 – 15	15 – 18	20 – 24	80 – 90

On the other hand, in September when the air temperature is 10° – 15° C and the earth temerature at the depth of 10 cm below the surface of the ground is about 5° – 15° C, the growth of the larva is markedly delayed, requiring 10 – 14 days or more before beginning to spin the cocoon. Some of the previous investigators of another species of *Bembix* (e. g. Wesenberg-Lund and Fabre) seem to have believed such a long period of growth to be a normal procedure; since, on the basis of such an assumption, they attempted to estimate the number of the young reared by one wasp for a season. But such a sluggish development seems to me not a normal one, for, *B. weberi* Handl. and *B. picticollis* A. Moraw. of Inner Mongolia showed the similar process of the larval growth as described here on *B. niponica*.

It seems of interest that the progress of the larval development is not proportional to the comsuption percentage of the total provision gathered progressively by the mother wasp. In general, the 4th instar larva, if eats 4 or 5 large victims well, would reach approximately 7/10 or 8/10 of its final size. After that, the larva eats usually more than as many flies as it has already eaten, but it does not so much increase in dimention as it will be expected. The reason for this seems to lie chiefly in the mode of eating of the large larva which is very rough.

c) *Mode of the moult*. It is very difficult to observe in detail the mode of shedding the skin of the larva. Because, the larva before the final instar is hardly able to be kept under our observation in the laboratory. The young larva is very apt to perish under the artificial rearing. By some reason or other, the moult may become difficult under such unnatural conditions. Or it may be so by the shock of the transportation. The following records are, therefore, all taken in the field, by using the artificial glass chamber and under the care of the mother wasp. The larva before moulting ceases its food taking and rests in quiet. But the resting period seems to be relatively short, probably 1 or 2 hours. I have never observed the actual process of moulting*. But I have had some larvae bearing the shed skin at the end of their abdomen. From such a larva I took off the skin after the method of Prell (1924),

* See Addendum

soaked it later in water in the laboratory and examined it under the mlcroscope. Though I could not succeed in making clear the number of the shed skins, I was able to observe the crevice on the cranium and the thorax of the skin. The integument of other portion of the body was entire. Judging from the data thus accumulated, the moult of the larva in this species seems to occur in the same manner as in many Lepidopterous larvae, with the exception that the larva does not creep out of the old skin for itself in the last stage of the procedure.

d) *Mode of eating.* As given previously, the larva of *B. niponica* eats a great many flies during the course of its development. Out of these numerous victims, however, those which are eaten before the 4th instar are only a few, namely 2 or 3 in number as a rule, occasionally even only 1. Accordingly the larva of the 1st – 3rd instar is not only small in size, but also very slender in form, being subcircular in the cross-section. Whereas, after the 3rd moult, the larva devours voraciously all the rest of the prey supplied by the mother wasp and rapidly attains full maturity. Indeed, the larva may be said to gain about four fifths or more of the final weight during the course of the 4th instar. The full-grown larva is somewhat flattened dorso-ventrally, bearing an extraordinarily swollen abdomen and a well-developed rounded tubercle on both sides of each bodily segment. The stigmata are located in an ordinary fashion. The large sized larvae, when fully stretch their bodies, attain nearly 30 mm. Their mandibles are hook-shaped, keenly pointed at the apices and are very nicely fitted for piercing and for tearing off the hard integuments of the victims.

The most frequently observed mode of their eating is to cut off the head of the prey first, and then to eat into the thorax from the wound. At that time the sclerite around the wound is more or less broken off and the opening is enlarged. As a rule, the larval wasp does not perfectly eat up the victims one by one, but, after devouring the thoracic muscles of one victim, it pulls out its head from the victim and begins to eat the next. Thus the larva is used to take a bit of flesh from all of the victims lying before it. Only when intact flies were all exhausted from within the bound of its reach, it returns to the remains of the victims again and dispatches the eatable portion from them. But as long as the mother wasp attends to feed it, such a scarce condition does not occur, because, before the intact victim is exhausted from in front of the larva, she always brings new victims again to it. Eating of the corpses that were already partly eaten occurs either after the mother wasp closes the nest permanently, or when the bad weather lasts for several days and prevent her from hunting. At any rate, in accordance with the abundant provisionment of the mother wasp, the mode of eating of the larval wasp is very rough and crude.. It leaves generally the head, sclerites of the thorax and the abdomen, legs, genitalia, etc. Usually several intact or nearly intact flies are found left uneaten in the cell containing the cocoon. Such a luxurious mode of diet can not be observed at all in any other fly-catching Fossores, for instance, many species of the genus *Grabro s. latr.*, *Mellinus*, *Oxybelus*, and so on. Only in rare occasions when scanty food is supplied, the larva devours every eatable portion of the victims lying before it. In such a case, small flies bearing a soft aclerite are perfectly crambled and eaten up, leaving only the wings or the scutellum of the mesothorax. But even in such a case, the exoskeleton of the thorax of most flies remains uneaten.

e) *Locomotion.* As a rule, before the final instar, the larva of *Bembix* does not leave the pedestal fly on which it was deposited as an egg. Probably the pedestal will supply the larva a solid foothold necessary for its moult. During the period of staying on the pedestal the larva eats the flies which are placed within the bound of its reach. However, once it leaves the pedestal, if necessary, it can move about awkwardly but fairly actively by means of a vermiculation. Its locomotion becomes most marked when it reaches the end of its growth and begins to search for the foothold for spinning the cocoon. Parker (1917) reported an interesting habits of the larva of *B. spinolae* and of *Bicyrtes ventralis*. He said that a newly hatched larva of these species moved up to the top of the empty egg-shell, remaining its caudal end attached thereto, made use of it as a tether, just as was reported by Fabre on some species of Eumenidae. Such habits, however, could not be seen in our species.

f) *Partiality for food.* I have attempted with success to rear the larvae of many species of hunting wasps with food of another kinds than those which are brought to them by their mother wasps. For instance, some larvae of *Sphex umbrosus* Christ have safely passed through their developmental stages into imagos in eating, instead of the grasshopper which is the natural food brought by their mother wasps, the cricket, the locust, the walking stick, the mantis, the cabbage caterpillar, the spider, the dragonfly, the cicada, the beetle and so on. The same experiment was attempted on the larvae of *B. niponica.* I selected some of the 4th instar larvae and gave them, instead of flies, weevils taken out of the nest of *Cerceris quinquecincta* Ashmend, small locusts plundered from *Tachysphex japonica* Iwata, caterpillars robbed of *Ammophila infesta* Smith and spiders (*Argiope bruennichi* Scopoli) taken in the course of transporation of *Batozonus lacerticida* Pallas. In addition to the above, were given dragonflies (only the thorax), larvae of the honeybee, a large ant lion which was the strongest enemy of the mother wasp, and a living larva of a Crabronid (*Ectemnius konowii* Kohl).

The larvae of *Bembix* did not show any sign of refusal against these unnatural food stuffs at first. All of them set about to eat any of them. But the insects of armour clad could not be eaten at all, owing perhaps to the lack of the proper instinct. Among the remainder the locust alone was soon afters refused. But all the rest were indifferently devoured. Strange to say, however, these larvae excepting for those which ate the thorax of the dragonfly and the larva of a Crabronid, all died before encasement. It was uncertain, however, whether the death of the larvae was dependent upon the strange food they ate or upon another cause. But according to my long experience, such a high percentage of death in the final instar larvae does not occur when they are reared with food that was taken out of their natural provision.

Judging from these results, it will generally be said that the partiality for food does not develop so high in the larval *Bembix* as yet. However, some unnatural food including the insects which were hunted by other fossorial wasps appears to become poison for their development.

In relation to the food quality of the larva and also to the habits of mother wasp to place each larva in a separate cell, it will be worthy to note here that two larvae of *Bembix*, if reared in the same glass tube, sooner or later would fight with each other and the stronger kills the weaker, devouring, in most cases, the entire corpse of the defeated. This cannibalism always occurs even when a mass of food is piled up between them. Either of them that has approached to full maturity begins to move about in the cell in preparation for the encasement. Soon it meets with the other and the battle is broken out. In my five trials, four of the defeated larvae were entirely devoured by the other. The larvae that ate the flesh of a brother or a sister mostly died sooner or later. But one of them succeeded in encasement and developed into the imago.

13. Provisioning activities.

a) *General problem concerning teh so-called progressive provisionment.* Provisioning activities of the Bembicine wasps are widely known since the time of Latreille as a special manner of brood-feeding and have been observed upon a number of species by numerous investigators. It is, however, rather curious to say that none of them have attempted to make sure the actural phase of the phenomenon, giving no more informations than the general aspect of the so-called progressive provisionment. It seems generally admitted that the Bembicine wasps have the habits of feeding their larvae from day to day, or rather from hour to hour, as long as it remains in the larval state. According to this account, it appears that the mode of feeding of the mother *Bembix* is much the same as in social wasps, save that they supply food as an intact insect, instead of making flesh-pellets of the prey. Strictly, however, the sentense is correct only in sofar as it concerns with "to bring food from day to day", but is wrong, in expressing "to bring food from hour to hour" and "to bring food as long as the larva remains in the feeding state". This is true at least as to *B. niponica*, and according to the literature, it seems also true in many species investigated heretofore. Because, in those species also, in the larval cell wherein a feeding larva is present, the same relation of food as is found in our species is always recorded by the investigators. First, I will describe the actual states of feeding activities of the mother wasp.

b) *Food actually found before the larvae of each instar.* One of the most important habits of the social wasps is to give the larvae a necessary quantity of food in time of necessity. Accordingly it does not happen that a large mass of food is accumulated at a time in front of each larva. The same phenomenon has also been ascertained in some of the subsocial Diploptera, e. g. *Synagris cornuta* of Africa and the members of Zethinae of the tropics of the Old and the New World. If the

Bembicine wasp has the analogous habits as widely believed, food supplied in front of the larva must always be very small in quantity or entirely be wanting. But things do not happen in such a manner in Bembix. The fact is readily realized by digging up their nests to examine the actual number of flies accumulated in front of the larva. Tables 11 and 12 are the results of my investigations.

Table 11. Number of prey supplied to the egg and the 1st – 3rd instar larvae

Stage / Prey / Obs. No.	Egg	1st Instar		2nd Instar		3rd Instar	
	Intact	Eaten*	Intact	Eaten*	Intact	Eaten*	Intact
1	1	0	1	1	2	1	1
2	1	0	2	1	2	1	1
3	1	0	2	1	2	2	0
4	1	0	2	1	3	1	3
5	1	0	2	1	2	1	3
6	1	0	2	1	2	1	3
7	1	0	3	1	2	1	3
8	1	1	3			1	3
9	2					2	3
10	2					2	3
11	2					2	3
12						2	2

* Only partly eaten.

Table 12. Number of prey supplied to the 4th instar larvae

Eaten prey \ Intact prey	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
1			1		3	2	3									9 *0* ⓪
2			2	1	3 *1*	3	*1*	1 *1*	1	*1*				1		12 *4* ⓪
3						*3*	1	1 *2*	*1*	1	1					4 *6* ⓪
4			1			2										3 *0* ⓪
5					*1*	*1*						*1*	*1*			0 *4* ⓪
6						①	*1* ①	*1*	①					①		0 *2* ④
7							*1*		*1*		①	*1*				0 *3* ①
8				*1*					①							0 *1* ①
9					*1*		*1*	①	*1*							0 *3* ①
10	*1*				*1*						①		①			0 *2* ②
11		*1*			①					①						0 *1* ②
20		①														0 *0* ①
Total	0*1*⓪	0*1*①	4*0*⓪	1*1*⓪	6*4*①	7*4*①	4*4*①	2*4*①	1*3*②	1*1*①	1*0*②	0*2*⓪	0*1*①	1*0*①	0*0*⓪	28, *26*, ⑫

Remarks. Numerals show the number of times of observation: 1, 2, 3 — in the early stage; *1, 2, 3* — in the middle stage; ①, ②, ⑧ — in the later stage.

From the tables we can summarize the number of intact victims found by each instar larva as follows : By the egg usually 1, rarely 2; by the 1st instar larva usually 2, sometimes 1 and 3; by the 2nd instar larva usually 2; by the 3rd instar larva usually 3, very rarely 0; by the 4th instar larva in the early stage 2 – 12, in the middle stage 1 – 11 and in the later stage 6 – 13.

As described above, in almost all the nests examined, a large mass of untouched food, in comparison with the developmental degree of the larva is accumulated.

This fact is important, because it indicates that the provisionment of *Bembix* is carried out essentially in accordance with the rule of the mass provisionment of other hunting wasps, excepting that it is repeated day by day. On the other hand, we can not overlook another important character of the provisionment shown in the tables. This is that the food supplied in the cell differs markedly in quantity according to the developmental degree of the larva; that is to say, generally speaking, the wasp brings a small quantity of food to the small larva, while she supplies a large quantity to the large larva. This fact seems to be more interesting than that the wasp supplies food from hour to hour with the request of the larva, although such a phenomenon does not occur in reality. Because the former requires higher grade of psychic ability (may it be merely an instinctive one) than the latter.

c) *Provisioning activities actually observed.* The following is the provisioning activities of a wasp for one larva based upon my observations:

Table 13. The time spent to bring the first prey

Wasp No.	Time of departure from the nest	Time of return with a prey	Duration
	h m	h m	h m
17	12. 10 p.m.	1. 30 p.m.	1. 20
55	1. 57	1. 59	. 02
98	2. 57	3. 48	. 51
100	10. 00 a.m.	10. 33 a.m.	. 33
115	1. 15 p.m.	2. 00 p.m.	. 45
117	12. 40	12. 45	. 05
123	9. 40 a.m.	11. 13 a.m.	1. 33
124	1. 25 p.m.	1. 37 p.m.	. 12
135	12. 25	1. 00	. 35

After the oviposition is finished, the wasp passes the greater part of the day in the nest, waiting for the hatching of the egg. She comes out of the nest only twice or thrice a day, probably to take a nourishment or refreshment for herself. During the time the accessory branch is dug in some nests. If we examine the nest at this time, we can find the wasp sitting quietly either in the accessory branch or in the tunnel just in front of the partition wall of the brood-cell, directing her head forwards. Towards the time when the egg is about to hatch, the wasp opens the closure of the cell and examine the egg (according to the glass tube method of observation), but it is yet uncertain whether such an examinbtion is performed once for all or several times. Then the wasp goes out and returns with the 2nd victim to the nest. At this time the egg is used to show the symptom of hatching out, but sometimes it cannot be perceived by human sensation. From that time the wasp passes the greater part of the day outdoors. But towards the evening she is used to return to her nest to pass the night.

For the 2nd and the 3rd instar larvae the wasp brings one or two victims more.

Occasionally, however, it is observed that the wasp accumulates 5 or 6 victims a day for the 3rd instar larva. But such a case seems to be an exception. During this period, in case more than one flies are supplied to the larva, they are brought in successively during a short period of time. Until this stage, apparently the activities of the wasp show a phase close to the real daily rearing. But after the larva sheds its 3rd instar skin, things become quite changed. The wasp comes, without exception, to bring in 5 to 10 or more victims a day to her larva. Such a large number of victims, however, are never brought in from hour to hour, or from morning till evening, as has been described by many authors upon another species of *Bembix*, but actually they are accumulated quite in concentration, during an hour or so in the morning. Only when the climatic conditions are unfavourable for the activities of the wasp and her work is commenced comparatively late in the forenoon, the work of the wasp is lengthened till the middle of the afternoon. But even in such a case, if the condition may allow, her provisionment is carried out concentratively during brief hours. The following instances will clearly show the usual manner of their provisionment under the normal condition.

1) Aug. 1, 1946. I found a wasp coming back to her nest with a prey at 9.00 in the morning. From that time onward till 9.52 a.m. she brought in 5 more prey to her nest, namely at 9.03, 9.10, 9.17, 9.40 and 9.52 respectively. At 10.20 I examined the brood-chamber. There were 7 intact flies piled up near the entrance in the cell. The larva was in the middle stage of the 4th instar. The wasp did not return till 5 in the afternoon, when I stopped the observation. However, when I examined the nest the next day before the work of the wasp began, two more flies which were not observed by me the previous day had been added in the cell. Therefore, they must have been carried in the nest in the previous evening after my observation was ceased.

2) The same day. Another wasp took the prey in her nest at the following hours : 8.57, 9.00, 9.03, 9.07, 9.10, 9.15. Then she gave the entrance-tunnel the permanent closure.

3) Aug. 11, 1948. A wasp brought the first victim of the day to her nest at 7.37 in the morning. She carried in thereafter 5 more victims successively to her nest, namely one at 7.44, 7.55, 8.15 and 8.25 respectively. Then she stopped her work till 4 in the afternoon, when I ceased the observation of the day.

Similar instances will abundantly be met with in the later section in connection with the analytical study of the behaviour of the wasp. Indeed, such a study was enabled only by utilyzing this habits of everyday-mass-provisionment. The manner of provisionment of *Bembix*, therefore, should be referred to as *progressive mass-provisionment* rather than mere progressive provisionment.

Similar phenomenon has hitherto been observed upon many species of *Bembix* by a number of investigators when the nests were examined by digging up. However, either they did not pay a special attention to the fact or they would attribute the phenomenon to the unusual accumulation of food in preparation for the unfavourable climatic condition. But such is nothing but the ordinary activity of the wasp and because of its ordinary phenomenon it will especially be worthy of notice as representing an intermediate condition between the habits of mass provisionment of the majority of the hunting wasps and those of the true progressive provisionment of the social wasps.

d) *Arrangement of victims in the cell.* The victims thus massively provisioned in the larval cell are all placed on their back near the entrance, with their heads directing inwards. The victims which are brought in later are, in turn, laid on top of others that were already piled up there. But those that are newly brought in are placed slightly more backwards, that is to say, towards the entrance. The larva is situated usually in the middle of the cell, with one or two victims placed near-bye. Remains of food were scattered on the posterior portion of the cell. As growth of the larva proceeds, the larva gradually proceeds towards the entrance and the mother wasp places the new victims more entrancewards, so that the cell is as much lengthened.

e) *The time of close of the provisionment.* Just as I have proved upon the fact that the feeding of the youg is not carried out by the mother wasp from hour to hour of the day, so I can as well verify that the feeding of the young is not continued as long as the young remains in its larval state. I have examined the developmental grade of many larvae whose nests have just been sealed up by means of the permanent closure. They are all in the 4th instar and in this respect things are quite unanimous. But their developmental degrees are very different. If we divide the growth of the 4th instar larva into 10 grades, the instances which came under my observation in

Table 14. Relationship among the developmental degree of the larva, the number of already eaten victim and the numbsr of intact victim left in the cell at the time when it was permanently closed.

Observ. No.	develop. of larvae	Number of eaten victims (A)	Number of intact victims (B)	$\frac{A}{A+B} \times 100$
1	3/10	5	12	29%
6	4/10	10	8	56
51	3/10	2	9	18
63	8/10	6	6	50
90	5/10	16	17	48
91	7/10	23	11	71
112	3/10	4	6	40
134	6/10	7	11	39
137	3/10	2	6	25
154	5/10	6	8	43
a	5/10	5	5	50
b	5/10	5	7	42
c	5/10	7	4	64
d	?	7	11	39
e	8/10	8	16	33
f	6/10	15	14	52

a – f … data obtained at chiba.

Sapporo were 3, 3, 3, 3, 4, 5, 6, 6, 7 and 8 in grade respectively. These instances indicate that *B. niponica* gives her nest the permanent or final closure, as a rule, prior to the full maturity of her larva. That is to say, this wasp stops her feeding activity usually at the time when the larva is yet in the early or middle stage of the final instar, only rather exceptionally she works till its later stage, but never till its full-grown state. The fact, when considered from the point of the time consumed, comes to be that the wasp ceases her provisionment at about 24 hours after the final moult of the larva, only rarely at 50 - 60 hours after that time. Whereas, the time required by the larva to pass through the feeding period of this instar is 80 - 90 hours under favourable condition. The fact, when considered from the point of the food consumption of the larva, is that the mother wasp stops her feeding work at the time when the larva has eaten only less than half, at most two thirds of the total mass of food stored in the cell. Table 14 shows the contents of the brood cells that have just been sealed up by the wasp by means of the permanent closure. It will best indicate the final phase of the provisionment in this species.

According to the evidences already described, it becomes that the activities of *Bembix* just before the permanent closure of her nest are carried out quite in the same manner as in other hunting wasps having the habits of mass-provisionment, excepting that the larva, instead of the egg, is present in the cell. Indeed, the *Bembix* gathers a number of victims during a short period every day and when she permenently closes her nest, she always leaves her young alone supplying it with a large quantity of food piled up in the cell which must take two or three days to eat thereater.

f) *Summary of the present paragraph.*

1) As soon as the nest is dug up, the wasp at once brings a victim to it and lays an egg upon it.

2) As a general rule, however, the mother wasp does not bring in the 2nd victim to the nest before hatching of the egg, only rarely she does, but never the 3rd victim.

3) As soon as the egg hatches out, the wasp hunts the 2nd victim and brings it in the cell, sometimes even the 3rd victim.

4) When the first moult has finished, the wasp takes one or two victims in the cell.

5) When the larva attains the 3rd instar, a few more victims are collected by the wasp. But sometimes only one or two victims are supplied to the larva before it develops into the 4th instar*.

6) For the larva of the final instar the mother wasp always places several fresh victims in front of it. The number thus accumulated is from 4 to 10 a day**.

7) Provisionment of a day is usually carried out massively and concentratively in a short period of the morning, never from hour to hour. Rarely one or two more victims added in the cell toward the evening.

8) The wasp stops her feeding activities. for the larva usually about 24 hours after its

* In one instance observed in Chiba, the larva was considered to be of the 4th instar just after moulting, but the victim already eaten by it was only a single *Stratiomyia japonica*, while the cell was stuffed with 12 intact insects of the same species.

** The instances shown in Table 12 which contain less than 3 intact victims in the cell are those that have not been fully provisioned as yet for the day.

final moult, rarely 50 - 60 hours after, despite the larva must continue its taking food for about 80 - 90 hours after the final moult. At that time the wasp stuffs a large amount of food in the cell in the same manner as in the majority of the hunting wasp and closes the nest permanently leaving the half-developed larva alone.

14. Permanent closure of the brood cell and the nest.

Carpenter (1930) in his interesting paper on the different methods of filling in the stocked burrow in Pompilidae and Sphecidae, notes that two species of *Bembix* have hitherto been observed to utilize the tip of the abdomen in pressing down the dirts which were swept in by the wasp to close the tunnel, namely *B. nubilipennis* Cresson and an unnamed species (*B. rostrata* ?). The one is derived from the observation of the Raus (1918) upon the N. American species. The other is said to be observed by O. W. Richards, but no detailed account is given.

In our species, the manner of permanent closure of the nest is very similar to that of *B. nubilipennis.* The wasp assumes her position at the bottom of the tunnel, with her head directing forwards. She bends the apical two segments of her abdomen ventrally and strikes and pounds quickly and succesively the sand grains with the dorsal suface of the curved segments. According to the Raus, *nubilipennis* uses the hind pair of legs, too, to cram and pack the dirts down, but in our species hind legs are used only to push away the sand grains backwards. The wasp sweeps in the dirts with the front pair of legs and then at once begins to press down the tampon with the tip of the abdomen. After a while she ceases her work, comes out, sweeps in the sand grains from the entrance, hurries in head first and turned around at the bottom of the hole, or retreats backward with a load of sand, and resumed her pounding work. Although her pounding activity is not so nimble as was seen in the members of the Pomilidae, her work is very skillful, turning the tip right and left and taps and strikes the bottom sand all over.

However, the utilization of the tip of the abdomen to press down the sand is not restricted to the case of permanent closure of the nest in our species. They show the same method when they make the partition wall of the cell as well as when they close the entrance of the nest from within at the time when they rest in the nest.

In addition, our *Bembix* shows sometimes another interesting behaviour at the time of the permanent closure of her nest. At that times she takes the material to close the tunnel from a constant spot in front of the entrance. Accordingly, with the progress of her work, a hole is made at the spot and it becomes deeper and deeper in proportion to the filling grade of her tunnel, resulting at last in a new tunnel that lies in the opposite direction to her closing nest. The wasp carries out the sand from the bottom of her new tunnel and carries it in her old tunnel. Thus burrowing and closing are carried out alternatively and simultaneously. This interesting behaviour was first observed by Dr. K. Yasumatsu in Kyushu. But so far as my observations go, such a behaviour occurs rather rarely. Moreover, out of several such instances only one was ascertained by me to be made up into a new nest. Others were all abandoned half-way. Probably the previous nest is adequately closed up before the newly formed tunnel reaches a favourable depth to make a nest.

The nest of *Bembix* which was permanently closed does not show the perfect closure throughout the tunnel. In most cases a more or less empty space is left between the closure of the entrance and that of the brood-cell. Both of the closure are, of course, more compactly and more thickly constructed than usual. Sometimes the closure of the entrance hole is not brought up exactly level with the surface of the ground, but remained opened for a short distance. These abandoned holes are sometimes utilized later as a favourable porch of their domiciles by some species of leaf-cutting bees or spider hunting Pompilids or the weevil killers of *Cerceris* that live in the same locality. At any rate, even when the entrance hole is perfectly closed up, our *bembix* would not take an effort to sweep away the debris heaped up in front of the nest, or to even the ground where the hole is made.

After finishing the closure, the wasp begins at once to search for the favourable place to make her following nest. As the permanent closure is usually carried out in the forenoon after the massive provisionment of the day, the next egg is mostly deposited within the same day.

15. Cocoon

The cocoon of *B. niponica* is composed of a layer of fine grains of sand, tightly glued together with secretion of the silk gland. It is elongate oval in form, measuring 20 - 25 mm in length and 8 - 10 mm in width. In the natural condition, the cocoon is hung up with the silk threads from the walls of the cell, directing the anterior end (= the broad end) forwards (= entrancewards) and more or less upwards, keeping its body somewhat obliquely and is located at the anterior end of the broodcell. On the broad end of the cocoon, there is a ring-formed trace of the silk funnel, on which the explanation will later be given. The so-called respiratory pores are arranged on the equatorial zone of the cocoon, varying in number from 6 to 17. The frequency of each number, so far as my examinations go, is as shown in Table 15.

Table 15. Number of the respilatory pore of the cocoon.

Number of pores	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total
Frequency	–	1	10	10	16	18	23	11	7	1	2	1	1	–	101

The respiratory pores are visible to our naked eyes. Though they are disposed on the equatorial zone of the cocoon, their distirbution is rather irregular, not only in the linear arrangement, but also in the intervals between them. Seen from outside, the pore is surrounded by a slightly projecting cone-shaped wall of glutinous substance, dark brown in colour. The orifice is 1/5 - 1/3 mm in diameter. Seen from inside, there is a rounded swelling with the diameter of 1 mm at the place of the pore. This swelling is composed of 3 layers of felt. The outermost layer, that is to say, the innermost layer if seen from outside, is the thickest of all. Occasionally its outer surface is covered with some glossy substance and is polished; usually, however, it consists of the same felt as that covering the inner surface of the cocoon all over. It is yellow or yellowish white or yellowish brown in colour, rarely pale brown. The middle layer is also swollen out, but less remarkably so than in the outer layer, and the basal surface is almost flattened. It is slightly darker in colour, namely yellowish brown or brown or dark brown. It consists also of the polyporous felt. The basal-most layer that constitutes the base of the outward projection of the respiratory pore is a more compact and more flattened layer than the other two and is usually brown or dark brown in colour. In most cases, this layer is perforated at the centre from outside by a small hole which sometimes hollows into the middle layer, rarely even into the surface layer and makes there the bottom of the respiratory pore. But in no case, have I found the pore perforating through the wall of the cocoon. Among the 3 layers, the surface layer can readily be torn off from the middle layer, while the latter is sometimes unable to be separated from the basal layer, especially in an old cocoon. When the basal layer is taken off, the base of the respiratory pore comes to appear, which is slightly broader than the outward orifice, measuring 4/5 mm in diameter (Fig. 5, B).

The inner surface of the cocoon is ununiformly lined with felt. This lining is usually thicker in the median- and the polar zones than the intervals, varying in colour from yellowish white to pale brown. In addition to this lining, the posterior (narrow) portion of the cocoon is painted with pitchy substance which is undoubtedly derived from the excretion of the larva.

As for the significance of the respiratory pore, it seems to me that it is useful not only for the circulation of the air, but also for the regulation of the humidity of the inside.

16. Encasement.

J. H. Fabre observed the method of the construction of the cocoon with the larva of *B. rostrata* L. His observation is, however, not of a complete one, owing to the improper arrangement employed. I have made the same observation with more than 20 larvae of *B. niponica* and have obtained the knowledge concerning the behabiour of the larva at that time. Two methods were adoped in my observations. In one of which I used the tube bottle of glass, with the diameter of 15 - 20 mm. I stuffed a mass of wet sand at the bottom of the tube to the thickness of 15 - 20 mm and hardened it so as not to cramble off when the tube was laid down horizontally. Then I introduced in it a larva of the 4th instar with its food and plugged the entrance either with a cotton plug or with a hard layer of wet sand, leaving the interval of 40 - 50 mm in length for the cell of the larva.

In the other method a Petri dish with a considerable depth was used. It is filled with wet sand level with the brim. A hollow of elongate ellipsoid of the proper size having a depth of 15 mm or so is impressed on the surface. A larva and its food are placed in it and the dish is put on with the cover. The behaviour of the larva can be observed through the cover of glass. This arrangement is very useful to observe the activity of the larva in its final course of the inside work in the constuction of the cocoon. Because, when the hollow is regulated to a proper shallowness, the larva is compelled to stick the upper portion of the cocoon to the glass-cover of the dish; whereas, the sand grains can not be adhered to the plain of glass, so that the portion of the cocoon is remained unset with the sand grains, only being lined with a semitransparent membrane through which we can observe the work of the larva inside the cocoon. The method of the encasement, or the forming of the cocoon observed by means of such arrangements can be summarized as follows :

The larva, when fully develops, moves about in the cell with a considerable activity. During the time it still picks up from time to time the remains of victims and eats the odd bits of flesh. At the same time, it scratches hither and thither of the surrounding walls of the glass tube with its mandibles. As the time goes on, the larva devotes itself to scratch the walls of the cell, epecially at the end where a mass of sand is stuffed compactly. As a result the sand grains are gradually scratched down on to the floor. In some instances, at this period of the work, the larva perfectly perforated through the sand wall supplied. In the field observations, we always find that the cell which contains a coccoon is, as a rule, by far the larger both in length and in width than that wherein a larva is still eating. At the same time, we can observe in such a cell the remains of victims sometimes covered with sand, sometimes left uncovered far behind the cocoon. These states can be best explained by supposing that the larva scratches down the sand-grains from the walls of the cell and proceeds forward in digging and scratching down the anterior wall. In the tube bottle, the larva then begins to shift the sand grains thus scratched down backwards by using the mandibles, and extends them flattly over the floor. This is *the first stage* of the encasement. The time spent for this stage is about 5 – 10 hours.

Next, the larva commences to spin the silk cocoon. First, silk threads are stretched between the lower portions of the lateral walls and also between the lateral wall and the sand grains of the floor. The larva stretches and turns its anterior body, proceeds forwards and turns around, weaving successively but rather irregularly a sheet of silken cloth or a hammock to get upon. On and on the silk-threads are attached to the upper portions of the lateral walls and the form of the hammock is gradually accomplished. It takes about 4 – 7 hours to make this hammock. This is *the second stage* of the cocoon formation.

The attaching points of the silk-threads are continuously shifted upwards and the threads come to be stretched between the lateral walls and the upper ceiling. Gradually and slowly it takes the form of a lengthened ellipsoid, enveloping the manufacturer within. The accomplished silk-cocoon is white in colour and semitransparent, with the anterior end directing towards the sand wall (in the natural condition always entrancewards) and always slightly elevated. While the posterior end is slightly lowered. At the anterior end where the cocoon remains still widely opened a sort of the silken funnel is attached, the apex of which is adhered to the sand wall of the tube bottle (Fig. 5 A, 1 and 2). This funnel is sometimes opened upwards and spread divergently forwards and downwards. At the posterior end the threads are converged into a thick bundle which bends suddenly downwards and is glued to the floor of the tube (Fig. 5 A, 2 ··· lateral view of 1). This is *the third stage* of the encasement. It takes about 4 – 5 hours.

Then *the fourth stage* begins. The larva proceeds forwards, stretches about one thirds of its body out of the opening of the cocoon towards the funnel and commences to gather the grains of sand. It catches a grain between its mandibles and then assembles a small amount of sand into the cocoon, moving its head back and forth and retreating itself little by little into the silken lodge*. It then glues several grains together into a block with the buccal secretion of the silk gland and pushes them over the inner surface of the silken capsule. The block is extended at once into a thin layer and the sand grains are inlaid in the silken wall of the pouch. Then the larva glues together the new sand grains gathered under its head, picks up several of them with its mandibles and inlays them in another portion of the cocoon. The manoeuvre is repeated right and left of the silken pouch. Towards the end of the first work of plastering, when the material comes to an end, the wall of the silken cocoon is inlaid with sand-grains as shown in Figure 5 A, 1 and 2. Then again the larva thrusts its body forwards out of the opening and collects the material in the cocoon. Then it resumes the sand-inbedding work as before. The same manoeuvre is repeated and the grains of sand are gradually inlaid in the silken wall of the cocoon. The order of the work is shown in the figure by small numerals (Fig. 5 A, 3). As the work proceeds further, the portion of the cocoon which is represented by cross-hatchings in the same figure (5 A, 4) is first set with the grains of sand, then the portion of simple hatchings and at last the posterior portion. Thus the sand-plastering work is commenced at the anterior end of the cocoon and is gradually extended towards the posterior end. Until the time when the posterior end alone remains free from the sand grains, the larva does not turn round in the cocoon. Therefore, in the work of plastering the posterior half, the larva folds its body into two (dorsad as well as ventrad) and stretches its anterior body backwards as long as possible. In order to inbed the material in the posteriormost wall, the larva turns round for the first time. It folds the body into two by thrusting the head and the thorax beneath the abdomen and pushes forewards the both halves of the body in the oppsite direction, namely the anterior half backwards and the posterior half forwards. At this moment the cocoon is markedly swollen in the middle part, owing to its high elasticity.

* In the same stage in *B. rostrata*, Fabre observed that the larva made selection in regard to the size of the sand grains and threw away unfavourably large material. Similar selection was conducted by the larval wasp of *Stizus pulcherrhimus* Sm. (Tsuneki, K., 1943). But in the observation with *B. niponica* none of the larvae showed the similar behaviour. However, it may be due to the fact that the sand grains used in the study were very uniform in size.

The material used to close the posterior end has been accumulated beforehand near the middle of the floor of the cocoon and the larva takes it up by thrusting the anterior body beneath the abdomen. After finishing the closure of the posterior end, the larva turns round again and recommences the sand inlaying activity. Thus, the work already done in a general way is repaired and replenished. If we examine the cocoon at this time of the procedure under the microscope, we can see the wall as yet only roughly inlaid with the grains of sand, leaving many a empty interval between them. The supplementary work is slowly but elaborately carried out. The time spent to inlay the grains of sand over the surface of the silk capsule is about 2 – 3 hours. Thus *the fourth stage* finishes and the next stage sets in.

In the fifth stage, the larva, after collecting the last material into the cocoon, begins to arrange the foundation of the lid. It gnaws the brim of the opening with the mandibles and pulls it inwards. The position gnawn and pulled by the larva is successively changed from one place to another, with the result that the brim turns into a more clear circle by the action of the buccal secretion and the opening becomes gradually smaller. Soon after, the work is turned to spin a convex lid over the opening. The threads are stretched radiately across the opening. When the mouth of the cocoon is covered with a thin layer of silk, the larva inlays it with grains of sand. The time spent for this work is about 30 – 50 minutes. This lid-manufacturing activity is *the fifth stage* of the encasement.

At this state, the cocoon is completely wet and very elastic, so that it allows

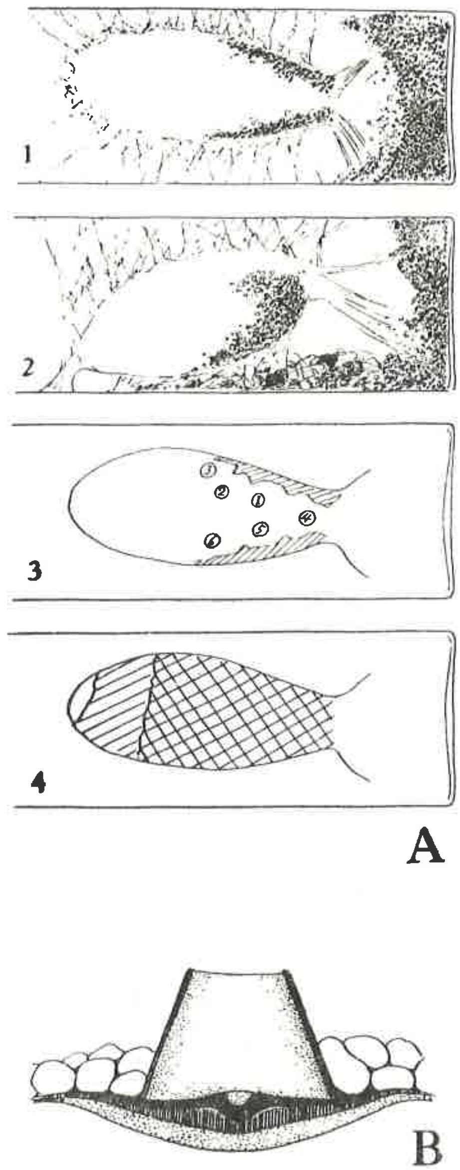

Fig. 5. A. Diagrams showing the order of the encasement.
1, The silk cocoon first spun by the larva, dorsal view. 2, Do, lateral view. 3, Do, dorsal view with numerals showing the order of the progress of the sand inlaying work. 4, The portion with cross-hatching is first plastered with sand and then the portion with simple hatching.
B. Diagram showing the structure of the so-called respiratory pore.

to change its form freely in accordance with the movement of the larva. The larva continues to work for about 3 – 4 hours further to accomplish the construction of the sand wall, turning and returning in the case. Toward the end of the work, the cocoon begins to dry up. If examine the cocoon at this state, we can observe the respiratory pores still distinctly perforating the sand wall. Probably they are prepared in the course of the mending work, when the mouth parts of the larva are frequently produced through the sand wall. Thereafter, the larva engages in the inside work of the architecture in weaving a silken sheet on the inner surface of the wall, as well as in spinning the three layers of the lining beneath the respiratory pores. It takes about 2 days for these inside works, *the sixth stage* of the cocoon construction.

In the above description, the time required for each stage of the encasement is given according to the instances wherein the work was smoothly carried out. The rate of the work, however, varies not only from one individual to another but also according to the temperature. Therefore, when only 3 hours are spent by one larva to scratch off the sand grains from the surrounding walls, it takes 8 – 17 hours for another. In the above described instances, the time spent in inlaying the sand grains over the surface of the silken pouch was only 2 – 3 hours, while in 5 other instances, it took 5, 7, 8, 9 and 15 hours respectively. Similar differences of the time required were observed in any other stage of the encasement.

It will be worthy of special mention that the convex lid that is attached to the front end of the cocoon in the 5th stage of the encasement is not planned in order to enable the just winged wasp to emerge from the cemented box easily. The suture at the circumference of the lid is not so loosly comented together as to permit the wasp to break it off with ease. Indeed, when the wasp comes out of the cocoon, it must attack the sand wall of the cell for 2 hours or more to cut open and the window thus made is not always unanimous with the form of the lid.

During the course of my rearing of more than 20 larvae of the wasp I have obtained 4 instances of the abnormal cocoons which are formed at the end of cotten plug, without using the grains of sand. In other respects they are similar in constitution to the normal cocoon, excepting for the respiratory pores. These cocoons are made of the silk-gland secretion only, having a perchment-like quality and are yellow in colour. They are somewhat smaller than the normal cocoon, probably owing to the shrinking caused by the lack of the solid support of the sand skeleton. On the equatorial zone are scattered irregularly and much more in number than usual the respiratory pores, most of which are, however, very imperfect in structure. Seen from inside, they are rather indistinguishable from the surroundings because of the disordered interior lining. The larvae in these abnormal cocoons were all failed to pupate and invariably died.

Several other instances that began to spin the cocoon at the end of the cotten plug failed to form the silken pouch. They made the hammock of irregular shape and spread upon it the secretion of the silk gland. In two other instances the larva, after spinning the normal silk cocoon, crept entirely out of it when it intended to gather the sand grains. It could not return to the pouch and after spreading the silk secretion over the floor, eventually died.

17. Rejection of the remains of food from the nest

I have frequently observed the wasp carrying out the remains of victims from her burrow, sometimes even the old cocoon. Undoubtedly a part of such a behaviour can be attributed to the clearing of remains of an old nest with which the wasp happened to encounter during her burrowing work. However, I have been able to ascertain also that such a behaviour is mostly aroused in the case when the wasp dust her nest. The following observations will give the definite evidences on the subject.

1) Wasp No. 28. Sept. 19, 1947. Simple nest. The wasp was in the accessory branch. A larva of the 4th instsr was in the cell. Two fresh prey were placed in front of the larva, but no remains of food could be found in the cell.

2) Wasp No. 125. Aug. 21, 1948. Simple nest. The wasp was absent from the nest. The larva was as large as in the above instance. Eight intact fresh victims were accumulated at the entrance portion in the cell and the larva had just begun to feed upon one of them. But no remains of food were in the brood-cell as well as in the tunnel.

3) Wasp No. 133. Aug. 25, 1948. Simple nest. The mother wasp was absent. The larva was in the 4th instar. It was situated at the posterior part of the cell. No food nor remains were about it, only a single newly brought fly was placed at the entrance portion.

The above instances were observed at the time when I dug open the nests. The following were ascertained in the course of my continuous observation by using an artificial nest of glass instead of the natural tunnel and cell.

4) Wasp No. 99. Aug. 12, 1948. I set a glass bottle in place of the natural brood-chamber and put in it a larva of the middle stage of the 4th instar and 2 prey. The mother wasp brought in 3 more prey on the day. The next day, however, when I examined the nest, the larva was beginning to spin the cocoon. Remains of two flies were there. But 3 others that were brought in by the mother wasp the previous day were all absent from the nest.

5) Wasp No. 94. Aug. 11, 1948. I placed in a nest a complicate labyrinth made of glass which contained 4 brood-cells and 3 larvae, each with some prey. Soon the wasp took in a fly. But after a short confusion in the arrangement, she took up an intact fly lying in a cell and dragged it backwards to the entrance orifice and abandoned it in front of the nest. Later when she came out of the nest again, she took it up once more and carried it backward for about 50 cm. There she flew up with the fly and threw it away from in the air.

6) Wasp No. 114. Aug. 17, 1948. I set in the nest a Y-tube of glass, with two cells and two larvae, one in each cell and provided with some food. The next morning when I examined the nest, one of the larvae were absent from the nest. On my search, however, the larva was found as yet alive on its pedestal fly, but which had been discarded on the sunny ground 15 cm away in front of the entrance.

These instances evidently indicate that the wasp, though on rare occasions, carries out the remains of larval food, or anything that appears strange to her, from her nest. In this respect *Bembix* should be said to resemble closely the social

Hymenoptera.

18. Enemies

The enemies that attack *Bemdix niponica* can be divided into 3 groups in view of the method of attack, namely the parasite, the predatory enemy and the robber. Among these groups of enemies the last named one has not come under my eyes as yet. But according to the observation of K. Baba, the robbery is commonly found in the settlements of the wasps on the dunes near the city Niigata. So that this phenomenon seems to occur rather provincially in our species. The robber of our *Bembix* is also a companion of the same settlement. It is said that some of the wasps that have failed in capturing the prey (?) in their foraging excursion, fall to robbing their more fortunate (?) companions. The robber (or robbers) attacks a home-coming companion carrying a prey and robs her of her booty. This phenomenon among the members of Bembix was first found by G. and E. Peckham upon a North American species, *B. spinolae* Lep. and has been considered by some authors as a sort of the labour-parasitism.

1) *Parasite.* As has been observed upon many species of *Bembix* of the world, our species is also harassed dy the perpetual invasion of parasitic flies. But the complete destruction of their nests caused by the paratisitism of these Tachinid flies (mostly *Myrtogramma* spp.) is occasioned rather rarely. In reality, the actual damage suffered by the wasp is, in most cases, merely a more or less loss of the stored food, because the maggot of the fly would not directly attack the living host. In view of these relations, they may better be classified as a commensalism. Indeed. I have observed several nests in which more than a dozen of maggots made an inroad, while the wasp's larva could invariably carry out its normal development. Notwithstanding which, we can not safely say that the parasitized host is always free from danger. Because I have observed also a few instances wherein the parasitized host was supposed to have starved to death, owing to the preoccupation of the stored food by a numberless maggots. It will be the condition of the nest at the time when the mother wasp gives it the final closure that determines the fate of the larva. In the case when the wasp stops her care of the larva in its earlier stage of the 4th instar and at the same time it happens that the nest has been invaded by a comparatively large number of parasites, the death of the wasp's larva will occur. The instances in which only the remains of food were found in the cell, despite that it is still in the midst of the wasps' season, seem to indicate such an occurrence. On the other hand, in the nest in which the mother wasp still continues her feeding activities, the larva does not starve to death in any case. Because, she will compenste as quickly the provision in the brood-cell as it is consumed by the larva as well as by the guests. Detailed proof concerning such an ability of the wasp will later be related.

As to the method of invasion of the parasite's maggots, there have been supposed or actually observed two ways on some species of the European as well as the

American *Bembix*. Fabre reported that the parasite deposited her maggots directly on the body of the booty of *Bembix* at the time when the wasp was about to enter her burrow, dragging the fly behind her. While G. and E. Peckham supposed another method of invasion. They saw several times a parasitic fly follow the wasp into her burrow, remaining within for half a minute. They supposed from such an observation that the fly might go in to lay her egg (!).

I have very frequently observed the parasitic flies penetrating into the burrow soon after the wasp carried in a victim. But I have had no opportunity of making a reliable observation upon the fact that a fly rushes on to the victim which is projected from under the abdomen of a wasp at the moment of her entrance to her nest. Indeed, a single instance of observation which I have actually made on the maggot-laying behaviour of a parasitic fly was performed in accordance with the supposed method of the Peckhams. A Tachinid fly that followed a wasp carrying a prey till her nest found it (*Eristalomyia tenax*) thrown aside in the tunnel within my sight and laid 2 maggots on it. In this case it seems of interest that the parasite, when first she found the fly lying there, would not lay her youngs at once, but only examined it carefully and came out of the burrow. She soon entered again, examined the victim once more, then deposited the maggots on it and flew away. The wasp came out, caught the victim and dragged it in backwards as usual, without noticing the maggots which had already hidden under the wings of the fly. That the parasite would not lay her maggots at once on the fly seems to be due to the fact that such a case is unusual for her habits.

On the other hand, I have observed an interesting behaviour of a parasitic fly (*Myrtogramma* sp.) depositing her maggots in an empty brood-cell of a species of the fossorial wasp. It occurred upon a nest of *Ammophila infesta* Smith. A parasitic fly that was crouching near the nest while it was stll being dug by the wasp came flying above the entrance-orifice. There she stops in flight and at once dropped a band of maggots into the unaccomplished burrow.

Judging from the two observations described above, it seems presumable that the following method of invasion will probably be made use of by the parasitic flies: A parasite, when entered a nest of which the entrance is not compactly closed may deposit the maggots in the empty tunnel in front of the entrance tampon of the brood-cell. The maggots thus deposited will wait for an opportunity and reach the victim at last when the wasp comes back with a booty and lays it aside in the tunnel while she is engaging in clearing the closure of the brood-cell. By such means the maggots will most efficiently be transported into the brood-cell of the wasp. Many observations made by me on the Tachinid flies penetrating in the incompletely closed tunnels of the wasps and staying there for a little while seem to give a strong supprt to the supposition that such a method of invasion may prevail among them under the natural condition.

2) *Predatory enemies.* This group of enemies falls in two classes, namely the enemies of the larva and those of the imago.

As predatoy enemies of the larva are known so far three species of insects, viz. *Craspedonotus tibialis* Schaumann, *Solenopsis fugax* Latreiile and the larva of some Ellateridae. *Craspedonotus tibialis*, a species of the Carabid beetle, occurs abundantly in the sand plains of the *Bembix* settlement, especially when the activities of the wasp approaches to the end. This beetle is frequently found in the nest of the wasp, devouring the larva as well as the stored flies. But it is quite doubtful whether the beetle particularly searches for the nest of *Bembix* for the purpose of getting food. Judging from the usual behaviour of the beetle, its entry to the wasp's nest seems to occur rather accidentally. Probably the beetle penetrates in an incompletely closed nest only with the intention of getting its own lodge and happens to find the delicious food there.

Solenopsis fugax is a famous thief ant that lives in the walls of nests of other large species of ants. The ants invade very frequnently the nest of *Bembix*, dissect the larva and the victims found there and carry them away. When the mother wasp knows the depredation of the ants, she is used to repeat several times the going in and out and at last gives up the nest, without attempting to drive the enemies away.

The larva of Elateridae is known as phytophagous insect, giving a serious damage to the cultivation. I do not know as yet whether or not the larva actually devours the young of the wasp, or the stored flies in the nest. But I have frequently observed the nests in which a few victims and an attending larva of the beetle alone were found and no trace of the rightful owner was there. In the observation of nest No. 75, the mother wasp transported her larva into the narrow accessory branch when the brooc-cell was occupied by a larva of the Elatrid beetle invaded throgh the posterior wall of the cell. These observations seem to me to give an evidence that the beetle's larva may be a dangerous enemy to the wasp's offspring.

Among the predatory enemies of the mother *Bembix*, the most dreadful one is the large ant-lion, the larva of *Acanthaclisis japonica* MacLachlan. This larva, despite of the inhabitant in sand, has not the pit-forming habits. When full-grown it reaches more than 20 mm in length. It buries itself shallowly beneath the surface of the sand plain, leaving only its large powerfnl jaws protruding. When some insect comes near its hiding place, it suddenly springs out, rushes upon the insect, seizes it with the jaws and pulls it backwards into the ground. The prey that fall to the jaws of this large ant-lion are grasshoppers, crickets, locusts, flies, sand wasps, dragonflies and so on. When the game is poor, the larva appears on the surface of the ground and shifts its hiding place. In this case, it does not walk in a clumsy manner, as usually observed in other pit-forming relatives, but rushes forwards. But it can not rush to a large distance at a time, so that it advances by repeating rush and hiding alternately. Its rush is so quickly carried out that it appears to us only as a whitish shadow. Any insect that happensd to be caught by the powerful jaws of this larva is quickly killed, ususlly before being dragged into the ground. A short struggle and succeeding quiverings of wings and legs, that are all. Out of many that have been observed by me the only instance that could escape from the dreadful jaws of this larva is *Scolia tokioensis* Betrem, a robust hunting wasp that preys upon the grubs of beetles. Probably the hard armour of this wasp could resist the jaws of the enemy while it was fighting with it. *Bembix*, if caught unfortunately by this enemy would be killed rather instantaneously. A comparatively serious damage given dy this insect to *Bembix niponica* is due to the fact that the insect chooses its hiding place very frequently just in front of the wasp's nest. Probably it has a habit of selecting some elevatad place as its hiding place, owing to the instictive conjecture upon the fact that such a spot gives a favourable resting place to the flying insects. Unfortunately the nest of our *Bembix* has a heap of dirts in front of the entrance which she does not scatter away even after completing the burrowing.

Usually the wasp is attacked by the larva when she comes back carrying a booty from her foraging excursion and is about to clear the entrance. In such a case the first assault of the enemy is most dangerous. But once she can save herslf from the first attack, she becomes very cautious thereafter and usually can escape from the death. Even in such a fortunate case, however, she is very frightened and drops her booty from between her legs, which is captured at once by the ant-lion and dragged into the ground. In case the insect lies in ambush for the wasp some distance away from the entrance, the wasp can enter the nest with the prey. But she is assaulted at the time when she comes out backing with a load of sand and approaches the hiding place of the insect. But in such a case, the wasp is seldom captured by the larva, because she throws a mass of sand before her and it acts as a substitute for her. The ant-lion, however, if unable to get its food, sooner or later may shift its hiding place toward the entrance and come to attack the wasp at the very spot of the nest gate. After taking notice of the enemy hiding at the entrance, the behaviour of the wasp becomes very deliverate. She does not alight at once on the surface of the ground in front of the nest, but lengthened her hind legs downwards, only touching the surface with the tips, while she keeps her stationary flight in the air, with loud buszing sounds. If she is attacked at that moment, she draws her legs at once and flies away. But her affection for her nest soon brings her again to the nest. There she resumes the same fruitless manoeuvre. After repeating such an attempt sevearl times in vain, the wasp appears to become too eager to enter the nest. She dare alight some distance away from the entrance and approaches there sweeping the sand. Again she is attacked and flies up. At last she comes to attempt to enter the nest directly from in the air. But all her attempt ends in failure and eventually she drops her booty to the ground. It seems of interest that the ant-lion would not rush upon the wasp in such an occasion, but attacks her only with its mandibles, hiding itself in sand as if it knows the danger of the open fight with the wasp. But owing to such a reserved attack, the insect can acquire a paralyzed fly repeatedly a day. Probably this condition will be better for the larva than to kill a single wasp at a blow.

I once observed a wasp at 11 o'clock a. m. flying away in astonishment from in front of the entrance of her nest, leaving an *Eristalis* fly behind her. I dug there at once and found a large ant-lion, measuring more than 20 mm, with an *Eristalis cerealis* and a *Lucilia caesar*, already dragged in about it. The prey retained as yet the softness at the articulation of the legs, showing that they were robbed of in that morning. I replaced the larva alone to the original place. At 3 o'clock p. m. I examined there and found 2 *Eristalis ceralis*, 1 *Lucilia caesar* and 1 *Villa limbatus* thrown out on the ground, all having been sucked out the body juice. The larva was as yet hiding there, but not the wasp nor the fly has been dragged in about it.

As indicated well by the above instances, the wasp will not abandon her nest that has been occupied by the enemy at the doorway. She continues the empty attempt to enter the nest, and sometimes she succeeds in entering, probably at the time when the antlion is sucking the juice from a victim of which it has just previously deprived her. But in most cases, however, the battle comes to an end either by the nest abandoment on the part of the wasp or by her death.

As another predatory ememies of *Bembix niponica* have been known two robber-flies, namely *Promachus yezonicus* Bigot and *Ommatius chinensis* Fabricius. The latter insect, strange to say, is also observed to be a victim of the wasp.

19. Persistence to the nest.

How strong is the persistence of the wasp to her nest will easily be supposed from the description given above in connection with the ant-lion. Such a persistence can also be observed when we dig up a nest or we disturb the surface of the ground where the nest of a wasp has been concealed. The wasp, on coming back with a booty, begins at once to search for the entrance to her nest. She alights exactly in front of her missing nest and commences without hesitation to dig the sand. At first she digs the place without letting off the prey, but after several minutes' work, she drops it off from between her legs and devotes all her energies in digging and in searching. The patience shown in her work in such a case is quite astonishing. She countinues her digging work for 2 – 3 hours or more without taking a least recess during the time. If the work is much lengthened, she frequently stops her digging, flies up, circles round and dashes straight to the site of the nest, as if to ascertain the spot by passing through the familiar course that may be fixed in her memory. On arriving at the place the wasp at once recommences the digging work. Later, however, the site of her digging is, from time to time, changed slightly right and left, effecting a large shapeless hole there.

When only the surface condition of the place is disturbed, the work of 5 – 10 minutes is sufficient to discover the missing tunnel. But even in such a case, the fly which has been dropped from between her legs during the course of her work, is mostly abandoned. She treats it as if it were a pebble and drags it away from the entrance of her nest to throw off. But rarely when the continuity of the tunnel is comparatively promptly discovered, she utilizes again the fly which is found from in the dirts during her work of sweeping and arranging in front of the entrance. But such an occurrence is rather exceptional.

The following instances will indicate well the astonishing persistence of the wasp to her nest :

1) Sept. 8, 1946. A wasp (No. 17) came back to her nest with the first prey at 1. 30 p. m. Ten minutes later another wasp (No. 19) returned with the second victim to her nest which was situated 50 cm away from that of No. 17. The nests of both wasps had been dug up by me and the surface had been evenly pressed. The nest of No. 17 was empty and that of No. 19 contained the 2nd instar larva within. Both wasps began at once to search for the nests. They continued their work of digging for one hour without taking a least recess, when I left the place. At 3. 20 p. m. I returned to the place and found No. 19 still continuing her work, but No. 17 was already absent. I don't know the end of her work, because I left the place again at once.

2) Sept. 7, 1947. At 12. 00, I found a wasp (No. 73) searching for her nest, the surface of which had been disturbed by my food-prints. It was supposed that she had been working for a considerable time, judging from the amount of sand dug out. I dug the place myself and found the tunnel. I left it opened at the bottom of a small hollow that I made. But the wasp could not find the entrance, probably on account of the difference of the surrounding condition resulted by my digging. She tried to dig only the flat place close to the hollow and continued her work till 2. 40 p. m., when she happened to find the entrance. In the brood-cell was a larva of the first instar.

3) Sept. 3, 1947. The surface of the nest of a wasp (No. 66) was seriously disturbed by the trample of the cattle. At about 2 p. m. when I found the wasp, she had already dug out a considerable amount of sand. At 5. 30 p. m. She dug 3 holes there and still continued her work. The next day, at 10. 30 a. m., I found the wasp still working at the place. As the hole she made was by far the larger than in the previous day, she was supposed to have worked for a long time on that morning. How and where she passed the night was unknown. At 11. 25, the wasp was observed still continuing the digging work. But 5 minutes later she was absent. I thought that she gave up her nest. However, at noon I was greatly surprised to find the wasp returned and digging there. How long did she continue her work thereafter, I do not know. But at 5 p. m. when I took notice of her, she had been already absent.

4) Sept. 6, 1949. At 9 a. m. a wasp (No. 166) was searching for her missing nest, the surface of which was disturbed by the trample of the passers-bye. She continued her work till about 11 a. m. and at last succeeded in finding it out. The next day, when I arrived at the place at 9 a. m., the surface of her nest had been heavily disordered by the passage of a wagon and the wasp was eagerly searching for her nest. At about noon when I payed my attention to her, she was still digging the ground. At 2 p. m. I found her coming back with a prey. The entrance of her nest was opened at the bottom of a fairly large hollow. The nest contained a larva of the middle stage of the final instar.

Generally speaking, the nest that contains an egg inside appears to be abandoned comparatively easily, but that which has a larva in it seems to give a strong persistence to the mother wasp. At any rate it is a great surprise to us that the wasp can continue that hard work of digging for so long a time without taking a least recess.

20. Terminal phase of the activities of the wasps

The end of the *Bembix*' activities comes in Hokkaido usually late in September.

The observation made in those days upon the last scene of the wasp's colony can be summarized as follows :

1) The number of the wasp working on the settlement diminishes day by day, but those remaine still continue their work, ·digging their burrows or carrying in their booties. Their activities, however, are confined to the warmer hours of the day.

2) Excepting for a short while of the out-door activities, the wasps are used to pass the greater part of the day in their nests, sitting either in front of the partition wall of the brood-cell or in the accessory branch of the tunnel. When dug out of their burrows, they cannot fly up at once, probably owing to the coldness of the interior of the nest.

3) These wasps, if dissected, always bear in their ovaries two maturated eggs. showing that they are able to continue their work if the climatic condition alone is favourabie.

4) Occasionally a dead wasp is found in the nest, sometimes sitting as if she were alive in front of the cell, someimes already decomposed into small fragments in the accessory branch; while in the former case, the larva is used to be still living in the cell.

5) Even in case the wasp is still continuing her feeding activities, the victims supplied to the larva in a day greatly diminish in number, at most 2 – 3 for the fourth instar larva.

6) At that time the development of the larva is markedly delayed. The egg can not hatch till about 5 – 6 days after being deposited.

7) Those nests in which the mother wasps are already dead or those to which the mother wasps do not return forever increase day after day. In such nests the prey stored are mostly rotten, while the larva or the egg is still living. The former when it is in the 4th instar, approaches the entrance of the cell, lifting its anterior body and drooping its head and remains quietly as if it were waiting for the mother wasp to bring to it a fresh vicitm to eat. But in these nests, the wasps are supposed to be already dead at some cerner in the field.

III. NOTES AND CONSIDERATIONS ON THE SPECIAL PROBLEMS CONCERNING THE BIOLOGY.

1. Biological significance of the accessory branch of the tunnel.

At the time when I was investigating the habits of this wasp in the suburbs of Chiba and Utsunomiya, I did not take special care of the significance of the accessory branch of the main tunnel. I thought it to be merely the beginning of the next cell. In fact in those nests which belonged to the compound type in structure it was surely the beginning of the next cell. But when I found the same structure in a great number of the nest of the simple type in the suburbs of Sapporo, I took notice for the first time whether it had some biological significance for the life of the wasp.

So I began to pay a special attention to the detailed conditions of the accessory branch and obtained the following results :

a) *Frequency of its occurrence.* Out of 143 nests which were specially examined on this point, 65 were provided with the branch (Table 16).

b) *Its situation.* Out of the 65 nests 41 were the instances in which the branch was made just or only slightly in front of the brood-chamber. While in the remainder it was burrowed 10 – 18 cm away in front of the cell. In both cases the partition wall of the brood-cell was always constructed in the main tunnel just behind the forking point of the accessory branch. In rare occasions the tunnel is closed with the tampon of sand not only at the forking point but also just in front of the brood-cell. A remarkable fact is that in most of the cases wherein the closure of the brood-cell is not constructed just in front of the cell, but away from it at the forking point of the accessory branch, the main tunnel leading to the larval chamber is turned or curved laterally from the forking point of the branch, and the branch itself forms the apical portion of the first straight part of the main tunnel. The same tendency is observed in the other case in which the brood-cell is situated just behind the forking point of the accessory branch.

c) *Time of its construction.* Table 16 shows the relationship between the existence of the accessory branch and the developmental degree of the larva. Judging by the evidences it is presumable that the accessory branch is usually dug soon after

Table 16. Relationship between the larval development and the presence of the accessory branch.

Larval development / Accessory branch	Empty	Egg	The 1st instar	The 2nd instar	The 3rd instar	The 4th instar	Cocoon	?	Total
Present	2	25	4	4	5	18	2	5	65
Absent	10	2	4	3	11	41	5	2	78
?	2	2	2	3	4	19	12	26	70
Total	14	29	10	10	20	78	19	33	213

Remarks. The ? in the column of Accessory branch stands for those instance to which no special attention was paid, but which seems highly probbably to be ones that have not the accessory branch.

the egg is deposited in the cell*. Two exceptional cases are shown in the table in the columun of the empty cell. But one is an instance which was observed late in the season when the wasp became inactive and prefered to pass the warm hours of the day in digging the tunnel rather than in hunting the prey. The other was found in a compound nest. The branch was near the end of a newly burrowed tunnel, the end of which was not formed yet into a cell. At that time the wasp was still engaging in her provisioning activities of the previous cell and the accessory branch

* It will be necessary to note here that the accessory branch is not effected casually by the removal of sand, in order to close the entrance of the cell. Because, if so, the branch must be made reverse in its direction.

in question, only 2 cm in length, was located 1 cm in front of the bottom of the tunnel. The previous day was cloudy and it was supposed that the wasp dug the new tunnel during her residence in the nest, prior to the completion of the previous cell. When such conditions are taken into consideration, it seems better to treat such instances as exceptions.

d) *Retention of the branch.* It is naturally supposed that the accessory branch, because of its situation in the tunnel, will easily be filled with sand every time when the wasp opens or closes the partition wall of the brood-chamber, especially when it is directed obliquely downwards. In reality, however, in a considerable percentage of the nests, the accessory branch is distinctly observed, sometimes even in the nests which contain the 4th instar larva inside. The fact indicates that the wasp must do a special work to keep the branch at the proper place and in the favourable form. Indeed, I often saw the wasp carry out the debris eagerly from the burrow just before she closed the entrance to start off on the next hunting excursion, or in the late afternoon when her activity of the day was already over. Probably she was working to reconstruct the accessory branch that might be filled with sand during her preceding activity.

e) *Relative decrease of its occurrence in the nests containing the 4th instar larva or the cocoon.* Table 16 distinctly indicates the presence of a relationship here mentioned. The wasp, when her larva grows larger, may lose her interest in reconstructing the accessory branch. The branches found in the nests wherein the 4th instar larva is present are usually shallower than usual. Moreover, in the nests of similar condition but not bearing the accessory branch, I often found a trace of the branch which was filled loosely with sand. Still further, I found occasionally a slight depression in the tunnel at the very spot where the accessory branch was usually located. Judging from these instances it seems probable that the branch is, as a rule, always present at the start of brood-rearing, but later when the larva grows large, it becomes to disappear in the course of the activity of the wasp. In the present state of the evolution of the wasp's habits, however, exceptions against this rule are not always few.

f) *Its actual utilization by the wasp.* When the nest is provided with the accessory branch, the wasp when in the nest without work is used to rest in this cavity, directing her head forwards. In case the wasp makes a second cell in the same nest, she always utilizes this accessory branch as the beginning of the new tunnel.

Among the accounts given above, the last stated shows one of the biological significance of the accessory branch; namely it serves as a sitting room for the wasp during her stay in the nest. Furthermore, the accounts (**c**) and (**e**) seem to have a suggestion that it may be especially useful for the wasp during the period when the nest contains an egg or a young larva inside. According to these informations the accessory branch is regarded to have a significance as a sitting room of the wasp during the period when she stays in the nest in order to wait for the hatching of her egg or to guard her helpless young. On the other hand, if such is the only significance of its occurrence, the benefit conferred upon the wasp from the accessory branch seems to be too slight. Because, the main tunnel will sufficiently fulfill the purpose of such a sort. At this point, the account (**b**) seems to me to give another suggestion. That is to say, the branch may be of great use for misleading the invading enemy from the true brood-cell, while the wasp is out of her nest. This suggestion is strongly supported by human experience when one digs the nest of this wasp that is provided with the accessory branch. Probably such a carnivorous intruder as *Craspedonotus tibialis* that happens to invade the nest of the wasp will return in vain from the bottom of the branch. Moreover, even if the beetle may try to dig the bottom for its own use, the larva which lives in another direction can remain without peril. According to this consideration, the utilization of the accessory branch by the wasp as her sitting cavity or as the beginning to her next cell comes to possess the secondary significance only. However, no matter what may be the significance of this curious accessory branch, it will safely be said that it has by no means the significance of primary importance for the life of the wasp, since, speaking in general, the nests without it can protect as safely the offspring as those with it.

On the other hand, as the accessory branch is very variable not only in its occurrence, but also, when occurs, in its position, in its direction as well as in the periods of its retention, the habits of making this curious branch-tunnel seem to represent the first step of the evolution of a instinct, not showing as yet the definite inclination of promotion, but merely exhibting the plastic variation. If any change in the environmental conditions of the wasp will give the existence of this accessory branch any important significance for the life of the wasp, then the presence or the absence of the branch will become a factor of the natural selection.

2. Biological significance of the manipulation conduncted upon the egg-supporting fly.

As mentioned in the previous chapter, our species has the same habits as shown by most of the members of the genus in executing a special manipulation on the first victim she captures, prior to the deposition of her egg. The wasp dislocates not only one of the wings of the fly to make it half open, but also one of the front and mid pair of legs of the same side. Now, what significance have these conducts of the wasp for the life of her larva? It has generally been considered that the dislocation of a wing is a device of Nature for the maintenance of the Diptera in an equilibrium, preventing the fly from being turned over by the very delicate young larva and thus insuring it against the injurious contact with the rough, sandy floor of the cell. As for the luxation of a mid leg, Ferton who for the first time observed the phenomenon regarded that the manipulation was a contrivance for preventing the luxated wing from returning to its original position, since the mid leg was firmly stretched and placed to press tightly the dislocated wing from above. His consideration has also been widely admitted. However, in this point it seems to me that the problem is still open to discussion, since the pressing of the wing is not so usual occurrence as in the wing dislocation. In my observation described previously such a phenomenon is confirmed in only 13 instances out of 21. The result seems to permit the introduction of another interpretation, that is to say, an interpretation that takes the manipulation as a natural device for pushing aside permanently the leg that will otherwise be a hindrance to the act of oviposition and also to the maintenance of the normal position of the egg. But the cases wherein the luxated leg is so located as to press the posterior border of the half-opened wing is too curious to be attributed to the casual happenings. Therefore, we may be better to consider it a habit that has the significance as Ferton speculated, but at the same time that is not so fixed as that which concerns with the wing.

In addition to the above, the states of the pedestal fly show that another interesting manipulation must be performed by the wasp. Because, it is lying usually killed or neraly killed*, though it is doubtlessly alive when it has been carried to the entrance of the nest. The reason for this operation seems to be to secure the perfect motionless state of the pedestal-fly, since, a movement of the pedestal insect will exert a decisive influence on the delicate procedure of the hatching of the egg.

It seems interesting that the wing and the leg of the same side are always selected by the wasp to be manipulated and that the egg is infallibly deposited on the base of that luxated wing.

3. Problem concerning the victim

a) *Is the small victim specially selected for the pedestal of the egg ?* According to the previous informations made by a number of authors on many other species of *Bembix*, it is generally admitted that the small fly is especially selected by the wasp for the pedestal of the egg. The first advocate for this habits of *Bembix* is J. H. Fabre. He accounted for the phenomenon as follows : (1) The prey captured by the wasp are (believed erroneously (?) by him to be) killed**. So that if a large fly is suplied to the egg it will become rotten before the hatching larva eats it up, because

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* Parker (1917) reported the following observations : "I carefully removed the fly and egg from the nest and placed them in a breeding cell in the basement of my house (on June, 13). The egg of the wasp (*Bembix spinolae*) did not hatch until on June 20 ··· the larva died on June 21. On 23 I removed the dead larva and pinned the fly. This fly was not dead at the time it was pinned and even after the pin had been thrust through the thorax it continued to move its antennae and its legs. In this case a fly paralyzed by the wasp lived for 10 days and might have lived longer, had I not killed it".

According to this description, *B. spinolae* seems to be different from *niponica* in reference to the manipulation carried out upon the pedestal fly.

** Fabre may generalize the result of his observation on the state of the pedestal fly upon other victims.

the large victim will need a longer period of time to be eaten up than the small one. (2) Generally speaking, a small fly has the softer body than the large one; accordingly it will better fit for the powerless jaws of the young larva.

The first account of his consideration is believed by most present-day investigators to have lost its basis, since the prey captured by his *Bembix* are found only paralysed instead of killed*. On the other hand, his second account seems to be widely admitted even in the present day, because the first victim that is captured by the wasp is believed to be smaller than others.

Apart from the first question regarding the states of victims, can we generally admit the account which forms the basis of these speculations ? Does the wasp select in reality the smaller victim for the pedestal of her egg ? Or, if so, how far her selection goes ? Observations hitherto reported seem to me rather inadequate on these detailed points. Accordingly, before entering upon the criticism on the prevailing opinion, we must faithfully reexamine the phenomenon and collect the reliable data concerning the subject.

Up to the present, 74 instances of the pedestal fly to which the offspring of the wasp, may it be an egg or a young larva, as yet attached have been observed by me. The species of the flies arranged in order of their body-size** and each total number are as shown in Table 17. Besides the directly observed ones above listed, 13 instances examined in the suburbs of Chiba in which the prey consisted of a single species (*Stratiomyia japonica*) give us furthur data. The number including these data was shown in the above table within parenthesis.

Now, if these species are divided into two groups of different body-size under the consideration on the usual food of the larval wasp (*vide* Table 3), Nos. 1 – 7*** shown in the table may be grouped into the large class and the remainder into the small one. The ratio between the total number of both classes comes to be 39 (59) : 35. Again if these species are divided into two groups according to the softness of the body, species 1 – 10a will fall in the hard group and the others in the soft one.

* This reason may not probably be applied to the Fabre's case in reality. At least it is unable to apply to our *Bembix*. Because, apart from other flies, the pedestal fly is killed or very weakened in our species (and probably in Fabre's species also). At least it becomes invariably dead by the time when the egg hatches out. Accordingly the question regarding the putrefaction or the deccication must be inevitably taken up. But, in reality, such a question has nothing to do with the life of the larval wasp, since the first fly is formally only a pedestal for the egg and not necessarily the first food for the larva. The detailed account concerning the problem will be treated in the subsequent section.

** In the strict sense, it is very artificial, because, each species treated here varies to a considerable extent in size.

***Fabre counted *Eristalis* as a small fly, but judging from the usual food of the larval wasp such a treatment seems to be unfair, at least in our species. The insects belonging to this genus bear a comparatively hard integument of the body and therefore, their thoracic sclerites always remain uneaen.

The ratio between such two groups comes to be 45 (58) : 29. Thus, the abolute ratios between such groups come, in both cases, to be entirely contrary to the general opinion of the previous observers. The results are sufficient enough to put aside

Table 17. Comparison of the size (represented by species) between the pedestal-flies and the general victims.

No.	Species	Size	Number in Pedestal		Number in general victims	
1	*Eristalomyia tenax*	large spp.	2		65	
2	*Stratiomyia japonica*		7 (20)		263	
3	*Tabanus mandarinus*		2		143	
4	*Villa limbatus*		1	39	83	1930
5	*Eristalis cerealis*		25	(52)	718	
6	*Ochrops fulvus*		1		99	
7	*Chrysotoxum japonicum*		1		19	
8	*Syrphus ribesii*	small spp.	1		3	
9	*Chrysozona tristis*		2		21	
10a	*Eristallinus sepulchralis*		3		99	
10	Ragionidae sp.		1		4	
10	*Sarcophaga carnaria* + spp.		15	35	162	636
10	*Lucilia caesar* + spp.		7		284	
10	Muscidae spp.		1		34	
11	*Musca domestica*		2		8	
11	*Theloria leucozona*		1		3	
11	Anthomyidae spp.		2		18	
	Total		74 (87)		2026	

any theory based upon such an erroneous imagination. However, these results do not give any evidence for themselves to deny a tendency of the selection made on the part of the wasp upon the pedestal-flies. Because, if we want to examine whether or not such a selection is made by the wasp, we must compare the ratio with that which is obtained from the total number of the victims of *B. niponica*. Now, if we try to make such groups with our material, the group with large-sized flies comes to contain 1390 individuals and the group with smaller flies 634 individuals, as shown in the right-hand column of the above table. Thus, the ratio between the large groups of the pedestal and of the total flies comes to 52 : 1930 (≒ 1 : 37), while the ratio between the small groups is 35 : 639 (≒ 1 : 18). In a rough calculation the ratio between the two results is 1 : 2. It means that the wasp captures small flies for the pedestal of the egg with the ratio of twice as large in number as the general victims. In other words, the selection percentage of the wasp for small flies in reference to the egg's pedestal comes to 67 %.

The above results were obtained from the whole data up to 1949 collected by me. But if they are separately examined according to the district they derived, we can find some interesting differences among them. Now, if we confine our data to those obtained in the suburbs of Sapporo, the ratio between the large groups of the pedestal and of the total victims comes to 28 : 1126, while that between the small groups 30 : 560, accordingly the selection percentage for small flies with regard to the pedestal of the egg is 69 %. On the other hand, if we confine our calculation to the data from Chiba alone, the percentage comes to 57 %. In conclusion we can say as follows :

i) The wasp prefers certainly the small flies for the first victim, the pedestal for her egg, in comparison with the general victims. But the selection percentage is comparatively low, only 67 % in general. It varies from 57 to 69 % according to the district of observation.

ii) But in the absolute number of the pedestal flies the percentage occupied by the large flies is distinctly larger than that by the small flies (63%).

iii) Any critical theory based on the conception that the pedestal fly is particularly small in size and has, accordingly, a soft body must be discarded by the actual data mentioned above.

iv) The fact (i) seems to show a tendency of such selection on the part of the wasp. But at least in the present stage of its development, it can not be considered to have any important significance for the life of the larval wasp.

b) *Does the wasp bring particularly small victims to her young larva* ? In connection with the accounts given above, it is also generally admitted that the Bembicine wasps bring to their young larvae comparatively small victims. In order to examine such a prevailing opinion, I have tried to compare the first three flies* brought by the wasp with the remaining victims. The data were collected from the actual observation of the cells containing a young larva inside, as well as from the presumation based upon the states of eaten victims or upon the arrangement condition of them in the cells of the 4th instar larvae. The species of such victims and each number are as shown in Table 18.

According to the table, the preference percentage of the wasp for the small flies to make them as food for the young larvae is $\left\{\frac{105}{671} \div \left(\frac{198}{1431} + \frac{105}{671}\right)\right\} \times 100 \fallingdotseq 53$ %. If the data obtained in the suburbs of Chiba are omitted, the percentage comes to 61 %, while those from Chiba are too small in number to draw any reliable conclusion from them.

According to the evidences, the matter is much more obscure than in the case of the pedestal fly, namely that the wasp seems to have a slight tendency of selecting small victims as food for her young larva, but the preference percentage is so small that it seems hardly to merit any special mention. Moreover, in the absolute number of the first three victims the percentage occupied by the large-sized flies attains 65 % of all. So that the same conclusions as drawn from the previous case can also be applied here.

* *Vide* Table 11.

Table 18. Comparison of the size (represened by species) between the first 3 victims and the general victms.

No.	Species	Number in the first 3 prey		Numper in general prey	
1	*Eristalomyia tenax*	6		65	
2	*Stratiomyia japonica*	56		263	
3	*Tabanus mandarinus*	7		143	
4	*Villa limbatus*	3		83	
5	*Eristalis cerealis*	80		718	
6	*Ochrops fulvus*	19	198	99	1431
7	*Ochrops bivittatus*	1		8	
8	*Gymnochaeta elegans*	2		9	
9	*Calliphora erythrocephala*	1		22	
10	*Chrysotoxum japonicum*	2		19	
11	*Chrysotoxum festivum*	1		2	
12	*Eristallinus sepulchralis*	7		99	
13	*Syrphus ribesii*	1		3	
14	*Chrysozona tristis*	5		21	
15	Rhagionidae spp.	2		3	
16	*Sarcophaga carnaria* + spp.	35		162	
17	*Lucilia caesar* + spp.	28		284	
18	Muscidae spp.	3	105	34	671
19	Anthomyiidae spp.	4		18	
20	Tachinidae (small) spp.	4		23	
21	*Chrysops suavis*	1		8	
22	*Musca domestica*	3		8	
23	*Syrphus corollae*	1		3	
24	Pipunculidae sp.	1		5	

The investigations made here in detail regarding the characters of the victims that are brought to the young larva as well as to the egg reveal that the prevailing opinion concerning the selection of prey by the mother wasp in accordance with the growth of her offspring is too much exagerated to be admitted unconditionally. Of course, the results here stated were obtained with *Bembix niponica* Smith and not with others. But, if the special care is taken in the observations on other species of *Bembix*, it seems highly probable that the same relationship is found in most of the foreign relatives hitherto investigated.

Now, why is such an exagerated opinion supported by many authors ? The first reason seems to me to lie in their negligence of observations on the victims that are supplied by the wasp to the developed larvae. The Bembicine wasps, so far as my investigations go, are used to bring to their developed larvae not only the large flies but also nearly as many small ones. The second reason may be the inproper classification of the large and small groups of the victims, basing probably on the lack of the rightful survey on the general victims of the species concerned, or basing on the incorrect preconception. For instance, if we put *Eristalis cerealis* into the small group, the selection percentage of the wasp for the small victims will become by far the larger. But such a division of size of victims is certainly unfair. If we take into consideration the general victims captured by the wasp, the relation will easily be recognized. Moreover, small victims are meant by those authorities to be soft and easily eatable. But *Eristalis* is not flies that bear the soft and easily breakable sclerite. For the third reason we can give 'the hasty conclusion'. The ratio of 2 : 1 (not in absolute number, but in comparative value against total victims)m ay allow the observations made on a few instance the chance that appears to show the perfect dominance of the small flies in some case. The fourth reason may be the apparent rationality of the reasons given to that opinion.

However, the essential fact against the opinion of Fabre and his followers is that the young larvae of the Bembicine wasps are able to eat the insects bearing harder sclerites than were supposed. Because, they have not only more powerful mandibles than hitherto postulated, but also a special technic of eating; namely, gnawing off the head of the victim first and then eating into the thorax from the wound. Besides, the larva, when the bodily part of the victim on which its mandibles happen to touch is too hard to rip open, does not continue to attack the place in vain, but shifts its mouthparts to another less hard portion, since the body of the fly has not the uniform hardness on all parts. Furthermore, the mother wasp always brings several fresh flies by the side of her larva, giving it a chance of selection of the suitable food. The reason why no difficulty can occur even when the first victim becomes rotten or it is too hard to eat lies chiefly in this fact. It will easily be understood from the following accounts.

c) *What is the victim first eaten by the young larva ?* The prevailing view that a small fly is specially selected for the pedestal of the wasp's egg seems to be based on the assumption that it is undoubtedly first eaten by the hatching larva. This assumption, however, can not be accepted without question. Because : 1) As described previously, the egg of *Bembix* is not fixed with its cephalic pole to the body of the pedestal insect. When hatches out, the larva stands upright, so that it must lean over the near-bye victim to begin to eat. The mouthparts of the hatching larva, however, is not always directed towards the pedestal-insect (p. 103). In such a case it will begin to eat whatever victim that comes to touch its jaws. In addition to the above, even when the hatching larva normally faces the pedestal-insect, if the latter is too small in size, the mouth of the young larva will fall upon the next victim across the thorax of the pedestal insect. Through the irony of chance, the smaller is the pedestal, the larger will be the chance of such a sort. 2) As stated also previously, the pedestal-fly is completely or nearly completely killed in our species. Such an insect, according to the conditions of the time, will promptly either decompose or deccicate and soon become unsuitable as food for the larva. In such a case, the larva will search for the eatable victim near-by and commence to eat any other fly than the pedestal. 3) The young larva, though it is attached to the pedestal with its caudal end, is able to alter its bodily orientation so as to reach the favourable food supplied around it, and the mother wasp always brings a second victim to the side of the pedestal, as if she were expecting the larva to eat the victim thus brought in anew.

These are the reasons for my question. As for the first reason described above, literature furnishes us an evidence for this. It is the observation made on a European species (*B. inimica*) by C. Ferton in Corse in 1911. He describes as follows : "Or il a deux petits mouches à sa disposition, et contraiement à tout ce qui j'avais vu jusqu'ici, il ne commence pas son repas par cell sur laquelle il a été pondu. Celle-ci, (*Geron gibbous* Meig. ♂) est exceptionnellement petite (3.25 mm de longeur, 1 mm de largeur au thorax); moin pesante que l'oeuf, qui était peut-être en outre dan une position défectueuse, elle n'a pu maintenir son fardeau en équilibre et a basculé. La mère *Bembex* a paré à cet accident en apportant une seconde mouche (*Geron gibbosus* ♀), qu'elle a placée prés de la première, de facon à ce que la larve, en s'affaissant du côté opposé au diptère qui la profait, vienne rencontre cette nouvelle proie ···" According to this description, Ferton appears to consider the phenomenon to be a quite exceptional instance caused by the very small size of the pedestal fly. Moreover, he seems to be of opinion that the presence of the 2nd fly by the side of the pedestal depends merely upon the fact that the accident was noticed by the mother wasp. My observation on our species, however, confirms that both phenomena are never exceptional- nor unusual behaviour of the mother wasp as stated below. As for the second and the third reasons no definite support is furnished from literature, though judging from the accounts given by some authors pertaining the states of the pedestal-fly and the situation occupied by the second victim, such cases seem very probable in some species of *Bembix*.

On the other hand, another case that completely denies the feeding of the hatching larva upon the first (= pedestal) fly is recorded by J. B. Parker on an American species (*B. spinolae*). But his instance will be better to be avoided here, because it depends entirely upon the very peculiar manner of eating on the part of the larval wasp, of which nothing similarity is observed in our wasp.

In order to ascertain the above mantioned phenomena, a special attention has been paid by me on the victim that is first eaten by the hatching larva. Thirty seven instances have been accumulated up to the present in which a young larva attaches as yet to the pedestal-fly. Among them 20 larvae are found either feeding upon the pedestal-fly or fed it first*. While in the remaining 17 instances, the victim that has been first eaten by the larva was not the pedestal fly. It is as shown in table 19.

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* The species of the pedestals and their frequency are as follows : *Musca domestica* 1, *Sarcophaga carnaria* 3, Rhagionidae sp. 1, Anthomyidae spp. 2, *Eristallinus sepulchralis* 1, *Eristalis cerealis* 10, *Villa limbatus* 1, *Eristalomyia tenax* 1. These instances will give unquestionable evidences for the fact that the power of the jaws of young larvae is by far the stronger than has bas been supposed.

Table 19. Instances in which the hatching larva first ate other fly than the pedestal.

No. of wasp	Larval instar	Species of pedestal	Remarks
5	4. 1/10	*Sarcophaga carnaria*	The pedestal (P) is rotten, covered already with mould. The larva (L) has eaten the 2nd victim (V), *S. carnaria* and is eating the 3rd victim, *Chrysozona tristis*.
16	2. -	*Eristalis cerealis*	P is discarded after being decapitated. L is eating a 2nd V (*Calliphora erythrocephala*) which is much harder and larger than P.
27	1. -	*Eristalis cerealis*	L has not begun to eat yet, but P is already covered with mould.
67	4. 2/10	*Cchrops fulvus*	P has only been gnawed. L is now eating the 3rd V (*Lucilia caesar*) across the 2nd V (*Chrysozona tristis*).
73	1. -	*Sarcophaga carnaria*	L has just begun to feed on the next V (*S. carnaria*), across the thorax of the pedestal itself.
83	3. -	*Eristalis cerealis*	P has only been decapitated and discarded. L is eating the 2nd V (*Ochrops fulvus !*) lying opposite side to L.
86	3. -	*Tabanus mandarinus*	L is eating the 2nd V (*Sarcophaga carnaria*) laid down on the opposite side to L.
93	1. -	*Sarcophaga melanura*	L has not begun to eat. But. it is facing opposite to P.
94	4. 1/10	*Lucilia caesar*	L is eating the 2nd V (*Lucilia* sp.), across the thorax of P.
114	1.	*Sarcophaga carnaria*	P is rotten. The 2nd V (*Lucilia caesar*) is placed by the side of P. L has not begun to eat yet.
123	4. 1/10	*Sarcophaga carnaria*	P is covered with mould. L gnawed the 2nd V (*Eristalis cerealis*) a little and is now eating the 3rd V (*Lucilia caesar*).
126	4. 2/10	*Eristalis cerealis*	L faces outwards and is eating the 2nd V (*Eristalis cerealis*).
127	3. -	*Eristallinns sepulchralis*	P is already musty. L is eating the next V (*Eristallinus sepulchralis*).
130	4. 1/10	*Sarcophaga carnaria*	L is eating the 2nd V (*Eristalis cerealis*) having the harder integument than P.
131	4. 1/10	*Musca domestica*	L is eating the 2nd V (*Sarcophaga* sp.). P has been discarded after being eaten a little.
142	3. -	*Eristalis cerealis*	L is eating the 2nd V (*Eristalis cerealis*), after gnawing P a little.
156	3. -	*Eristalis cerealis*	P is already musty. L is eatiug another *Eristalis* placed next to P.

The result makes it clear that in nearly a half of the instances observed the victims that were actually eaten first by the larvae were not the pedestal flies. The fact will give a sufficient proof to my presumed considerations. Moreover, it will also be accepted from the above data that the pedestal-flies are rather unsuitable for the larval food. Because, they are dead and are very likely to be rotten or to be desiccated promptly. Actual evidences for this are obtained from instance Nos. 5, 114, 123, 127 and 156 of the above table, wherein the pedestal flies have already been rotten and sometimes covered with mould. In addition to the above, observations that the young larvae would very frequently discard the pedestal flies after feeding very little of them seem to indicate that they have already been putrefied or desiccated and have become unfavourable as food for the larvae. The habit of the mother wasp to bring a second victim near-bye the pedestal fly by the time when the egg is about to hatch appears to have a certain connection with the fact that the first fly is killed.

Then, how should we account for the problem regarding the pedestal fly ? It has a tendency to be small in size; it is usually completely or nearly completely killed; it is dislocated at the base of one of the wings and also one or two of the legs on the same side as the egg is deposited. Before entering this problem, however, I must make some considerations on the interesting report made by J. B. Parker concerning the feeding habits of the newly hatched larva of *B. spinolae* and others.

d) *Notes on the Parker's report concerning the feeding method of the young larva.* J. B. Parker published a very interesting account on the larval locomotion in connection with the eating manner of young larvae of *B. spinolae* Lepeletier and *Bicyrtes ventralis* Say in 1917, which is as follows : "No more flies are placed in the nest until the larva emerges from the egg, which usually occurs at the expiration of one or two days after its deposition. The young larva does not leave the egg, but moves upward to the open end of the eggshell to which its posterior end remains attached. From this vantage point it can reach with its head to considerable distance on all sides. In no case observed did the larval wasp devour the fly on which the egg was placed. To do so would deprive the young larva of the advantage it enjoys in the position it occupies — a position that appears to be essential to its feeding upon the food provided by the mother wasp at this time. In no case did I succeed in rearing in my breeding cells a larva that was accidentally detached when small from the fly on which the egg was placed. — "

This account makes us remember the similar observation made by J. H. Fabre with regard to the young larva of a potter wasp, *Eumenes pomiformis* Fabr. In this case the egg is hung from the ceiling of a pot with its end-string. It is believed by Fabre that the hatched larva moves down to the cephalic end of the eggshell and remaining with its posterior end attached thereto reaches the food piled up below in the pot. Fabre says that in case the disturbance occurs among the half-paralysed caterpillars the larva draws itself promptly into the eggshell and thus makes use of it as a refuge for safety. But the same observation could not be repeated by any of the later investigators. Ferton, depending on his own observations, first published his mistrust on this phenomenon. I myself examined the nests of many species of Eumenidae occurring in my country, but in no case have I succeeded in corroborating the similar manoeuvre of the larval wasps. In my observations, as in those of Ferton, the larva slips out of the eggshell as soon as it hatches out and lying on top of the pile of the caterpillars, baldly sucks the juice of a victim nearbye one after the other. In many occasions, as described by Ferton, the caterpillars are packed in so much in amount that the suspending egg is pushed up on top of the pile of victims, so that any advantage whatever can be drawn from utilizing the eggshell as a refuge. Nevertheless, the larva devours the victims one by one and grows in safety. Moreover, even when the egg is detached from the ceiling of the pot and is placed on or amid the caterpillars, it can safely pass through its development.

Things are thus in the case of the potter-wasp. But, of course, the fact ascertained upon the potter-wasps can not be applied unconditionally to the case of another wasp with different habits and of the different pedigree. But it may serve as a sort of reference at least.

In our species of *Bembix*, as given previously, the larvae, in most cases, do not leave the pedestal-flies until the time of completion of their moults. Only rarely the larva of the 3rd instar is found leaving the foothold on the pedestal. The young larvae of *niponica*, attaching to their natural position on the pedestal, bear invariably the shed skins at their caudal ends. Probably the eggshell, too, will be included in that shrinkled substance. But in no case have I found the larva at the top of the empty eggshell, remaining with its caudal end attached thereto and feeding on a victim that is placed some distance away from the pedestal. Parker considered this situation of the larva "the vantage point". But the reason for what purpose it is vantage he did not give. If it is only for the benefit of obtaining much food from a distance, it must be a nonsensical device, since the food taken by the young larva is very little in quantity and a victim or two will be sufficient for the purpose. Moreover, even if the pedestal-fly is unfavourable for the larval food, the larva need not search for it for itself, because the mother wasp, in case of necessity, will bring a fresh victim at once by the side of the larva. When cosidered thus upon our *Bembix*, no advantage whatever can be supposed with regard to such behaviour of the larval wasp.

But, of course, our wasp is not *spinolae* and the fact that our larval wasp has not such a habit is not a positive proof that *spinolae* has not likewise. At any rate and at least in our species the newly hatched larva does not make use of the moulted eggshell as a tether of itself. However, it keeps its original position on the pedestal, attaching to the base of a wing with its posterior end till the completion of its larval moults, that is to say till it attains the final instar of the larval life. The reason for such an attachment appears to be to ensure the solid support necessary for shedding the skins. Thus, our wasp in the early stage of its larval life enjoys the same degree of advantage as in *spinolae* without making use of its eggshell. And it seems quite needless to utilize the eggshell if only the solid support for the moult is requested.

4. Considerations on the problem regarding the first victim of the wasp

The wasps bearing an instinct similar to the Genus *Bembix* in relation to the manner of oviposition are those which belong to the Nyssoninae Tribes Stizini and Bembicini*. The egg of these wasps is, without exception, attached to the pedestal with its posterior end and stands upright. Among them those which are grouped into the most advanced form from the ethological point of view, are, so far as is known, *Bembix olivacea* Vyrillo (= *mediterranea* Handlirsch and auctt), *B. brullei* Guer., *Stictia carolina* (Fabr.) (= *Monedula carolina* Drury), *S. punctata* (Fabr.), *Zyzzyx chilensis* Eschs., *Microbembex monodonta* Say, *M. sulphurea* Spin., *Bembecinus tridens* (Fabr.), *B. errans* (Kohl), *B. japonicus* (Sonan) and *B. formosanus* (Sonan). All the wasps of these species deposite their eggs prior to the hunting activities, accordingly, not on their victims but directly on the floor of the brood-cell. Their eggs are always placed in an erect position on the caudal pole. In some species, namely *Bembix olivacca*, *B. brullei*, *Microbembex monodonta*, *M. sulphrea*, *Bembecinus errans*, *B. japonicus* and *B. formosanus*, it has been ascertained that the base of the egg is either carefully supported by a cluster of large sand grains or glued to the top of a special pedestal which is formed sometimes by a single small pebble and sometimes by a lump of fine grains of sand.

On the other hand, such species as *Stizus pulcherrimus* Smith, *S. ciliatus* Fabr., *Rubrica surinamensis* De Geer, *Bicyrtes quadrifasciata* Say, *B. parata* Popov, *B. variegata* Oliv., *B. discisa* Taschenb., *B. ventralis* Say, *Bembix spinolae* Lep., *B. comata* Park., *B. integra* Panz., *B. inimica* Kohl, *B. oculata* Latr., *B. rostrata* L., *B. sinuata* Latr., *B. handlirschiella* Ferton, *B. weberi* Handl., *B. picticollis* A. Moraw., *B. niponica* Sm, *B. taiwana* Bisch., etc. (all that have been investigated as regards the biology except the first group) are known to glue their eggs directly on the body of the first victim they capture**.

Among the species belonging to the two groups mentioned above, those which have come directly under my observations are *Bembecinus japonicus* in the first group and *Stizus pulcherrimus*, *Bembix weberi*, *B. picticollis* and *B. niponica* in the second group. Since the matter requests the detailed knowledge, I will confine the basis of my discussion to those instances with which I am most familiar. Fortunately, the species of the three genera observed by me seem to represent a different developmental

* *Crabro claudii* (*Sphex haemorrhoidalis* and *Rhopalum latronum*) alone makes exceptions. The former, a South-American aphid-hunting species, is said to lay several eggs in a group prior to the hunting activities. Her nest is made in a hollow stem of grass and it is reported that the laid eggs are attached to the bottom of the brood chamber with their posterir ends, standing upright. The other two show the progressive manner of provisionment as in Stizinae. (As to *S. haemorrhoidalis* : Tsuneki, K. 1946 Seibutsu. Vol. I, No. 1, pp. 46 - 49.)

** Besides these species, some species of *Stizus* and of *Sphecius* are known to have the similar habits, but detailed points concerned here remain unknown.

grade respectively in the evolution of their egg-laying habits :

i) *Stizus pulcherrimus* Smith*. This species is nearly as large as *B. niponica* and has the habits of hunting the Orthopterous insects**. The wasp digs a shallow nest of the compound type in the earth which contains inside 2 – 9 larval cells. General structure of the nest is very similar to that of the compound nest of *B. niponica*. When the first brood-chamber is dug up at the end of the tunnel, the wasp goes out in search of the victim. Soon she secures it and comes back carrying it in the same fashion as in *Bembix*, save that she holds it, in addition, by the antennae with her mandibles. She retains her hold upon it while she opens the entrance to the nest, but only by the antennae. The victim — usually a nymph of the locust — is laid on its side in the cell and an egg is attached with its posterior end to one of the buds of the anterior wings which happened to come to the upper surface. But, unlike in *Bembix* it is not placed in a upright position, but stands aslant. Frequently it lays down upon the wing and appears to be attached with its side or with its anterior end. But always such is not the case. This species, as in *Bicyrtes*, does not wait for the egg to hatch before bringing in the subsequent victims, but proceeds at once to complete the provisionment of the cell. So that the cell is usually closed before the egg hatches out. Then she digs a branch tunnel and constructs the next cell at its end. The same manoeuvre is repeated until the cell attains several in number. In one occasion, however, I found a young larva in a cell which was yet in the course of the provisionment. This instance seems to indicate that the wasp can show the similar progressive method of provisionment as in the case of *Bembix* according to the condition (probably climatic) of the time. The larva of this species always begins to eat from the first victim captured by the mother wasp, upon which it is laid. Because, the size of the victim is comparatively large and the egg is laid with the anterior part close to the victim.

ii) *Bembecinus japonicus* (Sonan). This is a small species measuring only 10 – 12 mm in length and invariably makes her nest in the sandy area. The structure of the nest always belongs to the simple type. The burrow is about 10 – 15 cm in length and enters obliquely and shallowly in sand. It ends in an enlarged pocket wherein a single larva is reared. When the burrow is dug up, the wasp gathers several to scores of fine grains of sand and forms a lovely pedestal. Then she lays an egg upon it in an upright position. Sometimes, however, the egg is attached to the side of the pedestal with its lateral surface of the posterior end, in a similar fashion as in the case of *Bembix niponica*. After depositing the egg, the wasp closes the entrance of the nest,

* Tsuneki, K. 1943. A Naturalist amid the Battlefield, Osaka, (In Japanese).

Tsuneki, K. 1943. On the nesting habits of *Stizus pulcherrimus* Smith. Mushi, 15, pp. 37 – 47 (in Japanese).

** The following species belonging to Acridiidae and Locustidae have been known to be captured as the victim : *Paraplourus alliaeus* Germer, *Aiolopus tamulus* Fabr., *Xiphidion maculatum* (le Gouillon), *Acrida lata* (Motsch.), *Staurodsrus schmidti* Ikon., *Trilophida annulata* Thunb., *Oxya* sp. and *Chorthippus dubius* Zub.

then carefully scatters and sweeps the sand thrown out in front of the spot where the mouth of the burrow is concealed. The activities of the wasp shown thereafter are quite similar to the case of *Bembix*, save that she preys on the small Homopterous insects. The essential points in the subsequent habits of this apecies are : (1) No food is brought in the nest, as a rule, until the egg hatches out, (2) the mother wasp ceases her breeding activities, accumulating a mass of food in the cell, prior to the full maturity of her larva, probably soon after the completion of the larval moults.

Now, when we compare these two species in regard to their habit-types, *Stizus pulcherrimus* seems to indicate evidently a primitive stage of development. In this species the progressive method of provisionment occurs rather rarely, only through the unfavourable condition of the environment. The first victim supplied to the larva is always alive; it is only in the condition of deep paralysis. The egg is deposited on the body of the victim; it is placed nearly flat thereon, though it is attached, in reality, only with its caudal end. These conditions make us remember the habit-type of those hunting wasps which prey on several victims and at the some time which lay their eggs on the first insect they capture. Many species of *Sphex*, *Tachytes* and *Tachysphex*, some species of *Ammophila* and so on will fall in this criterion. The only essential difference between the habit-types of these wasps and of the *Stizus* lies in the fact that with which end the egg is attached to the body of the victim.

On the other hand, the habit-type of *Bembecinus japonicus* seems to show a more advanced stage of development, in reference not only to the method of provisionment, but also to that of oviposition. Especially as for the oviposition, a special remark must be given to the point that the wasp utilizes an inanimate object for the pedestal to glue her egg.

When we thus compare the habit-types of the *Stizus* and the *Bembecinus*, we can easily understand that our *Bembix* lies in the intermediate stage between them in relation to her habit-type. At the same time we can realize the significance of the manipulation given by the mother wasp to the first prey she hunts; that is to say, to the pedestal of her egg. It is killed or nearly killed and very frequently it becomes musty and is covered with mould by the time when the hatching larva begins to eat. Notwithstanding such conditions, the larva attached to it can safely continue its development. This result is entirely dependent upon the fact that the larva under such a condition eats other victims than the pedestal. This means that under such a circumstance the first victim that support the egg is no longer food for the hatching larva, but merely a pedestal for the egg. The fact seems to be very suggestive. But some one may say, such a state is nothing but an exception. It may partly be true, but that the first victim is killed or nearly killed is not of an exceptional matter. The latter fact seems to indicate that the wasp intends from the first to make the first prey into a mere pedestal for the egg and not brings it as food for the hatching larva. This consideration is supported by two evidences derived from another sources. One of which is that the mother wasp brings invariably a newly paralysed victim within the reach of her young larva by the time when it begins to eat. The other is that the dorso-ventral axis of the egg is not always placed in such a position that the mouthparts of the hatching larva is to face toward the pedestal (*vide* Addendum).

When we thus consider, the fact that the larva falls on the pedestal-fly and feeds upon it may be rather a casual phenomenon, representing an old condition which we now find in the habits of *Stizus pulcherrimus* Sm. Still further, the fact that even when the larva begins to eat the very pedestal-fly, it soon ceases to feed on it as a rule (probably on account of the unsuitable condition of the victim) will serve as another evidence that can support my consideration.

The manipulation given upon the legs and one of the wings of the pedestal-fly seems to have merely the secondary significance regarding this habits of the wasp. It will be nothing but a mechanical adaptation concerning the technic of oviposition.

According to the above consideration, the oviposition-type of our *Bembix* is quite intermediate between those of *Stizus pulcherrimus* and *Bembecinus japonicus* in the point that it lays its egg on the first insect of its victims, but at the same time it utilizes the insect merely as a pedestal and trests it as if it were an inanimate object. Here we can perceive the most interesting significance of the curious manipulation conducted upon the pedestal-fly of the wasp's egg. Besides, according to the view, the preference of the mother wasp for the relatively small fly in reference to the pedestal of her egg has no significance whatever in itself. It may be a mere reservation of the old habits that might have a significance once in supplying the softer insect as the first food for the larva.

5. Homing —— Place recognition

Parker (1917) in his interesting observation on the habits of *Microbembex monodonta* gave a conclusion to the question "how do these wasps find the entrance to their burrows ?". According to his consideration, they do so through the sense of smell or some power similar to smell. His conclusion is based upon the observations that the wasps can find their nests without confusion, no matter how greatly the appearance of the surface of the ground is changed either through the natural accidents or through the artificial methods of his experiments. His conclusion, however, seems to be too hasty, since his experiments were not conducted under the method of analytical cantrol. Indeed, he observed a great change on the surface conditionns of the nesting site, caused by wind, rain or trampling of animals. Besides, he changed himself the nearest surroundings of the nest either by dashing baskets of water over the surface or by placing leaves or rabbishes about the mouth of the nest, or by making a small pile of sand on the entrance to the burrow. In no case, however, could he change the general scene of the place which was constituted with a number of landmarks scattering on and around the wasp's colony. Furthermore, no attempt whatever has been made by him to deprive the nesting site of its odour factor. The observations and the experiments carried out by him were only able to ascertain the fact that the wasp could not be disturbed by the change of the topographical conditions of the nearest surroundings of the nest. No further conclusion could be drawn from the data obtained by him.

The observations of such a sort were already reported as early as 1856 by J. H. Fabre on a European species, *B. rostrata* L. According to him, *rostrata* could not also be deceived by the change of the surface condition around the nest.

On the other hand, E. L. Bouvier (1900) reported that a wasp of the same species as that treated by Fabre (under the name of *labiata* Fabr.) was thrown into a marked confusion when he razed the sparsely growing plants from the surface of 70 – 80 sqare cm around the nest. He also described a success of a learning experiment in connection with a flat stone which he placed on the entrance to the nest. However, in the similar experiment made with another individual of the same species, he could not obtain the same results. From such data he considered it possible to conclude that "la mémoire de lieu et la vue jeuent un rôle essentiel, si non exclusif, dans l'habileté vraiment admirable avec laquelle le *Bembex labiata* retrouve l'entrée de son nid".

In the same year E. Marchant made a similar observation on the homing of the same species and arrived at the same conclusion as Bouvier's. He considered that in a case he observed "le voisinage du moulin et le pied de *Vincetoxicum* étaient pour la Guêpe des points de repère qui lui permettaient de s'orienter pour retrouver son nid. Le premier, visible de très loin, lui rendait cette orientation très facile en lui permettant de filer droit dessus, le second indiquait l'entrée du port, c'est-à-dire du nid".

I have not as yet accomplished the thorough-going investigation concerning the problem upon our species of *Bembix*. But I am strongly of the opinion, with Bouvier and Marchant, that visual cues may play a leading rôle in their place recognition. Because we can not account for the manoeuvre of the wasp exhibited during the so-called orientation flight, unless we suppose the connection of the behaviour with the memory of the place acquired through visual cues. Moreover, the nest-searching behaviour of the wasp in the case when her nesting site has been seriously disturbed gives us the same suggestion. Because, with the increase of difficulty of finding the entrance, the wasp repeatedly rises on the wing and circles widely once or twice around the place and invariably returns straight from some distance in front of her nest to the position where the entrance to her nest had been, as if she were guided by the distribution-balance of landmarks around the nest.

Nevertheless, I can not believe that the surface condition including some small objects at the nearest surroundings of the nest does act as a definite landmark of the entrance to the burrow. Because, quite in the same manner as described by Fabre and Parker on their respective species, our *Bembix* are able to find the exact position of their nests, even after the great change occurred on the topography around their nest. In this respect Bouvier's experiment on *B. rostrata* gives, too, the same evidence. Because, when he first changed the surface condition by placing a flat stone on the entrance to the burrow (in order to make the wasp learn it), the wasp could easily find the exact position of her nest, despite the change occurred.

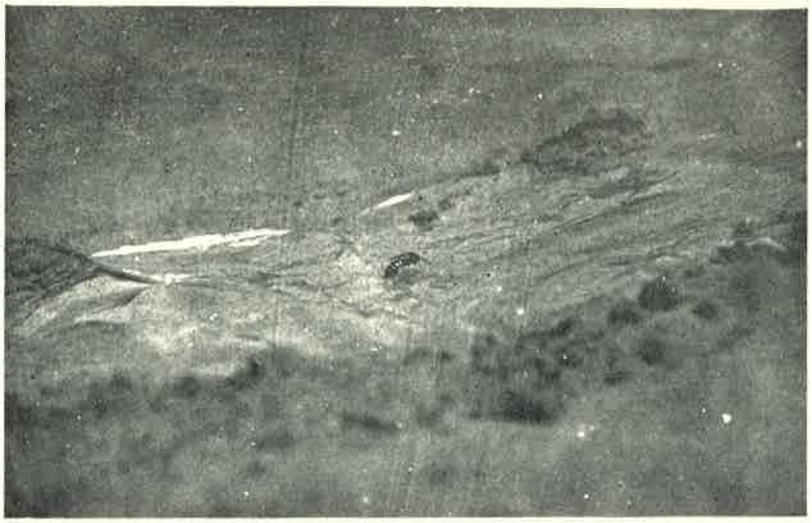
All the learning experiment hitherto carried out by me, though discontented as yet in method, have arrived at the negative conclusion. I placed from 3 to 5 coloured round plates, 1.5 - 2.0 cm in diameter, around the entrance of a nest which was situated in a clear sand plain and was just in the course of digging. I repeatedly frightened the working wasp and made her fly up from her burrow. She flew about a while, then alighted in front of the entrance and resumed her digging activity. By means of such a forced repetition of the return to the nest, I expected the wasp to obtain an associative memory between the plates and the site of her nest. After repeating such a behaviour from six to ten times, the wasp closed the entrance and started on the hunting excursion. During her absence I swept and evened the surface of the ground around the nest and shifted the set of the round plates some distance away from the nest and arranged them as before. On coming back from her hunting journey, however, in no case did the wasp go to the plates. All of them I studied went invariably to the correct position of their nests, despite the change introduced around it.

In my experiments conducted upon *niponica*, I was used to cover the entrance to the nest with a large Petri dish (20 cm in diameter) in order not to permit the wasp to enter the tunnel while I was examining the contents of the nest. The wasp, when came back, always alighted upon the dish of glass without showing the least disturbance and rasped the surface of the instrument violently with her front pair of legs, with a loud squeaking sound (Fig. 6). Whatever smell or some other volatile substance like the smell could stimulate the wasp in such a case ? Nevertheless, the wasp alighted just above the entrance door and swept the surface of the glass as if she were opening the closure. In no case have I observed the wasp strive to penetrate from beneath the lateral wall of the dish. In order to ascertain the phenomenon more exactly I tried recently the experiment of similar sort by using a sheet of colourless cellophane (35 × 45 cm) instead of the Petri dish. The wasps when came back either carrying the booty or empty-handed always alighted on the transparent paper just above the entrance to their burrows and continued the behaviour of clearing the sand stoppage. Figs. 7 and 8 will most eloquently tell the results of the experiments.

I infer, basing upon the data obtained up to the present, that the sensory cues that will guide the wasp to her burrow must be visual in order. Rabaud (1928) divided the mechanism of homing phenomenon of the flying insect into three steps, namely : (1) Departure in the correct direction and maintenance of it as far as the immediate vicinity of the nest is reached, (2) recognition of the site, (3) recognition of the nest. If such steps are applied to the homing of our *Bembix*, I believe that the second and the third steps must depend upon the sense of vision, apart from the first. As for the second, my opinion agrees well with that of Marchand in the essential point. In this step, what will lead the wasps to their nesting site may be the memory of the general survey of the place. Probably it will be an indistinct image like a vaguely outlined pattern of the place, constituted by the distribution of objects or spaces that differ in brightness or in colour (if colour is visible to them). Such a pattern will be registered in their memory chiefly during the course of their flying about in the neighbourhood of their birth place. As to the third step, however, I am of the different opinion from that of Bouvier and Marchand. According to my observations, it happens rather in rare occasions, provably secondarily and passively, that the wasp memorizes some special object such as a potsherd, a chip of wood, a pebble or some weeds located by the side of the nest in connection with the precise position of the

Fig. 6. A wasp which returned with a prey and alighted on the Petri dish that was placed on the entrance of her nest. Notice the front pair of legs that are in the act of sweeping the sand ! (Photo. K. Tsuneki).

entrance to the burrow. In the usual case it seems to me that in the Bembicine wasp there is no recognition of the nest itself nor the associative memory concerning some conspicuous landmarks close to the nest. What guides the wasp to the exact position of her nest seems to be the memory of the background seen from in front of the nest. The image may be a vague pattern of brightness (and colortion), but it will have a special combination of brightness (and coloration), like that remembered by human aviators with regard to their own aerodromes. It will first be obtained by the wasp during her selection flight in search of the nesting site and strengthened in her frequent flights during digging. But it will be most exactly fixed to her memory during the time when she repeatedly poises in the air in front of the nest in the course of her orientation flight. It will become more and more accurate later by repeated recognition whenever she comes back to her nest. If, in such a case, there is around the nest some object that is sufficiently marked either in its brightness (or in its colour) or in its size to occupy an important part of the pattern, it would become secondarily utilized as a landmark of her nest. The condition recorded by Bouvier seems to represent an instance of such a case. In every case it is presumable that the pattern is utilized as a whole by the wasp. Accordingly the change occurred partly



Figs. 7 and 8. A wasp which landed on the cellophane paper covering the nest just at the very spot where the entrance is concealed.

in the component of the pattern will have nothing to do with the recognition of the site of the place. The change of the surface condition of the nearest surroundings of the nest or alteration of the situation of trivial objects around the entrance will be quite out of the queation to the wasp.

6. Does the wasp rear more than one larva at a time?

Having a special feeding habits, the wasp belonging to the genus *Bembix* requires, in general, a comparatively long period of time to breed one larva. Therefore, old investigators believed that they would have several nests having each larva inside and feed them at a time. They had a concept that unless the wasp has such habits it can not rear sufficient number of larvae to retain the prosperity of its species. But according to the later investigators, in no species observed heretofore could such habits have been confirmed. The Peckhams particularly investigated on this problem with *B. spinolae* by means of marking each of the wasps and of their nests. But at length they failed to discover the phenomenon. According to Parker, *B. nubilipennis* of North America makes a branched burrow in sand. The wasp separates the end of each branch into 2 or 3 linearly arranged brood-chambers and breeds several larvae within a nest. Nevertheless, she does not rear more than one larva at a time. On the other hand, it has come to be believed in general that the time needed for feeding one larva was too much exagerated by old authors. Indeed, Parker shows that a larval wasp of *B. spinolae* spends only four days under a good condition to complete its growth from the egg to its encasement. The matter is in our species very similar to *spinolae*. It needs usually a week to complete its growth. The long duration of about a fortnight is spent by the larva only when the climatic condition becomes bad in the late season of the Bembix' activities. According to these evidences it becomes that even when the wasp rears her larvae one after the other, she can readily leave behind her a sufficient number of offspring to ensure the prosperity of the next generation. Now-a-days, therefore, investigators of this group of wasps appear to have agreed in their conviction that the wasp feeds but one larva at a time.

In our species, however, very rare as it is, the phenomenon of simultaneous rearing of more than one larva occurs in reality. In this respect *B. niponica* is worthy of a special notice. With regard to the observations carried out in the suburbs of Sapporo with a great number of individuals, no such case could be ascertained excepting but one. But the evidence obtained near the City Chiba shows distinctly the phenomenon occurring in the wasps' colony. As stated previously, nearly all the nests observed at that place belonged to the compound type. In these nests usually from 2 to 6 larvae were reared, The detailed data regarding the compound nests are as shown in Table 20.

From the table we can first underatand that *B. niponica* does not continue the care of her young until the time of its encasement. If she does so, the table will give decided evidences to show that the members of the colony rear rather habitually more than one larva at a time. But, as shown in the foregoing section, most of the individuals of this species cease their feeding activities before the full maturity of their larvae. Therefore, instance Nos. II and V, though they each contain 2 larvae inside, can not be accepted without question as evidences of simultaneous rearing of more than one larva in the same nest. In these nests, probably the larger larvae might have already left their mothers' care at the time when I dug the nests. Nest No. VII, however, indicates a more interesting situation. Judging from the records, the larva must be in the 3rd instar or very early stage of the last instar. Victims

Table 20. Contents of the compound nests observed in Chiba.

No. of nest	No. of cell	The young of wasp	Species and number of victims: Eaten	Species and number of victims: Intact	Total number of prey	Remarks
II	1	L. 20 mm	St 7	St 4	11	
	2	Egg	—	L 1	1	
	3	—	—	—	-	Accessory br.
IV	1	Egg	—	St 1	1	
	2	—	—	—	-	Accessory br.
V	1	L. 20 mm	St 5	St 7	12	
	2	L. 7 mm	—	L 3	3	Larva, 2nd inst.
	3	—	—	—	-	Accessory br.
VII	1	L. 12 mm	St 2	St 6	8	
	2	Egg	—	St 1	1	
	3	—	—	—	-	Accessory br.
IX	1	Cocoon	St 13	—	13	
	2	none	St 17	—	17	Parasite ?
	3	?	?	?	?	Provisioning !
XI	1	?	?	?	?	Parasite ?
	2	Cocoon	?	?	?	No record
XII	1	?	?	?	?	
	2	Cocoon	?	?	?	
	3	Cocoon	St 15	—	-	
	4	Cocoon	St 18	—	18	
	5	Cocoon	St 8	—	8	
	6	L. 25 mm	St 4, Sa 1, L 21	Sa 4, L 3	33	
XIII	1	None	St 7	—	7	Parasite
	2	Cocoon	St 7	—	-	
	3	L. 15 mm	St 3, T 2,	St 7, T 2	14	Larva, 4th inst.
	4	—	—	—	-	Accessory br.
XVI	1	Cocoon	St 9, Sa 3	—	12	
	2	None	St 12, Sa 4	—	16	Parasite
	3	Cocoon	St 9	—	9	
	4	L. ? mm	St 7	St 11	18	Larva 4th inst.
XVII	1	L. 20 mm	St 5	St 5	10	Larva 4th inst.
	2	L. 10 mm	St 1	St 4	5	L. 2 - 3 instar
	3	Egg	—	Sa 1	1	
XVIII	1	Cocoon	St 15	—	15	
	2	None	?	?	?	
XIX	1	Cocoon	St 18	—	18	
	2	Cocoon	St 12	—	12	
	3	Egg	—	St 2	2	

Remarks for abbreviation : St --- *Straytiomyia japonica*, Sa --- *Sarcophaga carnaria*, L --- *Lucilia caesar*, T --- *Tabanus* sp.

stored by the side of it are only 8 in number. The conditions apparently possess every possibility of allowing us to suppose that the mother wasp will bring victims at least one day more to the larva. On the other hand, cell No. 5 of nest No. XII, cell No. 2 of nest No. XIII and cell No. 3 of nest No. XVI indicate that 8 flies accumulated are not necessarily too small in number as a diet for one larva. That is to say, when considered from the lowest standard of provisionment, this cell, too, can not be denied to have been completed.

When we examine nest No. XVII, however, we can not deny from every point of view the occurrence of simultaneous rearing of more than one larva in the same nest. In the nest in question, cell No. 1 might have been already completed. But cell No. 2 has every possibility of imcompletion. The larva is believed yet in the 2nd or the 3rd instar. The victims supplied are only 5 in number. Whereas, in cell No. 3 the egg has already been laid. The mother wasp must inevitably bring food to the two cells of her nest.

But, what we must give a special attention in the states of affairs is that one of the offsprings in question is as yet in the stage of the egg and the other is a fairly developed larva. In other words, for one of them no special care is needed on the part of the mother wasp and for the other her care is expected to cease soon. To put the things in the concrete, the mother wasp, at the time when her feeding larva attained the state wherein it required only the provisionment of one day further, laid her next egg in her next cell. Therefore, when the egg hatches out, the feeding work for the previous larva will have already finished and no need will remain for the mother wasp to supply food to her two larvae at a time. In this instance, care of the mother wasp for two cells at a time is, in reality, confined to the time only when she brought a pedestal-fly to the next cell. Nests No. V. and No. VII, viewed in the light of the knowledge obtained here seem to have a high possibility of having passed the same procedure. Furthermore, the fact that the wasps observed in Chiba tend to cease the care of their larvae much earlier than those investigated in Sapporo, seems also to support the probability of frequent occurrence of the above stated phenomenon. Judging from these evidences and presumations, the phenomenon of rearing more than one larva at a time seems not always rare among the wasps living in that district.

At any rate, it seems especially of interest that the fact found here indicates one of the primitive phases of the multiple rearing of the larvae in the insect world. Because, in this case only two offsprings are reared at a time, and furthermore, such simultaneous rearing occurs only in a limited period of time, at the transitional point from the provisionment of the previous cell to that of the next.

In the suburbs of Sapporo, I have opened more than 200 nests of this species. Nevertheless, no such an instance could be met with except only one, probably on account of the rare occurrence of the compound nest. The only instance was as follows:

Sept. 3, 1949. At 12.15, I saw a wasp enter a nest with her *Eristalis cerealis*. I dug it from behind and found it composed of two branched tunnels. One of which had at its end a brood-chamber containing an egg which was attached to *Theloria leucozona*. The other was missed in my digging and the contents of the chamber were unknown. But, judging from the activity of the mother wasp, the missed cell must be in the course of provisioning and the *Eristalis* which I saw must be taken in it. I was so interested with the fact that I replaced the natural brood-chamber with an artificial glass cell and put the egg with its pedestal fly in it. At 3.30 p.m. I dug the nest from the entrance and found the wasp resting in the accessory branch which must be made by her after 12.40. In the glass-bottle the egg had just hatched out. This condition shows clearly that the wasp was continuing her provisioning activity for the previous cell during the time of her waiting for the hatching of the next larva — the condition completely agreeing with that which was previously observed in Chiba.

7. Honey-robbing

Some species of the hunting wasps have been known to take their own nurishment from the victims they capture for their larvae. Some are reported to imbibe the blood of the victims, while others are known to lick the syrup pressed out of the crop of the prey. The former instances have been known among the hunters of the caterpillar (*Ammophila*, members of the Eumenidae, etc.) and the latter among those of solitary and social bees (*Philanthus*, *Cerceris*, *Palarus*, etc.). Fabre, in his observation on *Philanthus apivorus*, recorded the phenomenon and attributed it to the instinctive precaution of the mother wasp for preventing her larva from honey-poisoning. As for *Bembix*, so far as I know, no definite observation regarding this problem has been made up-to-date. C. Ferton, however, in connection with the states of victims reported by Fabre and Wesenberg-Lund, supposed that the wasp might crush the thorax of the victims at the time when she takes her own nurishment from the captured insect.

In the course of my investigation in the suburbs of Sapporo from 1947 to 1950, I have twice had the opportunity of observing such an occurrence, though in both cases the wasp did not crush the thorax of the victim. One of them came on Aug. 29, 1947. At about noon I saw a wasp alight on the ground with a prey and begin to show something wonderful behaviour moving the fly between her legs. I approached her by stealth and succeeded in going about half a meter from her. She crasped the fly (*Eristalis cerealis*) ventral side upward with her mid legs, but more anteriorly than usual, and was inserting the long stretched labrum into the anterior portion of the thorax of the fly. As I could not confirm the exact point of insertion, I approached more. But this resulted in threatening the wasp and she flew away with the prey. This observation did not permit me to give a conclusion whether the wasp was imbibing the sweet juice from the oesophagus of the fly, or she was giving the imperfectly paralyzed victim a supplementary operation by using the pointed labrum as a lancet.

While, the second observation which was made upon wasp No. 134, on Aug. 25, 1948, was more conclusive. The wasp came back at 10.07 a.m. with an *Eristalis cerealis* to her nest. She alighted on the sand plain 3 meters away from her nest.

Fortunately it was only 1 meter in front of my sitting place. At once she began that strange manoeuvre of which I have just mentioned above. She pushed the fly forwards which was grasped as usual ventral side upward. Then the wasp straightened her long pointed lubrum and inserted it into the throat of the victim. The labium was distinctly observed entering into the wound with the labrum. Both organs were repeatedly pushed in and pulled out. I approached more and could closely observe the bebaviour of the wasp, from the distance of only half a meter away from her. The action of drinking honey was three or four times repeated, then she pulled out the organs from the wound and recaptured the fly as usual under her body and went flying to her nest.

According to my presumation based upon the obserations on the behaviour of the wasp inside the nest, such a habit of honey-robbing from the prey seems to occur rather frequently inside her burrow. But I do not regard the behaviour as instinctive precaution of the mother wasp to prevent the larva from honey-poisoning. Because, the greater part of the flower-flies found in the brood-cells is used to have the abdomen filled with honey-dew, but in no case have I found the larval wasp poisoned by devouring such a prey.

Addendum : The following observations were all conducted in the suburbs of Sapporo in 1951, after the manuscript was written.

3) Wasp No. 189. Aug. 21, at 10. 20 a. m. The wasp brought a flower-fly (*Eristalis cerealis*) to her nesting ground and alighted 2 m away from her nest. She grasped it from the back and stung it very slowly on the throat. The apex of her sting appeared to be directed towards the victim's thorax. Then she rolled the fly with her legs and made it upside-down. She pushed the fly forwards until it became face to fo face with her. She then stretched her labrum and inserted it into the mouth of the flower-fly, just behind the labium. The labium of the wasp was also inserted and twice and thrice it was deeply pushed in and pulled out. After the manoeuvre, the wasp carried the prey to her burrow (obserbed from only 30 cm away from the wasp).

4) Wasp No. 186. Aug. 22, at 9. 00 a. m. At the entrance to the wasp's burrow, an *Eristalomyia tenax* suddenly and violently beated her wings and succeeded in escaping from between the legs of the *Bembix*. The latter at once pursued and easily recaptured the fly and landed 5 m away from her nest. She then stung the fly and sucked the crop of the victim. The manner was quite the same as in the above instance. (Observed at a distance of 50 cm from the wasp).

5) Wasp No. 194. Aug, 22, at 10. 41 a. m. The captured *Eristalomyia* violently beated its wings at the entrance of the wasp's burrow and fled away. The wasp recaptured the fled victim and alighted 10 m away from her nest. She rolled the fly and made it venter to venter with her. But as the fly beated its wings once more, she rolled it again and caught it from the back and darted her sting at the throat of the fly. After stinging, the wasp inserted her labium together with the labrum into the mouth of the fly. Deeply and very slowly, four times she pushed them in and pulled out. Then she carried it to her nest.

6) Wasp No. 195. Aug. 23, at 10. 20 a. m. In this case also the fly flesd from between the lege of the wasp. It was recaptured and stung. Then the syrup was sipped out from the crop of the fly, quite in the same manner as in the prevous instance.

7) An unnumbered wasp. Aug. 22, 10.58 a.m. The wasp recaptured the fled fly and stung it in the same manner as mentioned and then imbibed the content of the crop by inserting her mouthparts in the mouth of the victim.

All the observations mentioned above were made upon the flower-fly, and moreover, upon those that have fled from between the legs of the wasp. Therefore, the behaviour of imbibing syrup from the crop of the victim may have some significance in weakening the stout victims.

8. Familiarity between the inhabitants of the same colony

Some authors referred to the wasps of the genus *Bembix* as subsocial, because of their gregarious habits. But, if a certain species of insects that nests gregariously within a limited area is to be called as a subsocial insect, most of the solitary wasps and bees will fall within the criterion, since these insects, as a rule, return to their native place to make their nests side by side with sisters ond cousins, forming the so-called colony or settlement on the same place from year to year. In reality, however, between the neighbours of such a colony there is usually no such familiar relationships as those found among the comrades of the social insect. Each of them lives an independent life and when happened to confronted with each other they are used to show a furious hostility, especially in wasps. They fly up in the air to fight and the battle is continued till one of them is driven away or goes out of sight. As a rule, however, they do not invade to one another. Nevertheless, all of them appear to take the neighbours as enemies. In some species, moreover, the robbery comes to occur among the individuals of the same colony. Such being the case, they do not deserve the name, "subsocial insect". As for *Bembix*, some species are known to have the robbery habits as mentioned previously, for instance *B. spinolae* of North America. From the point of view of the intimate nature among the neighbours, therefore, these *Bembix* belong completely to the non-social insect.

On the other hand, in our species at least, in so far as my observations go, things occur somewhat otherwise. Among the inhabitants of the same colony there is no such a hostility, no such an absurd battle and no such a labour-parasitism*. When the colony is very crowed and the surface of the ground is disturbed by the observer, a confusion is often broken out. It occurs sometimes that some wasp enters by mistake the nest of a neighbour which remains opening at that moment. In such a case the two wasps come inevitably to meet with each other in the tunnel. But never the battle is broken out between them. The wasp that wants to go in goes in, rather elbowing her way, indifferent to the presence of the other wasp. The owner makes no effort for hindering her to enter, but she becomes excited and begins to repeat the going-in and coming-out. The strayed wasp begins also to make the ingress and egress. Thus they come to meet with each other more frequently in the tunnel. But they never grapple nor bite with each other. They close or open the entrance quite independently

* K. Baba, however, reported the phenomenon at a colony in the sand-dune district in Niigata Prefecture.

in excitement, or they sweep the tunnel or the ground in front of the nest. Meanwhile the strayed wasp comes to know, as a rule, her own mistake and goes to her own place. This familiarity, though not of an active one, is always observed in their settlements. Our species therefore, seems to merit the name, "subsocial wasp", not only in the relationship between the mother and the young but also in the relationship among the inhabitants of the same colony.

III. BEHAVIOUR INSIDE THE NEST

1. Method of observation

With regard to the behaviour of *Bembix* inside their nests no actual investigation has been undertaken up-to-date. Many previous observers only supposed the subterrenean behaviour of the wasp only through the examination of the brood-cell. Fabre (1856), in his attempt to investigate whether or not the mother wasp could recognize her own larva, uncovered the tunnel and the cell of a nest. He observed the wasp, when returned, thrown into confusion. The wasp, even when she trampled upon her larva, could not recognize it, striving only to find the entrance to the nest. Bouvier (1900), on the other hand, tried to lead the wasp to her exposed cell by shortening the tunnel gradually from outside. All his trial, however, failed in the end. The failure of these attempts, however, seems to me nothing but a natural result, since they both neglected the manifestation-order of the instinctive behaviour. In the natural procedure, the wasp must first penetrate from the entrance to her nest, prior to the contact with her larva. This order is mechanically decided from the beginning of her life and can not be altered by any change of the environmental conditions. So, when the wasp is compelled to alter this a-priori order, it is clear that she can not show any adaptive activity to the confronted states of things which otherwise should appear in some later course in her behaviour system.

In my method, therefore, precaution was particularly taken not to disturb the order of the successive manifestation of the elements of the behaviour system. In no case have I destroyed the entrance to their nests. Every time when I wanted to see the behaviour of the wasp in the nest, I uncovered the brood-chamber from behind. At first I examined the curvature of the tunnel by inserting a stalk of grass from the closed entrance. With knowledge of the general direction of the situation of the brood-cell, I excavated a broad hole with depth of about 15 – 20 cm in the direction, 40 or 50 cm behind the entrance. I then enlarged the hole toward the entrance by shaving off little by little the sand wall with a knife until I found the cell.

At first I observed the behaviour of the wasp in the cell that was partly or wholly left exposed. But soon I found the method very inconvenient. Because, a) the wasp was likely to fly out of the brood-cell through the opening when she was disturbed, b) it was entirely impossible to make a successive obseration. Besides the above, c) in this method the cell must be directly dug at, but such is very difficult owing chiefly to the unexpected curvature of the tunnel. For these reasons, I changed the method and put an artificial brood-chamber in the place of the natural one. It was made of glass and was similar in form and dimention to the natural cell and was provided with a stalk of 1 cm both in length and in diameter, in order to connect well with the end of the tunnel. But, later when such a specially made glass-ecll was not at my hand, I used a common tube-bottle of favourable size in place of the ellipsoidal one. The results were utterly identical in both cases.

In addition to the glass-bottles, I used also glass-tubes of various length and curvature, with the diameter of 1 cm, in place of the natural tunnel of the nest. The results were as good as in the case of the glass-bottles. By applying a various sort of glass-tubes to the open end of the natural tunnel, I could not only utilize all the nests that were failed in digging directly at the brood-cell, but also shift the position of the brood-cell anywhere I wanted. Moreover, only by using such instruments of glass, I could alter the structural condition of the nest as freely as I wanted to enable the analysis of the psychical ability of the wasp.

The instruments were usually covered with sand when not observed, but sometimes they were left exposed, only the direct sunshine being intercepted with a wooden plate and the like. Every time when the wasp was thrown into confusion by the stimulus of the light, the arrangement had at once to be covered with sand so as to keep the interior dark. The use of the red cellophane paper was also tried for the same purpose, but then the observation became somewhat difficult, unless a sheet of white paper was placed under the instruments.

2. Taking-in of the victim

Bembix, in carrying the victim in her nest after clearing the entrance closure, always pushes it backward from beneath her abdomen and drags it behind her, crasping it with her hind legs and goes in the tunnel. Nothing of the further behaviour of the wasp has hitherto been known. Many observers seem to believe vaguely that the wasp goes on in the same manner in the tunnel up to the blood-cell and there opens the closure of the cell by the same method as used at the entrance. However, in reality, the victim is always laid aside sooner or later in the tunnel and the wasp opens the 2nd tampon of the burrow free-handed. She then enters the brood-cell head first, examines the larva with her antennae, or toutches it with her legs, turns round and goes back to the victim. There she grasps it usually by the neck with her jaws and drags it backward into the cell.

In the manner of taking-in of the prey, *Bembix* (and also the allied genera) has been considered exceptional, since she enters the nest without letting off the prey, and moreover, goes in the tunnel head first. By the above stated observation however, it has been made clear that such is merely the first scene of the procedure. In reality, inside the nest, *Bembix* too, follows the general rule prevailing among the hunting wasps, that is to say, first laying aside the prey, then examining the cell and finally dragging the prey backward into the brood-chamber. The apparent difference is only due to the fact that the first manoeuvre is somewhat delayed and occurs in the tunnel and out of sight.

When the larva is in the 4th instar, the victims thus carried in are placed near the entrance within the cell. They are all placed on their backs and piled up one above the other. The wasp when brings a new victim backward into the cell, tramples over those already heaped up and puts it on top of others. Owing to the narrowness of the cell and to the structural character of the fly, the victims that are taken in later are respectively placed slightly more entrancewards, with their body-axis kept aslant. In the usual case the time spent till her work of opening the 2nd tampon finishes is half a minute or so. But sometimes she spends 1 - 2 minutes or more inside the tunnel before she comes in the brood-cell. At first it was an unsolved question to me for what purpose she spent such a long time in the tunnel. But after I observed the wasp's habit of taking her own nurishment from her victim, I came to believe that something like that sort of behaviour might be carried out during the time. This belief seems to be supported by the fact that such stagnation of the process occurs only from time to time and especially when the wasp comes back with the first victim of the day.

In case the inner portion of the tunnel is replaced with a tube of glass, we can observe the wasp proceed inside, repeating the sweeping movements with her front pair of legs. This sweeping movement, probably reflexive, is almost always observed in her forward progress in the tunnel, excepting a rare omission at the time when she hurries to the victim left alone in the tunnel from her trip to inspect the brood-cell. It will be the same sort of reflexive behaviour as usually observed outside her nest when she proceeds on foot.

After taking in the victim, the wasp seals up the entrance of the brood-chamber with a tampon of sand. But when a glass tube is applied in place of her own tunnel, she cannot actually gather the sand to seal up the tube. Nevertheless, the wasp exhibits the sealing behaviour in the tube. And after repeating certain times of that fruitless work, she appears in the entrance gallery, closes there and goes on the next hunting excursion. The sealing of the brood-chamber is performed as follows: First the wasp proceeds from the chamber a few steps into the tube, sweeping automatically the floor with her front pair of legs. Then she stops and at once begins to retreat, with her front legs curled inward as if they were supporting a mass of sand behind them. Near the entrance of the cell she stops again, sweeps the floor of the tube with a big motion as if she were pushing away the carrying burden behind her. Then she proceeds again with the sweeping movement and resumes the sand-gathering behaviour. However, in the case when the tube is not long, whilst the wasp thus repeats the absurd manoeuvres, a small quantity of sand is gradually gathered from the sand tunnel into the tube. Finally, at the time when provisioning activity comes to an end, the tube is used to be more or less closed with sand. The time spent in such manoeuvre in each case is about half a minute or so. Then the wasp appears at once in the entrance of the nest. But sometimes she stays 5 - 10 minutes in the tunnel, probably to take a rest.

3. Preparation for oviposition

I have attempted several times to observe the behaviour of the wasp in the very act of oviposition. But I have never succeeded heretofore in confirming not only the behaviour of oviposition but also that of manipulation conducted on the victim which must be done prior to oviposition. However, what I have observed up to the present will be worthy of description, since they seem to give some suggestion to the subsequent investigators as to the problem.

One of the obserations was made upon wasp No. 70, on Sept. 4, 1947. At 11.30 a.m., I saw the wasp enter a nest carrying a fly. The small sand heap in front of the entrance told me that the nest was soon after having been dug up. So, I at once uncovered the nest from behind and fortunately succeeded in digging at the end of the burrow. It had not been enlarged into a cell, as was expected, and no victim had been placed inside. I put there a tube bottle, 12 mm in diameter and 10 cm in length, connecting its mouth with the opened end of the burrow, and waited for the wasp come in. While I arranged the bottle, I did it in great haste lest I should be behind time. Because, the tunnel was only 20 cm in length and if the wasp came in without delay, it might take her only a few second. Against my apprehension, the wasp did not come in the bottle at once. I waited and waited for her coming, but she did not appear within my sight. At last, after 7 minutes from her entering, she showed her head at the entrance of the glass-chamber. She came in slowly, empty-handed and came on until the end of the bottle. There, she began, without hesitation, to dig the burrow, sweeping and scratching the glass-wall with her front pair of legs. The behaviour of the wasp did not show any such confusion as caused often by the stimulus of the light. If she was confused by light she must scratch the upper wall of the tube-bottle instead of the bottom-wall, since the former was exposed to light, while the latter was inserted in sand.

The wasp worked there for about 3 minutes, then turned round and went back in the narural tunnel. Soon she returned in the cell of glass and resumed the same behaviour as before. This time, too, her work was continued for about 3 minutes, then she went back again in the dark gallery. Soon she reappeared in the bottle and once more scratched and swept the end wall of the bottle in vain. After 2 minutes' labour she returned in the tunnel again. For the 4th time of her entering, the wasp came backing with the victim in the bottle. There she laid it aside and once more tried to dig the end wall of the tube. After a hard attack of about 4 minutes against the obstacle, she returned in the tunnel, trampling indifferently on the lying fly. I covered the end of the tube bottle for about 2 cm with sand, so as to darken the interior. But, on her return, the wasp repeated the same absurd manoeuvre again and again. After the 6th attempt she stayed in the tunnel for a while. While she was absent, I reflected the sunlight into the bottle by means of a mirrow and observed the state of the fly. It was a species of Muscidae and was placed on its back with the head directing inwards. But not a trace of manipulation given upon the wing and the leg could be observed.

After a while, the wasp emerged from the entrance, amazed at me and rose on the wing. She circled round about the nest and then flew away. I took up the tube-bottle and filled the end half of it with wet sand and replaced it as before, putting the fly in front of the packing. The wasp did not come back for about 10 minutes, so that I closed the entrance of the nest with sand, placed a pebble on it and returned to other nests which were also under my obrervation. At 12.30, I went to the nest and found the pebble moved and the entrance opened. Inside the bottle, the wasp was digging the sand that I had packed in. She loosened it as usual, carried it to the entrance and threw out of the nest. Soon the packed sand became exhausted and the wasp came to struggle once more against the end wall of the bottle. For the last time she carried out the sand from within and having amazed at me, flew away. I again placed a pebble on the entrance. But it remained untouched until the noon of the subsequent day and it was clear that the nest was abandoned. So I examined the nest. The fly had received no manipulation whatever either on the wing or on the leg, but no definite sign of life was also left upon it.

In three other instances that I have observed the matter progressed in much the same manner. The time spent by the wasps in the entrance gallery before they came in the bottle, was 5, 6 and 9 minutes respectively. Therefore, such a stay seems to occur rather habitually before the wasp transports the first victim to the end of the tunnel. But it has been still uncertain what they are doing in the tunnel during the time of their stay. Whether they are waiting for the good physical condition of oviposition or whether they are giving some operation upon the victim will be the problem which should be dissolved by the future study. But the fact that the wasp is used to complete the brood-chamber after capturing the first victim seems to be clarified.

4. Care of the young

It has been a long unsolved mystery whether the Bembicine wasps take actual care of their larvae, or merely automatically store a necessary quantity of food only in progressive method. Judging from the viewpoint that the insect's behaviour is governed in the main by the hereditary memory or the instinct, the latter consideration seems to be more probable. Indeed, according to the Morgan's canon, it seems more scientific to consider that not only the process but also the pace of the work of the mother wasps is already prescribed in their nervous system, quite independently from the developmental degree of their larvae than to presume rather anthropomorphically that the mother wasps take special care of their larvae in accordance with the developmental degrees of them. My observation, however, revealed that, against our expectation, the latter presumption is an actual fact in our species. The following instances of my observations will most eloquently tell the various aspects of the mother-wasps' care of their youngs. They will also show the common behaviour of the wasps inside their nests.

(1) Wasp No. 52. Aug. 8, 1947. The nest belonged to the compound type, having two cells inside. In one of the cells the larva has already encased, in the other it was in the 2nd instar and supplied by the mother wasp with 3 victims. The larva attached yet on to the pedestal-fly and was feeding upon it. I closed the branch tunnel that led to the larval cell and opened the other and replaced the end cell with a bottle of glass. In the bottle were put the larva and the victims of the 2nd cell. As a result the tunnel was straightened and at the same time it was shortened by 10 cm. At 11.20, the mother wasp came back empty-handed and at once penetrated from the entrance. After working a while to arrange the tunnel, she came within my sight in the bottle. She trampled over the larva and the flies quite indifferently, arrived at the end wall of the cell and begun to scratch there, probably owing to the shortened passage. Soon she ceased the work and walked about in the chamber. During the time she trampled and kicked the larva as well as the flies. Meanwhile, however, she abruptly took up the larva between her jaws and transported it to the entrance portion of the cell. There she dropped the larva and then walked about again in the chamber, trampling on and raking aside the victims indifferently. At that moment she felt the light and began to dart against the glass wall, so I was oblighed to cover the bottle with sand. But I left a small window in the cover, through which I peeped into the chamber. The wasp sometimes took up the larva, sometimes the fly. But she did not hold either of them long. Once she dropped the larva among the gathered flies, as if she had selected the favourable place for the larva. But the next moment she trampled on it and laked it aside as if she were treating an obstacle in the tunnel. In the meantime she felt the light again and fell into confusion. So I covered the cell perfectly. After 3 hours when I uncovered the cell the larva was placed in the middle of the cell and was peacefully feeding upon a fly. The flyes were also arranged and were put to the side of the larva.

(2) Wasp No. 60. Aug. 29, 1947. The nest was simple in structure and the tunnel of 25 cm led to a brood-chamber, in which was a larva of the early stage of the last instar together with 10 flies. Out of the victims 2 were already eaten, 2 were decapitated and being eaten and the remainder were intact. I put the larva in the glass-cell and replaced the natural chamber with it, removing all the victims from the cell. At 12. 07, I examined the nest and found the wasp already working in the burrow. She dug a new tunnel in parallel with the cell, probably owing to my in accurate setting of the instrument, and had just perforated the sand wall that I had pressed from behind. She flew out of the hole in the air. So, I connected the cell of glass to the opening she had made. The wasp soon returned, entered the burrow and at once appeared in the cell. She walked about in the chamber, trampling indifferently on the larva as in the previous instance. Then she felt the light and was thrown into confusion. I covered the cell. A short time later I uncovered the cell. The wasp was at the end of the tunnel, directing her head toward the cell. Then she turned around and went in the dark tunnel. Soon she showed her anterior body at the entrance and found a fly that had been discarded there and half covered with sand. She grasped it with the mandibies and dragged it in backward. At once she came backing near the cell, dropped the fly, turned round and approached the larva in the cell. She took up the larva between her mandibles without hesitation and went backing in the tunnel. Then she appeared at the entrance empty-handed, amazed at me and flew up. I retreated a step. The wasp returned soon and enter the nest again. Thenceforth she began and continued the work of throwing out the sand from the tunnel and did not come in the bottle. So, I earthed the cell. At 12. 15, the wasp sealed up the entrance and flew away. In the cell the larva was replaced again and was calmly eating the fly which had been placed by the side of it.

(3) Wasp No. 75. Sept. 9, 1947. This is one of the most interesting instances I have ever

observed. In this nest there were two entrance-openings with the interval of 1 cm between them. By inserting a stalk of grass from outside and by digging from behind I found the two tunnels cross in the interior, as shown in Figure 9. According to my supposition, the wasp, having lost her original entrance by some accident (possibly by my foot-print), made a new tunnel in her search-digging and succeeded in finding the brood-cell; but she passed through the original tunnel in her outgoing and thus the two entrance-tunnels were accomplished. In fact, during my subsequent observations, she was used to enter the nest through either of the tunnels. In Fig. 14, A is a short blind tunnel, probably the trace of her search-digging or beginning of the 2nd cell. B is a formal cell. C is a typical accessory branch, directing obliquely below and tapering toward the apex. In the nest, when I dug, a very interesting event was happening, In the cell (B) the victims, about 10 in number and already eaten in a different degree, were scattered, but the larval wasp was not there. Instead, a larva of some Skipjack was in the posterior portion of the cell, apparently eating the remains of the flies. The larval wasp had been forced in the narrow accessory branch. It was about 20 mm in length and was in the later middle stage of the final instar. The cavity in which it was pressed appeared too narrow to receive such a fat, plump larva. In front of it, at the entrance of the branch was offered a flower fly, to which, however, it had not touched as yet with its mouth. The mother wasp was absent. The occurrence might be caused by the intrusion of the Elaterid's larva and the larval wasp must have been transported by the mother wasp.

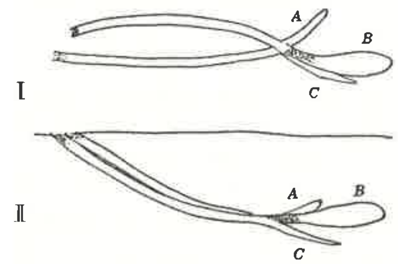


Fig. 9. The nest of wasp No. 75, I, seen from above; II, seen in profile.
A … A short blind tunnel, B … the brood-chamber, C … the accessory brauch.

I removed the Elaterid's larva and replaced the larval wasp in the original cell. The ground was cut open perpendicularly from below C, and a lateral wall of the cell was removed. As a result a horizontal terrace appeared 10 cm below C. Covering the exposed nest with a card board from the direct rays of the sun, I left the place to fetch my camera. After a few minutes I returned there and found a very interesting event going on. On the terrace lay the larva, possibly it had dropped from the opened cell. A wasp was mounting upon it. She stood high on her legs, holding the larva between her jaws by the neck and was striving hard to proceed forwards. However, the larva was too heavy to carry it forward with ease. After a few trials the wasp began to beat her wings with buzzing sounds Probably while I was away, the mother wasp came back and fell off the brood cell with the larva, or they might fall off the nest separately and the mother might find the young on the terrace. I removed the cover in order to observe the process of the occurrence in detail. The wasp was frightened, dropped the larva and flew away. I excavated the inner side of the brood-cell a little, lest the larva should fall off there and put back the larva again in the cell. The mother wasp returned soon and entered the nest. She appeared in the opened portion of the tunnel with the usual sweeping movement. But as the tunnel had been cut off on one side, she soon lost her footing and fell over the criff. Having risen up, however, the wasp, without showing any confusion, continued her walking progress on the terrace, sweeping the floor as usual, as if she were passing through the tunnel. Meanwhile she ceased the sweeping progress, went to the foot of the perpendicular criff and degan to climb it up, beating her wings violently. At last the wasp succended in reaching the brood-cell and there she found the larva. She examined it with her antennae, held it between her mandibles and moved it slightly hither and thither. At that moment the wasp missed her footing and dropped again on to the terrace with the larva. She rose on the wing in amazement, but at once went to the entrance and would penetrate there. Hindering her entry with my hand, I hurriedly deepened the groove of the tunnel and replaced the larva again in the cell. As soon as the interferance was stopped, the wasp at once entered the nest. She came soon to the exposed portion of the nest, but without being disturbed by the light, passed the tunnel as usual, sweeping the floor with her front pair of legs and arrived at the brood-cell. There, she passed over the pile of victims that I had placed and came to the larva. Again she touched it with her antennae and held it with her jaws, but the next moment she laid it on the floor, moved it a little, held it again and then, dropped once more from the chamber on to the terrace with the larva. The wasp flew up and went at once to the entrance. The same series of manoeuvre and happening was repeated three times further. For the fifth time the wasp caught a fly which had been left aside in front of the entrance since the first time and carried it as usual in the nest. When she came in the exposed tunnel she left the victim on the floor and came to the larva and resumed the same behaviour as stated above.

This observation was made during 10 minutes from 10. 30 a. m.

(4) Wasp No. 78. Sept. 10, 1947. The nest was simple in structure, containing in the cell a larva of the early stage of the 4th instar, with 2 eaten and 7 intact flies. At 10. 30 a. m. I arranged in the nest 4 brood-cells as shown in Figure 10. In A were put the larva of this nest and 2 half-eaten victims, in B a just moulted 4th instar larva of another nest and 2 intact flies, in C 2 untouched flies without a larva and in D 7 intact flies alone. I covered the arrangement with thick layer of sand and left it unobserved until 3 o'clok in the afternoon, when I dug it open. On examining each cell, I found that a very interesting change of contents had been carried out by the wasp. In A were added 7 flies, in B 2 flies, while in C and D the flies were all removed. Moreover, in the tunnel just in front of the entrance to A one more fly was placed. This fly, judging from the species, must be newly brought from outdoors by the wasp.

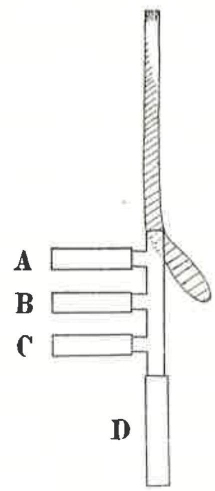


Fig 10. Experimental arrangement in the nest of wasp No. 78.

I exchanged the bottle A together with its contents for C. But I removed two flies from A and put them in C. The next day I saw the wasp repeatedly carrying in a victim to her burrow in the morning. But I left her alone. At 1. 45 p. m. , however, I saw the wasp closing the tunnel permanently, using the tip of her abdomen. So I examined the nest. The contents of each cell were as follows: C — 5 flies, that is to say 3 flies had been added, in spite of the absence of the larva. B — The larva became full-grown and the victims had been all devoured. Careful examination of the remains, however, showed that one fly had been added. A — The larva were also nearly full-grown. Remains of victims showed that 2 flies had been newly brought in. D — Empty. Moreover,

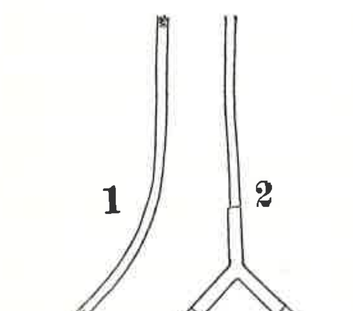


Fig. 11. The nest of wasp No. 102 (1) and the experimental arrangement (2).

in the gallery, between the entrances of B and A one flower fly was left lying.

As to the significance shown by the results, discussion will be given in Part Ⅱ of this paper. But it will be evident that the mother wasp takes special care of the larvae.

(5) Wasp No. 102. Aug. 14, 1948. I dug the nest at 9.20 a.m. The form of the nest and the experimental arrangement set by me are as shown in Figure 11. In the original chamber was a larva of the middle stage of the 4th instar with 12 flies, of which 11 were already eaten. The single intact fly (*Eristalis cerealis*) was taken in at 8.40 in the morning under my observation. So that this nest was one of the interesting exceptional instances wherein the wasp brings the victim to her larva after the store of food has been entirely devoured up. I put in bottle A two intact flies without the larva, while in B the larva and the intact fly.

At 9.37 the wasp came back empty-handed. She came in the tunnel, leading to A, without hesitation. But after entering a step, she stopped, retreated and turned her way to cell B. However, only thrusting her head in the direction, she turned round and went back in the tunnel. She then emerged from the entrance but at once reentered the burrow. At the branching point she again proceeded a step in branch A, but turned at once her way into B and came in the brood-cell. There, she caught the larva between her mandibles and turned it over. As a result the larva came to face backward. The wasp trampled on it to the inner wall, struggled a little against the glass, turned around and went back in the tunnel. She emerged, closed the entrance and flew away. At 10.30, the wasp returned without a booty and entered the nest. But she did not came in the tunnel of glass and soon after flew away. At 10.53, when I examined the nest, the wasp was resting quiety in cell A, with her head directing forward. I covered the bottles with sand. Two minutes later I uncovered the arrangement and found the wasp in her own sand tunnel. From cell A, however, the two flies had been all carried out. One of them was transported in cell B to offer the larva, while the other was carried out of the nest and discarded in front of it. I covered the arrangement again.

At 11.02, when I saw the nest, the discarded fly was disappeared. On examining the cell, I found it placed in cell A. The wasp was still in the tunnel. At 11.30, cell A remained as before, while in cell B one fresh victim was added. The larva in cell B was calmly eating, facing as before inwards. I then introduced 3 maggots of a parasitic fly in cell B, each about 7 mm in length. Moreover, I removed from the cell 2 intact flies, leaving a single half-eaten fly alone. At 11.52, the wasp took in a prey. I uncovered the cells of glass and waited for her coming. She came in cell B straight, touched the larva, turned round and went back in the tunnel. Once more she appeared in the brood-chamber empty-handed, examined the larva, holding it between her antennae, and returned in the tunnel. For the 3rd time of her entrance, she came backing carrying the fly. She trampled over the larva, dragging the victim and placed it just below the mouth of the larva. At that moment her hanging antennae appeared to touch the parasitic maggots, but she paid no attention about them, turned round, strided over the larva and went in the tunnel. At 10.55, she closed the entrance and flew off on the hunting excursion. I removed all the victim once more from both cells, leaving the larva and the maggots in cell B.

At 0.22, I saw the wasp closing the entrance, so I examined the nest. Both the host and the parasites remained as before, indicating that no battle was broken out between them. By the side of the wasp's larva 2 green-bottle flies had been placed and the larva was feeding upon one of them and the maggots upon the other. I exchanged the positions of A and B for each other, placing A on the right and B on the left. At 0.50, the wasp carried in another victim. She came out two minutes later, when I caught and marked her with coloured lac. The victim (*Villa limbatus*) had been taken in cell A, as if to show that she had transported it automatically in the direction of the previous brood-cell. At 2. 50 p. m. I examind the nest. Cell A had become empty, while in cell B had been brought 2 fresh flies and the host and the parasites were all in good condition. In front of the nest had been discarded a newly brought fly and was being dragged by a troop of ants. Nowhere could be found the *Villa*. Probably it also might be discarded and already carried away by the ants. At 4, I examined the nest again, but no change had happened upon the larvae. The next day at 9. 50 a. m. I found the wasp digging a new burrow at another corner of the colony. Two days later I examined the previous nest. The larva in cell B was spinning the silk cocoon., But neither the maggots nor their pupae could be found there. Probably they had gone out of the glass-cell in search of sand to penetrate. The prey were all fragmental, but the close examination made it clear that no flies had been stored in the cell since 2. 50 p. m. of the 14th.

A great many instances showing the mother-wasp's care of her young have been observed, some of which will be described later in connection with some experiments. But the knowledge regarding the problem concerned here can be summarized as follows:

1) Behaviour of mother wasps is variable to a considerable extent according not only to the individual but also to the circumstance. That is to say, they are very plastfc in behaviour. But the general behaviour is:

2) When the wasp carries a booty in her nest, always she lays it aside in the tunnel and comes in the brood-chamber empty-handed. At that time the wasp shows one of the following behaviour: a) Touching the larva with the tip of her antennae, b) touching the larva between the antennae, as if to measure the size, c) touching the larva with her legs during her walking in the cell, d) only thrusting her head in the cell and going back in the tunnel without examining the larva. See Pl. VIII.

The antennal examination according to method (a) mentioned above is most usually observed, while method (b) only rarely occurs. But, when the inner conditions of the nest are changed by some experimental technic and the wasp is forced to obey to some disorder to find her larva, this method of examination, when she meets with the larva, is invariably observed. Method (c) is also observed under the altered condition. Apparently it occurs during the time when the wasp is still more or less in confusion; for instance, when she enters the brood-cell for the 2nd time after the discovery of the larva. While (d) is usually met with during the period when the provisionment of the wasp is very busily carried out. In such cases it appears that the wasp can recognize the existence of the larva througn the sense of smell. But judging from the fact that the same behaviour is also observed at the time when the wasp gathers food in the cell from which the larva has been already removed, it seems also that the wasp makes such behaviour rather automatically.

3) When the food to eat comes to an end or comes to be scanty by the side of the larva, the wasp brings one or two victims to it. The states of the larval food seem to be perceived by the wasp during her examination of the larva, though any special manner can not be observed as to the examination of the victim. The flies that are brought to the larva in such a case are either dragged from the pile accumulated

at the entrance portion of the cell or pulled in directly from the tunnel where a newly brought fly was left alone.

4) The wasp, when the larva of the 4th instar comes too near to the pile of food stored at the entrance portion of the cell, is used to transport it to the middle or posterior portion of the chamber, capturing it between her mandibles. Then she brings several of the flies to it. Thus, it appears that she wants to keep some distance between the larva and the store of food.

5) The wasp, when given under some experimental condition a branched tunnel having an artificial cell at each end, is used to search for the larva in the labyrinth. When she find it in one of the chambers at last, she examines it very carefully. The transportation of the fly that has just been carried in the nest to the brood-cell is always done after she finds the larva. If, in such a case, some victims are placed in the other cell, the wasp would carry them, or some of them, to the larval cell later during her stay in the nest.

6) When the larval cell is long exposed to light, or when something occurs that renders the wasp warn of —— e. g. a sudden change of illumination of light, an approach of a moving shadow or some mechanical shock, etc. —— the wasp always transports the larva to another place, usually to the dark portion of the tunnel.

7) As a rule, the mother wasp takes care of her larva at least until it finishes the final moult in its larval stage. However, once it arrives at the last instar, sooner or later, she ceases her care before the full maturity of it and seals up permanently and elaborately the entrance of the cell. The time of the close of her care seems to vary according not only to the individual, but also to the structural condition of the nest. In general, the care seems to be stopped more early in the nest of the compound type than in the simple one. This tendency was very marked in the instances observed in Chiba.

5. Yet unobservable facts regarding the mother-wasp's care.

The above accounts have been actually observed by me in the course of my investigation. The following, however, have not been able to confirm as yet. Probably such behaviour as described below will not occur in our species.

a) *Trophallaxis.* The trophallaxis or the mutual exchange of food between the abult and the young, this well-known phenomenon among social wasps, ants and termites was also found by E. Roubaud (1910) in *Synagris cornuta*, an African solitary Vespine wasp that feeds her young with masticated pastes of caterpillar. Because of the fact that our *Bembix* shows an interesting relationship between the adult and the young, a special attention has been paid to see if similar phenomenon has been established between them. But, so far as my investigation goes, no such relationship could be observed in our wasps. I have also tested the larvae of the 3rd and the 4th instars of our *Bembix* by touching them with a pencil point, but in no case would they secrete the liquid from their mouth. Whether or not things are the same in the larvae of the earlier instars, I can not say. But judging from the observations made under the natural conditions, the presence of such a relationship seems also to be very improbable.

Trophallaxic relationship is generally admitted as an important element in the phylogenetic development of the social life among the carnivorous insects. Speaking from this point of view, our *Bembix* should be said to stand out of the promising way toward the social life. Then, what is the factor to render the mother wasps of *Bembix* take care of their larvae ? What is the first step toward the social life in them? Quite unknown. It seems certain, however, that there is something on the part of the mother wasp that plays a more important part than the trophallaxic relationship in the first step toward the social life. Something — that may be something like an interest or a curiosity in looking after the egg and the larva that suddenly appeared in the nervous activity of the mother wasp.

b) *Specially prepared food for the hatching larva.* In his biological accounts on *B. spinolae*, J. B. Parker (1917) described as follow : "It is my conviction that the flies on which the young larva first feeds are crushed or macerated for it by the mother wasp. In no case did I find a newly-hatched larva in my breeding cell able to feed upon house-flies that were given to it intact and a number of such larvae died for me before I discovered this. By crushing the flies thereafter so as to permit the larva to reach the internal organs it fed freely and after a day or two it had no difficulty in feeding upon flies that were given intact".

As previously stated, the victims that were fed upon by the newly-hatched larva of our *Bembix* are either the pedestal of the egg or the 2nd or the 3rd fly that is placed by the side of the pedestal. And so far as my examinations go, no special manipulation for such a purpose as supposed by Parker has ever been observed upon any material dealt with by me. The newly-hatched larva is always observed feeding upon the intact fly. But I have the same experience as stated by Parker in that the breeding of young larvae is never succeeded in the laboratory. Whether or not the fact is caused by the mechanical shocks given in the course of transportation of them from the field to the laboratory, I have not as yet confirmed experimentally. But the larvae of the last instar that were brought to the laboratory by the same way have been reared very easily. On the other hand, the young larvae that were fairly roughly treated in the field but that were placed again under the care of Bembicine nurses, were observed to develop as safely as in the untouched companions. These data seem to me to give a suggestion that the mother wasp may give some help to the young larva. But what is that help I can not say. It seems to me quite improbable, however, that such particular care on the part of the mother wasp as stated by Paker occurs in our species also. At any rate, it is certain that the larva of our *Bembix* is always fed with, and can feed upon, intact flies from the first.

6) True phase of the feeding habits of *Bembix*

It was pointed out in detail elsewhere in this article that the provisioning activities of our *Bembix* are carried out progressively from day to day until the time when the mother wasp stops the care of her larva, but at the same time it was shown that the hunting and the bringing-in of the prey is not made according to the request of the larval appetite or from hour to hour during a day. Indeed, the wasp is used to *store* the larval food in a corner of the brood-cell, and besides she collects it rather concentrically within a short period of the morning. Speaking from such a point of view, the food-getting habits of our *Bembix* should be referred to the category of progressive mass-provisiorment rather than to that of the simple progressive provisionment.

According to the literature regarding other species of *Bembix* similar phenomenon seems to occur rather universally in the memberes of the genus. However, no investigator has ever paid a particular attention to the fact. Fabre, when he observed a large number of victims stored in a cell, attributed the phenomenon merely to the mother-wasp's precaution for the unfavourable weather. He was of the opinion that the wasp had a presentiment of the coming bad weather and stored food of the larva in such a case in abvance to feed it during the time. In the normal case, however, the wasp, he supposed, brings the victim in accordance with the request of the larva from hour to hour as in the social wasps. But, in reality, the phenomenon that he odserved is nothing but the normal procedure of the wasp's activity.

When it is true that the mass-provisionment repeated daily and progressively by the mother wasp is the normal procdure of the feeding activity of the *Bembix* it is naturally supposed that the adult wasp, like other hunting-wasps, will show no concern whatever as to the food once it has been taken in the larval cell, and that the larva will eat by itself the food thus piled up in a corner of the cell one after the other from behind. Contrary to the supposition, despite that the method of gathering food is carried out according to the fashion of mass-provisionment (only repeated from day to day), the manner of feeding the larva in her nest is, in reality, quite different from our supposition. Things occur rather in the same manner as has been supposed by Fabre for the case of the unfavourable weather. That is to say, the mother wasp is used to bring food from time to time from the store at the entrance of the cell to the side of the larva. At the same time she pays an attention lest the larva should approach too near to the store of food. Therefore when she finds the larva by the side of the store of food, she catches it between her jaws and carries it to the middle or posterior portion of the cell.

According to the knowledge summerized here it will generally be said that the feeding method of *Bembix* has been appreciated too much with regard to the outdoor activities and too little with regard to the activities inside the nest. In reality, their activities outside the nest are somewhat more primitive than have been accepted by many investigators and at the same time more interesting from the point of view of the development of instinct. While their activities inside the nest is more advanced and more interesting than have been supposed by the previous authors. The former shows an intermediate state between the mass-feeding of the majority of the hunting wasps and the progressive feeding of the social wasps; while the latter indicates a state very close to the behaviour of the ants, save that the prey are offered intact.

ADDENDA

1. **Moulting.** In Aug., 1951, I had a chance of observing the process of the larval moulting. When I took notice, a 3rd instar larva in one of my glass cells was shedding its skin. The head of the 4th instar larva had just appeared from the crevice at the first bodily segment, just behind the old cranium, which, with the trembles of the larval body, slowly slid along the ventral side of the trunk. Soon it reached about the middle of the abdomen and stopped there. At this stage the moulting appeared to be practically finished. The larva, after a short rest, soon began to eat. According to three other instances which occurred under my eyes in the same year, it seems to be a normal procedure that the moulting is practically finished at this stage. Because in all these instances the larva began to eat, with the shed case of the head attached to the middle of the ventral surface. Moreover, in one instance it was still observed *in situ* on the following day, after about twenty hours. The skin is apparently shed gradually afterwards by the increasing plumpness of the larval body.

2. **States of the pedestal fly.** In the year 1951, I observed with particular care the states of the pedestal insects with which I happened to meet. In the greater part of the instances, the flies were completely dead, corroborating the results of my previous observations. But in some cases, the fly was fairly vivid after the egg was deposited and remained still alive even on the following day. After 24 hours, however, they became very weakened and were nearly in a dead state. In this respect they, too, do not form any exceptional instance against my opinion regarding the significance of the first prey in this species. The details are as follws:

1) Aug. 7. The fly was *Musca* sp. It was examined 3 hours after being taken in the nest. The egg was normally deposited. The pedestal insect was completely motionless, showing no sign of life.

2) Aug. 7. *Sarcophaga* sp. The egg was without any symptom of hatching out as yet, though the time of capture of the supporting fly was undecided. Possibly it had been brought in the cell within several hours. Despite that, it was completely in a motionless state, showing no movement whatever at any part of the body.

3) Aug. 16. A large specimen of *Sarcophaga* sp. At 9.30 a.m., the fly was seen to be carried in. At 10.20 a.m., when examined, it showed no sign of life.

4) Aug. 16. *Heterochrysops van-der-wulpi* Kröber. The fly was observed to be taken in at 9.10 a.m. An hour later when I examined, it was already completely dead, though the body remained still soft and vivid.

5) Aug. 21. *Musca domestica* L. The egg was as yet very fresh, but the fly showed no mevement whatever at any part of the body.

6) The same day as above. A large specimen belonging to Stomoxyidae. It was carried in the nest at 2.36 p.m. when examined, the fly showed no respiratory

nor visceral movements at all. But a very feeble trembling was observed on the left front tarsus alone. The next day at 7 a.m., it was completely dead.

7) The same day. A large specimen of *Sarcophaga albiceps* Meigen. The egg was very fresh, showing no symptom of hatching out. Only the very weak respiratory movements could be observed on the abdomen of the fly. Five hours later, however, it can hardly be observed.

8) Aug. 23. A small example belonging to Tachinidae. It was observed to be taken in the nest at 1.27 p.m. When examined at 3.40 and at 8 p.m. respectively, a fairly active respiratory movement and a rather dull movement of the proboscis could be observed on the fly. On the 24th, at 8 a.m., the movements were fairly active as before and some excretion had been made. At noon, however, all the movements became very feeble. At 6 p.m. of the same day, the fly were in a completely motionless state. Possibly it was dead.

9) Aug. 23. At 0.30 p.m., the pedestal fly (*Sarcophaga* sp.) was taken in. At 3.00 p.m. when dug out, the fly showed a fairly clear respiratory as well as a visceral movement. In addition, the mouth parts were repeatedly protruded and contracted. At 6.00 p.m., the movement remained as before and moreover, the insect had excreted. However, at noon of the subsequent day, only a very faint respiratory movement was observed on the abdomen of the insect. This state continued till 6.00 p.m. with increasing faintness of the movement. At 9.00 p.m. when I examined the fly, it was completely dead.

That the flies of the last two instances, although they were very active in the vegetative movements when observed several hours after being operated by the wasp, quickly became inactive before 24 hours elapsed seems to give a strong support to my consideration. When we compare the longevity of these flies with that shown in Table 8 (p. 99), it seems most probable that some particular manipulation has been given upon the flies by the wasp before oviposition are carried out.

3. **Orientation of the egg.** In connection with the observations mentioned above, a special attention was given on the orientation of the wasp's egg upon the pedestal fly. Out of the above described nine instances, two (Nos. 2 and 4) showed that the egg supported by the fly was abnormally deposited, that is to say, deposited with its ventral side not directing toward the pedestal. In No. 2, it faced forwards and outwards, and in No. 4 nearly completely outwards. Though the eggs were desiccated in my laboratory, it is naturally supposed that the larva hatched out from such an egg will eat first other flies than the pedestal under the natural condition.

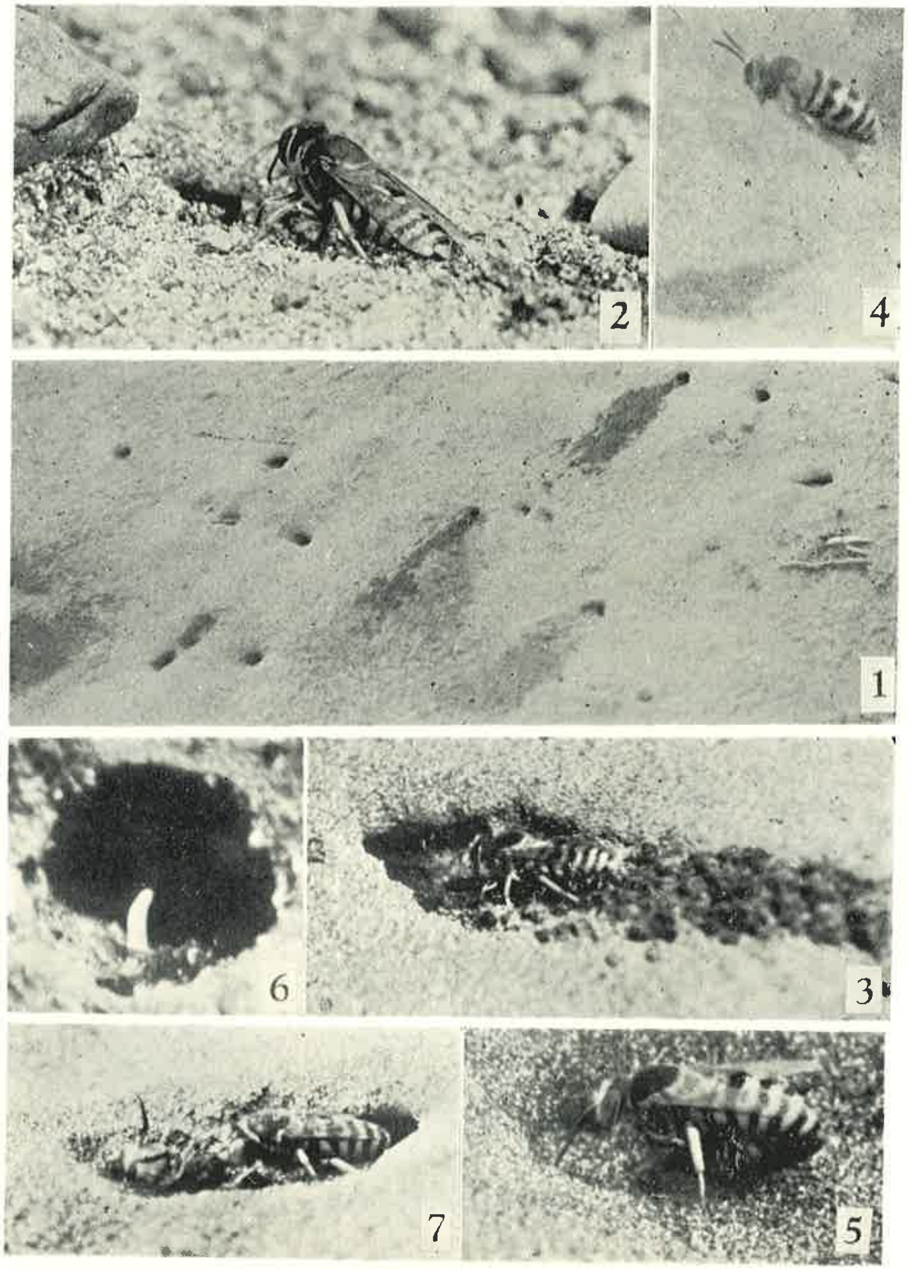
4. **Shift of the nesting site.** Judging from the strong instinct of homing in *Bembix* it seems natural to suppose that the wasp, once she determines her nesting place in a certain place forming a colony with her comrades, would live on within the area during her lifetime. In the course of my investigation on the structure of the nests succedingly constructed by the same individual wasp, however, I became aware of the fact that my numbered wasps gradually disappeared one after the other from the settlement. I could not persue the activities of a wasp concerning more than

three of her nests. Among them some might escape from my eyes depending in the main upon the weakening marking. But as I carefully numbered them by placing a coloured lac on the median segment, lest it should be denudated during their subterranean activities, such individuals were expected to be small in number. Despite that, the wasps bearing the number-marks disappeared day after day and, on the contrary, nearly as many of the unnumbered wasps joined the members of the colony. Probably each wasp has a habit of shifting its nesting site from time to time from one settlement to another. This phenomenon seems rather curious in the members of the so-called subsocial wasps, but it may have some biological significance in relation to the dispersion of the species —— dispersion not directly of the adult wasps, but of the progenies.

Explanation of Pl. V.

1. A colony of *Bembix niponica* Smith, with working wasps and abandoned burrows.
2. A burrowing wasp.
3. Ditto.
4. A wasp coming back with a prey.
5. A wasp clearing the entrance closure, with a booty under her abdomen.
6. A standing egg, seen from the entrance of the cell.
7. A wasp returns from the inspection of the brood-cell and is about to catch the fly left in the tunnel (photo. after the tunnel is dug open)

(Photo. K. Tsuneki)



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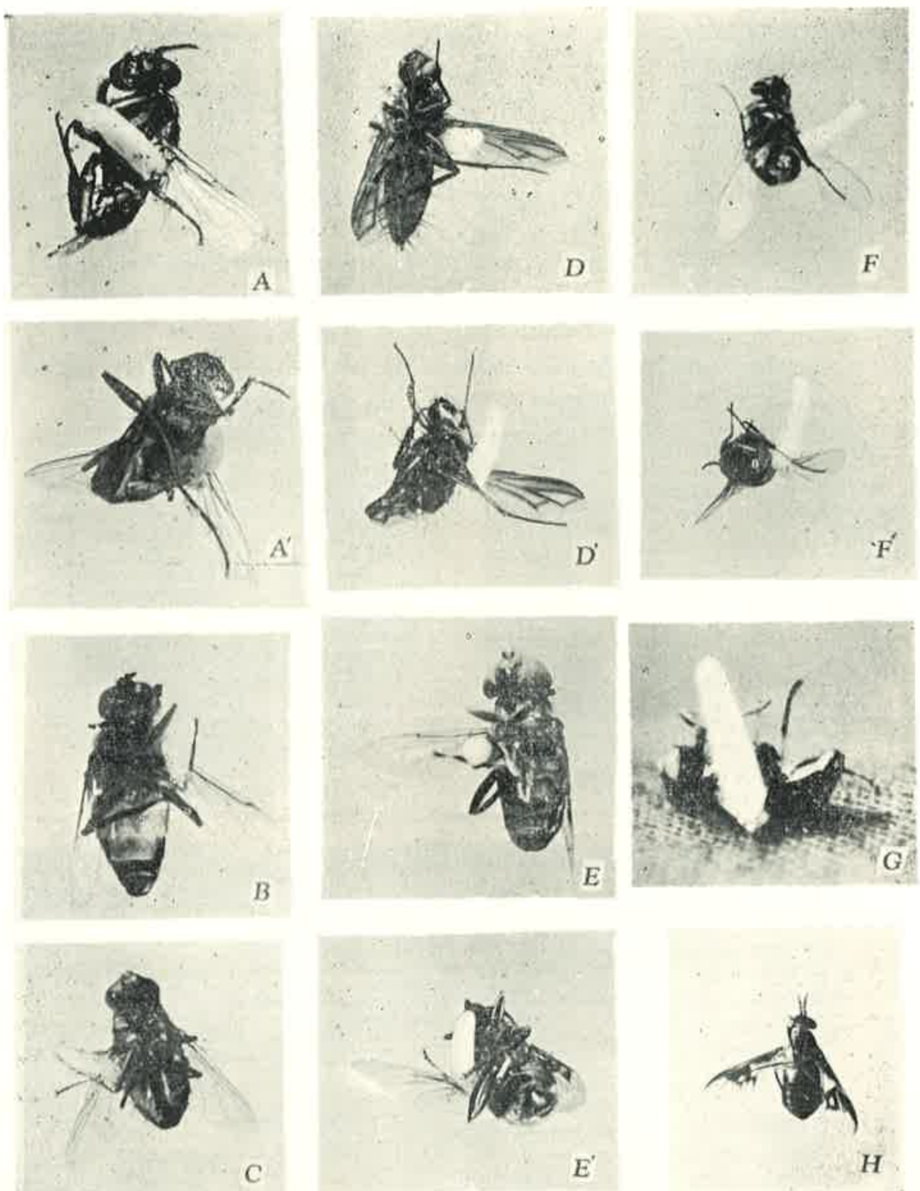
Explanation of Pl. VI.

Pedestal flies each with a wasp's egg. Those marked with the same letter (one with a dash) are the same individual viewed in the different direction. Notice the middle leg of the fly dislocated and pressing from above the half opened wing in Figs. A (A′), D (D′), F (F′) and H. In these instances the front leg of the same side is also distinctly dislocated and stretched forwards. While in others the middle leg is only dislocated, but not manipulated in such a manner as in the others, the manipulation on the front leg being also slight.

(Photo. K. Tsuneki)



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Explanation of Pl. VII.

A … The instars of the larva, numerals 1 – 4 showing respectively the 1st, 2nd, 3rd and 4th instar (4/5 of natural size).

B … The larva of the final instar in the artificial chamber in the Petri dish.

C … The most dreadful enemy of *Bembix niponica* Sm., the larva of *Acanthaclisis japonica* MacLachlan (5/4).

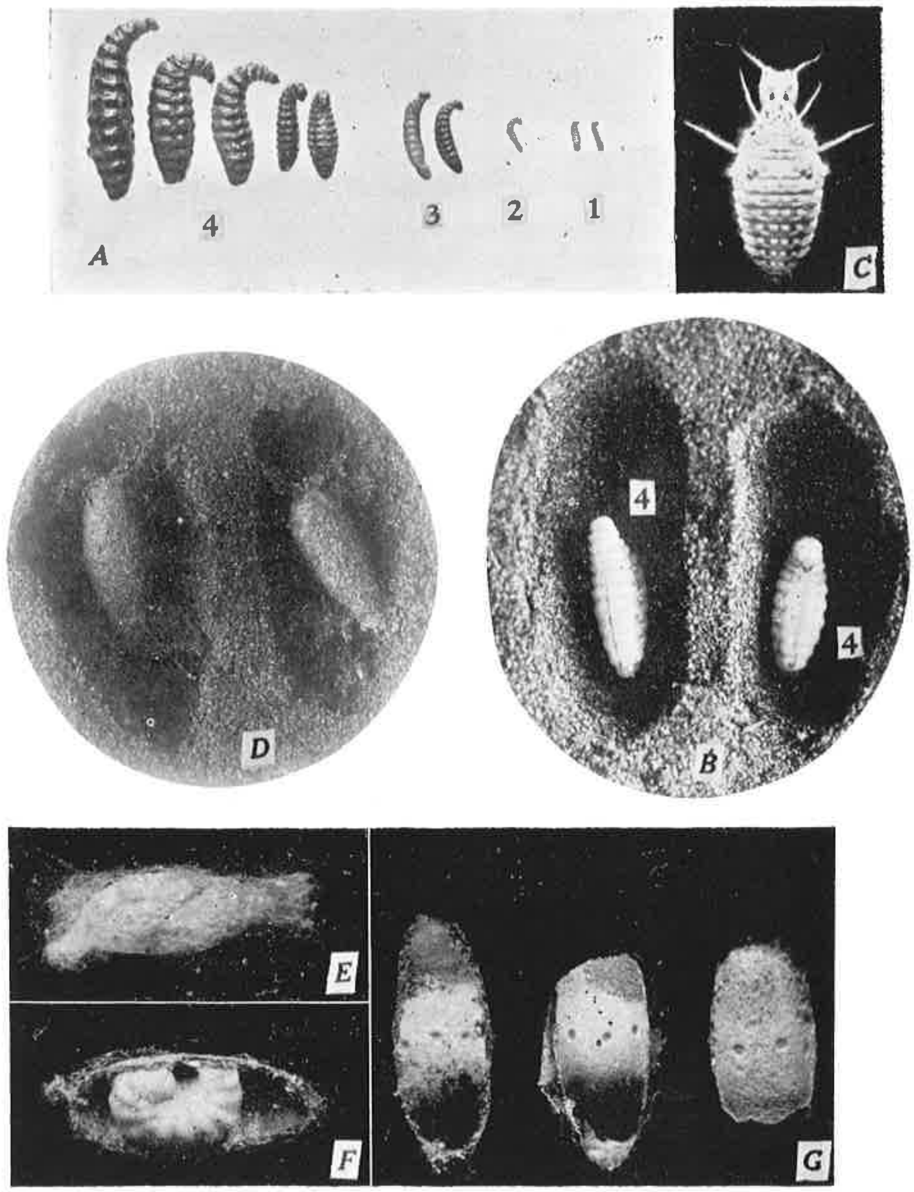
D … The cocoon of the wasp, made in the artificial chamber in the Petri dish. At the broad end, the trace of the funnel can be seen (4/5).

E … The silk cocoon that is first spun by the larva.

F … The so-called prepuppa of the wasp in the cocoon.

G … Inner surface of the cocoon, showing the respiratory pores.

(Photo. K. Tsunei)



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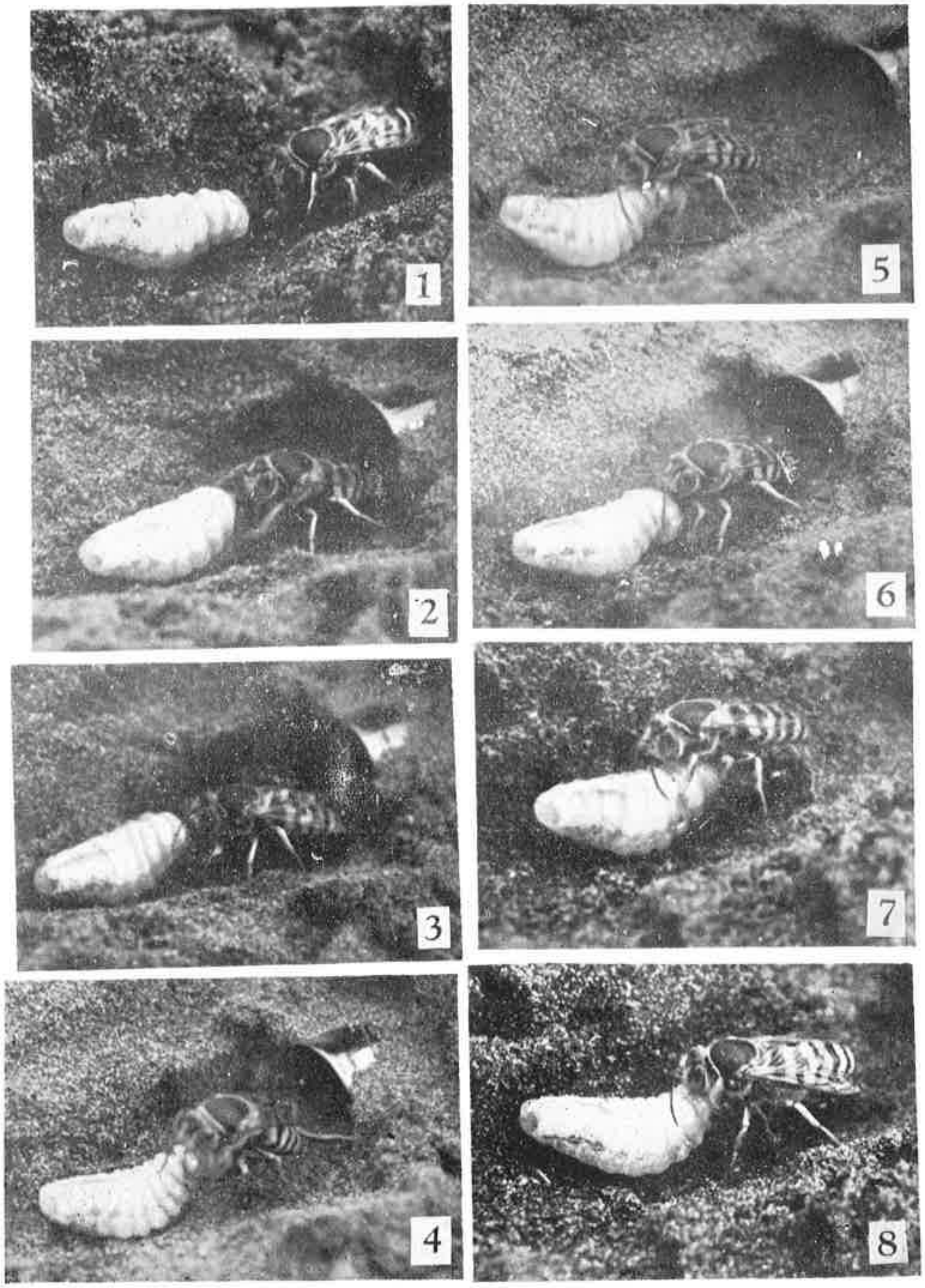
Explanation of Pl. VIII.

The mother wasp's care of her young.

Photographed after removing the glass chamber and placing the larva on the exposed hollw. The mother wasp came in the brood cell (1), touched the larva with her antennae (2 and 3), examined it carefully between the antennae (3 - 7), and caught it with the jaws to drag it to the dark portion of the tunnel. Near the upper right corner (2 - 6) the end of the glass tunnel can be seen.

(Photo. K. Tsuneki)



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