

Occasional Publication of the Biological Laboratory Fukui University, Japan

No. 38.

GLEANINGS ON THE BIONOMICS OF THE EAST-ASIATIC NON-SOCIAL WASPS (HYMENOPTERA)

I. Some Species of Oxybelus (Sphecidae)

By K. TSUNEKI (Biological Laboratory, Fukui University)

GLEANINGS ON THE BIONOMICS OF THE EAST-ASIATIC NON-SOCIAL WASPS (HYMENOPTERA)

I. Some Species of Oxybelus (Sphecidae)*

By K. TSUNEKI (Biological Laboratory, Fukui University)

Introduction

Under the title above given I will treat in a series the nesting biology of mainly the fossorial and diplopterous wasps occurring in East Asia, some of which were once published in Japanese. In order to contribute to the worldwide knowledge, however, I am intending to reproduce them from my original notes. Most of the unpublished data were obtained more than a score of years ago. But I believe that they are as fresh as those recently obtained.

The purpose of the present and the following papers is to provide the persons interested in this field with the raw material and not to synthesize the knowledge hitherto acquired in regard to the species, genus, tribe or the family to which the observed specimen(s) belongs. As a rule, therefore, the comparison with the data of other regions is confined to the minimum. But, some of the knowledge obtained in Japan by some other authors and published in Japanese will comparatively be summarized as occasion demands.

OXYBELUS VENUSTUS SICKMANN

On the ground of our camp, while I stayed in Peking, North China, as a called-out soldier at the beginning of the so-called Chino-Japanese Conflict that preceded the Second World War, I found a flourishing population of the small wasps of this species making their nests. The place was used by the soldiers as a tenis court or a base-ball ground in the evening every day and their nesting site was seriously disturbed and damaged by the hobnailed shoes. Every forenoon, therefore, I saw many of the wasps hovering over the ground with their prey in search of their nests. The males and other undisturbed females were seen crowded on the flowers of the pot-planted orange trees and I could catch them with my fingers as many as I would.

On June 2, 1938, in the evening after my task was over I went to a spot outside the tenis court and dug two nests. The ground was roamy, but was mixed with abundant fragments of bricks, roof tiles and plaster and the tunnel of the nests was sometimes irregularly turned and bent to avoid the obstacles.

Nest 1. The tunnel went to the north for 2 cm in a gentle inclination and suddenly turned at a nearly right angle to the left, then became somewhat steep and proceeded 2 cm further. It again turned a little to the right and penetrated in a steep inclination into the ground. The tunnel was about 3 mm in diameter and seemed to be comparatively broad as the nest of such a pigmy wasp. At the end, about 12 cm below the surface, I found the wasp sitting and behind her an incompleted broad-chamber. In the chamber a paralysed Musca-like fly was placed without carrying the egg of the wasp. The chamber was somewhat broader than the tunnel, but the inside wall was not polished.

Nest 2. The tunnel went obliquely for the first 4 cm and then steeply entered the ground, forming more than 70° inclination with the surface of the ground. At a depth of 13 cm below

^{*} Contribution No. 127 from the Biological Laboratory, Fukui University, Japan.

the surface the inclination became gentle and the tunnel was somewhat enlarged. There I found the owner of the nest and 4 flies. The body orientation of the flies was uncertain, some being side up and some others venter up. I could not find the egg of the wasp on any of them.

The entrance of the nest was very simply closed when the wasp stayed inside. The closure was so loose and thin that it was easily opened by a blow or two of my breath. While the wasp was out, however, the closure seemed somewhat compact and the returning wasp had to clear the way by the quick movement of her fore legs.

Nest building. The manner of burrowing of the wasp was very much like that of the Bembicine wasps. She bit off the surface soil with her mandibles and swept the debris backward through the underside of her abdomen with her front pair of legs. Her movement was considerably prompt and the hollow was soon deepened to make the working wasp invisible. At intervals the wasp came backing out of the tunnel with a burden of soil or a pebble to throw it backward at the entrance. When the burrow became fairly deepened, if not completed, the wasp closed the entrance temporarily and flew away. At the time of her departure she gathered together the closing material from the surroundings, keeping her abdomen in the tunnel to support the material collected. But it was pulled out little by little and the rôle of the stopper was replaced by the material. She then leveled the surface once or twice before flying off.

Methed of the prey carriage. While the wasp was very slowly flying with a prey in search of her nest the surface of which had been disturbed I carefully observed her to know how she held her prey. Certainly it was held by the wasp venter to venter under and somewhat behind her abdomen, but it was hardly possible to ascertain by which of the legs the fly was kept. Apparently it was held by the hind pair of legs. But the thought was soon denied by seeing that the wasp stood on her head using the hind legs at the entrance to her nest to remove the filling soil and that as soon as the wasp entered the nest with the prey the loose soil was pushed out and closed the entrance, probably by the hind pair of legs. On the other hand the rôle was not played by one or both of the middle pair of legs as usually done by many of the hunting wasps, because I could confirm with care while the wasp stood at the entrance that none of the 6 legs was used to support the fly. I further observed at the same time that the end segment of the wasp was strongly bent down like a hook and the fly was distinctly protruded beyond the tip of her abdomen. Did the wasp hold the prey by such curious means using the flexible caudal segment of the abdomen?

Before arriving at the final conclusion I had to go to the front, but the next year I returned to the Peking camp again. On May 20, I again had a chance of observation upon the wasps of this species. Despite the apparent serious disturbance they received the wasps of the previous year certainly succeeded in leaving a number of their offsprings and these wasps formed a flourishing colony as in their previous generation, although the everyday disturbance of their nesting site remained quite unchanged.

Soon I reconfirmed repeatedly my observation done the year before. Certainly the wasp who carried a prey always bent down the last segment of her abdomen. In some of the wasps the fly was transversely held, producing its abdomen sideways. I thought that the prey was held by the neck with the strongly bent caudal segment of the huntress¹⁾.

Nest 3. On May 22, 1939, I dug 5 nests and with 3 of them succeeded in following the

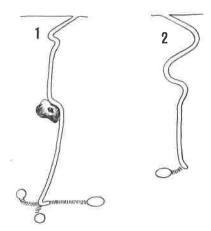
¹⁾ In my "A Naturalist at the Front" (in Japanese) I wrote the method of the prey carriage in this species as such. But the later studies on other species of the genus, especially on O. bipunctatus made it clear that my observation was incomplete and in this species also the method related by the previous authors was supposed to have been adopted (see section of O. bipunctatus).

tunnel up to the brood-cells. This was the first one of them.

The entrance tunnel was gentle in inclination for 2 cm, then suddenly turned downwards and almost perpendicularly penetrated into the ground for 9 cm to reach the end. The place was not the simple closure at the entrance to the larval cell, but was very hard as if to be the end of the incomplete tunnel. But I enlarged the excavation around the place for trial and could quite unexpectedly dig out 5 flies in a mass. The state of the brood-cell and the tunnel to it were, of course, unobservable. Also the egg or the larva of the wasp.

Nest 4. In this nest (Fig. 1) also the entrance gallery was gently sloped for 2 cm, of which the first half was filled with soil. Then the tunnel curved downward nearly perpendicularly, drawing a spiral on the way and went onto a stone. It proceeded gently along its surface for 1 cm and again penetrated almost perpendicularly to 14 cm below the surface. There it abruptly became horizontal, but soon reached the end. I searched the extention of the cul-de-sack which was tightly packed with soil and after 3 cm excavation could discover a cell. In the cell there were 3 flies stored, but they were heavily covered with mould into a mass and the offspring of the wasp had already been missed. I further enlarged the excavation to know if there were other cells hidden, because the structure of this nest suggested to me that it was compound in form.

As I expected I could find out 2 other cells each lying in a different direction, 2 and 1.5 cm respectively distant from the end of the perpendicular tunnel. The cells were melon-shaped, 7-8 mm in length, about 5 mm in width containing a cocoon within. The cocoon was about 6×3.5 mm in dimensions, ashy brown in colour, without being inlaid with sand particles, contrary of the case in the Japanese congeners. It was attached to the inner wall of the cell with one of its ends and covered with the remains of the flies. These remains informed me that the prey offered to the larvae were 3 and 4 in number respectively. I cut open one of them and found that the larva was soon after cocoon-spinning and before entering the prepupal stage, because in its abdomen the blackish feces could be seen.



Figs. 1-2. Nests of Oxybelus venustus Sickmann (lateral view).

.Nest 5. The tunnel (Fig. 2) was curved and turned without any obstacle. By enlarging the excavation from the end of the tunnel I could find out only one larval cell which contained a cocoon in it. It was located at the same level as that of the tunnel end and 12 cm below the surface of the ground. The cell and the cocoon size and their characters were approximately the same as in the previous nest.

Summary. This species nests in the hard clayey ground and builds the compound nest. The cells are located 12-14 cm below the surface and provisioned with 3-5 flies of the *Muscatype*. When the wasp leaves the nest she closes the entrance and leveled the debris. At the first departure the wasp shows behaviour which is considered to be the locality study. The prey is not held with any of the legs, but is supported with the strongly bent end segment of the abdomen. Probably the sting is used to impail the fly. The prey collected in the incomplete cell do not carry the egg of the wasp. The coccon is not inlaid with sand grains.

OXYBELUS NIPPONICUS TSUNEKI

On the biology of this species I already briefly touched on in No. 16 of this Publication in connection with the description of the species. But, for the benefit of the comparison I will reproduce the account in the following.

The records written on my old notebook were the incomplete observations attempted while I stayed in the barrack in the suburbs of Chiba, east of Tokyo, as a called out soldier about 40 years ago. The nesting site of this species was found on a small bare patch of the ground located between the roam bank and the broad way running along the sea-shore. The patch of the ground was leveled, abandoned and sunny, with a favourable hardness for nesting of the fossorial wasps. So the area was beloved by the sand wasps of various species such as *Bembix niponica* Smith, *Bembecinus hungaricus japonicus*, *Cerceris arenaria*, *Cerceris albofasciata* and frequently utilized as their nesting place by some vagabond spider wasps. Among them the tiny wasps of the named species formed a scattered colony.

The earth was loamy and considerably tight for the upper 2 cm, but below there it became sandy and was easily crambled.

(1) July 9, 1932. I found a number of small openings on the place, 2.5–3.0 mm in diameter and dug several of them. I could collect the following knowledge on this species:

Most of the tunnels went in the earth perpendicularly from the beginning, but sometimes it made a certain (usually fairly steep) angle with the ground surface and in some nests the tunnel was curved on the way. Usually it ended 6-8 cm below the surface in turning horizontal and was somewhat enlarged into a brood-cell. In such cells I found 5 cocoons, all being inlaid with sand grains and mostly the old ones that were cut open at an end. They were elongated egg-shaped and about 5×3 mm in size.

- (2) The same day I dug one other nest to which a wasp carried in a prey. The tunnel went in the earth in a gentle inclination and the larval cell at the end was located 7 cm below the surface and 8 cm horizontally apart from the entrance and contained 4 flies, 2 being the gnat-shaped ones of about 1.5 mm in length and the remaing 2 the common fly-shaped of about 2.5 mm in length. The egg of the wasp could not be discovered.
- (3) July 16, the same year. When I arrived at the place to study mainly the life of *Bembix niponica* the surface of the earth was evened and tightened by the rain of the day before. While I was waiting the return of the marked *Bembix* I tried to examine several nests of the *Oxybelus*, but in only 2 of them I could find the larval cell, all others being either the incomplete nests or the old ones.

The larval cell of one of the succeeded nests was located 8 cm just below the entrance of the nest and contained 8 small flies of the 2 types mentioned in relation to No. 2. On none of them, however, could I find the egg of the wasp.

The other nest also penetrated into the earth almost perpendicularly and around the end of the tunnel I found 3 cells, located different in direction and also somewhat different in depth, 8, 9 and 9.5 cm below the surface.

- Cell 1. 7 small flies of probably Simuliidae or the like and 1 somewhat large fly of Anthomyiidae
 - Cell 2. 15 small gnat-like flies, with a small larva of the wasp.
 - Cell 3. 6 small flies and 2 somewhat large flies of probably Anthomyiidae.

In cells 1 and 3 probably there was a larva or an egg of the wasp but I could not find them out.

(4) July 23. Near the end of the almost perpendicular tunnel, about 10 mm in depth, I obtained 34 flies, all being less than 3 mm in length. The flies were dug out by a scoop of a driver and the details regarding the cell or cells in which they had been provisioned remained unknown. But I found on one of them an egg of the wasp which was attached to the underside of the neck and laid crosswise. It was about 2 mm in length, wax-white in colour and slightly curved.

Summary. The nest is simple or compound. The prey, flies of Simulidae? and Anthomyidae, are possibly stored provisionally in the cell. The cells are made 6-10 cm below the surface. The egg is attached to the underside of the neck of the prey and laid crosswise. The cocoon is made of sand grains.

OXYBELUS STRANDI YASUMATSU

An observation in Tokyo. While I was a student, in a small orchard in the (old) city of Toky I happened to find a small wasp carrying something under its body. It walked about on the ground within a certain limited area under the peach tree. Possibly it searched about for the entrance to the nest which was disturbed by my foot-prints. As it could not succeeded in finding out the nest and as I was not allowed to observe such a thing during the practice hour I captured the wasp with its prey. The prey was a fly, a male of possibly a Muscid fly. I hurriedly dug out the place where the wasp obstinately walked about and from about 7 cm below the surface I could obtain 2 flies of the same species as was carried by the wasp and 1 other black glittering fly. My digging was a disordered attempt and anything about the larval cell or the offspring of the wasp could not be confirmed.

After my return to my lodging I could know that the wasp belonged to the genus Oxybelus and the flies were 3 Fannia canicularis L. and 1 Ophyra leucostoma Wied. This was the first of my encounter with this species. It was June 3, 1930. Several years later the wasp was named by Mr. K. Yasumatsu in honour of the famous Entomologist as strandi.

Observations in Sapporo. Fifteen years later, in 1945, when I was given a post as an assistant at the Zoological Institute of Hokkaido University, I happened to find a colony of this species on the deserted lane in the Botanical Garden of Sapporo. Near the end of World War II, the Garden was ill-kept. The flower beds were all planted with potatoes and cabbages and the lanes were occupied here and there by the colonies of various species of the digger wasps and solitary bees. During my study on the homing ability of Cerceris hortivaga (Tsuneki: Etizenia, 9, 1965) I knew that a number of the wasps of this Oxybelus lived at the same area, They occupied mostly the side part of the lane, while the Cerceris mostly the central part, thus showing a phenomenon of the so-called 'habitat segregation'.

Similar to the nest entrance of the *Cerceris*, in this species also a small mound of soil was piled up at the opening, but it was smaller than that of the *Cerceris*. The entrance of the nest was usually left open, but sometimes partly or wholly closed loosely with soil. When the wasp came back she did not drop the prey at the entrance to clear the stoppage of the tunnel, but dashed into it with the prey immediately from in the air and penetrated further with it. When the entrance is more or less closed with the soil she opened it with her front pair of legs, without letting the prey off.

During the transportation of the prey the wasp did not use any of her legs to hold it. It was ascertained by observing that a wasp carrying a prey stood on its six legs when she alighted near the entrance to the nest. I saw at the same time that the end segment of the abdomen was

strongly bent down as if to hold the prey by its neck. I could not confirm, however, whether or not the sting was used in this case as was mentioned by J. H. Fabre. But it was certain that the hind legs did not play any part in carrying the fly against the opinion of G. and E. Peckhams.

- Nest 1. August 11. The nest (Fig. 3) was comparatively shallowly made and the tunnel was throughout loosely filled with soil. The larval cell at the end of the tunnel was laid 3 cm below the surface up to its ceiling. It was about 10×6 mm in size and contained 3 prey of Ophyra leucostoma, but the egg of the wasp could not be found on any of them.
- Nest 2. The nest was as given in Figure 4, a and b. It was also made shallow and the larval cell was filled with the cocoon of the larva and the remains of its food. The cocoon was made of sand grains, $6 \times 3.5 \times 3.5$ mm in dimensions. In this nest the larval cell was somewhat inclined and the ceiling of its main part was situated about 3 cm below the surface.
- Nest 3. During the work of digging of nest 2 I found at the same depth the other larval cell which also contained a cocoon. But the tunnel leading to it, together with its entrance was unknown. But probably the cell did not belong to nest 2, but to the separate one, because in the case of such a shallow and simple nest the occurrence of the compound type could not be considered.
- Nest 4. August 24. I saw a wasp, after a moment's slow flight above the opening, directly fly into the entrance carrying a fly at the end of her abdomen. She at once pushed out the soil behind her. I at once dug the tunnel to follow her. She was proceeding in the tunnel by clearing the loose packing of soil without letting off the fly. Soon, however, she took notice of my digging immediately after her, dropped the prey and flew off. I independently followed the tunnel by discerning the loose filling from the hard texture of the surrounding earth and could reach the larval cell which lay exceptionally deep in this species at about 7 cm below the surface. In the cell were already stored 4 flies of Ophyra leucostoma and on one of which lying toward the interior was attached the egg of the wasp. It was wax-white, slightly bent, about 2.5 mm in length and was glued to the neck of the fly, slightly deviating from the central line to the left, with its cephalic end and with the caudal end reaching between the fore and middle legs of the other side.

This nest was suggestive as to the time of oviposition of the wasp. In the cell was already present the wasp's egg and yet she was carrying in the prey.

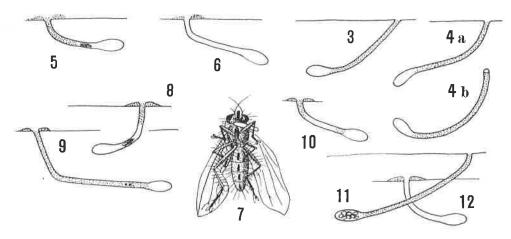
Nest 5. September 3. The entrance of the nest was open at the centre of the semispherical mound of soil and the tunnel went nearly perpendicularly in the earth for about 7 cm. But before reaching there I found 2 flies of Lucilia sp. buried in the filling of soil. Apparently there was no larval cell at the end, though I dug broadly around the end of the tunnel in search of the completed cell.

This nest was also suggestive in regard to the method of provisioning.

- Nest 6. The same day. I saw a wasp close the entrance by using the soil that formed the entrance mound and then simply level there. When she flew away I at once dug the nest. From about 3 cm below the surface I dug out 3 flies of *Lucilia* sp., all without the egg of the wasp. But the details regarding the larval cell could not be observed.
- Nest 7. (Fig. 5). The same day. The tunnel was short and loosely filled with soil throughout and the larval cell was made shallow, only 12 mm below the surface to its roof. The wasp was found sitting in front of the brood-chamber with her head forward. The cell was melon-shaped, measured 12×7 mm (comparatively large) and included 8 male flies of Ophyra leucostoma. Their body orientation was uncertain, though their heads were invariably directed inwards. I could not find out the wasp's egg on any of the flies provisioned.

Nest 8. (Fig. 6). The tunnel was throughout fairly compactly packed with soil and in the larval cell 5 prey of Anthomyiid flies, the same species and all males, were stored. On one of the prey that was laid venter up and at the innermost portion of the cell I found an egg of the wasp. It was attached to the underside of the neck of the fly with its anterior end (Fig. 7). It was slightly less than 3 mm long and wax-white in colour and very faintly curved.

Nest 9. September 4, on the same day nests 10–13 were also observed. The entrance of nest 9 was closed and around it a small mound of soil was heaped up. A female wasp that I later caught and confirmed came from time to time to the place and tried to enter. Everytime however, after penetrated 1 or 2 cm she was hurriedly came out and flew away. After her final attempt I saw in the half-opened tunnel the face of another wasp. I dug the nest and knew that



Figs. 5-12. 5-6, 8-12: Nests of Oxybelus strandi Yasumatsu (lateral view, 4b ... dorsal view of 4a). 7: A prey carrying the egg of the wasp.

the wasp sat in front of the larval cell with her head outward, with the entrance gallery closed. The cell was shallowly made, only 2 cm below the surface and the tunnel leading to it was only 3 cm in length, at the first half nearly perpendicular and loosely closed with soil and at the final half in a gentle inclination and open where the wasp was present. The entrance to the larval cell was without the packing and the cell appeared to have been completely built in structure, but it was still empty (Fig. 8).

It seemed to me that the first wasp was the owner of nest 6 that was situated 20 cm distant from nest 9 and was destroyed by me the day before. After my examination the wasp of this nest was seen several times to return to the place and to try to dig the leveled ground in search of her nest.

This nest gives us an information that sometimes at least the larval cell is completely constructed prior to the collection of the prey.

Nest 10. In this nest (Fig. 9) the larval cell was 3 cm below the surface and the tunnel was thoroughly closed with soil. Obviously the nest was an accomplished one. It was interesting that a fly was left in the tunnel about 1 cm in front of the larval cell, buried in the packed soil. In the cell were collected 7 flies, all being head in, but with their body orientation uncertain. The mode of placement of the prey was not disordered, however, but was apparently for a special purpose — for keeping the bodies inside and the wings outside as against the central axis of the cell. Near the centre of the mass of the prey a larva of some parasitic fly, probably about 24 hours after being laid was discovered. The prey at the inner portion of the cell were ravaged

and the waspling was undiscovered, probably having been devoured by the maggot. The prey were all *Ophyra leucostoma*.

Nest 12. The tunnel, 6.5 cm in length and shallowly made, was filled with soil throughout the length and at the inner third the filling was considerably compact. The cell that was located 2.5 cm below the surface involved 4 flies of Lucilia sp. All the prey were placed head in, but the outer—and uppermost one dorsum up, the middle two side up and venter to venter with each other, while the innermost one venter up, thus forming an envelop with their wings. The egg of the wasp was found attached to the innermost and the largest fly at the underside of its neck with its cephalic pole and its caudal pole producing sideways from in front of the front coxa of the dexter side.

Nest 13. In this nest (Fig. 11) also the tunnel was throughout loosely filled with soil and 8 prey of Ophyra leucostoma were provisioned in the larval cell. The mode of packing of the prey showed the tendency as given in other instances, to keep the bodies inside and the wings outside. At the underside of the neck of the innermost prey where the egg of the wasp was usually laid a very small larva of the parasitic fly was discovered, probably it was just after sucking the egg of the wasp. This nest also provided me with an information that the egg of the wasp was laid on the prey that was put at the innermost part of the cell.

Nest 14. September 5, the same year and at the same place. At 11:52 I saw a wasp enter her nest with a fly and push out the soil from within. After some ten seconds the wasp appeared at the entrance, raked together the soil in the entrance and flew away. I covered the entrance with a bottle. At 11:55 the wasp came back carrying a prey. She repeated coming and going to and from the bottle-side on the wing and I at last removed it to make her enter the nest. Again I covered the entrance with it to confirm the time of her departure. At 12:18 the wasp came out of the tunnel and entered the trap. I let her go and again covered the entrance with the bottle. While I was working with the Cerceris I frequently paid attention to the bottle, but until 13:00 I could not see the wasp come back there, when I dug the nest.

The nest was very simple (Fig. 12). The larval chamber was 1.5 cm below the ground surface and horizontally also 1.5 cm from the entrance. The short tunnel was loosely filled with soil and the cell contained 4 prey, all *Ophyra leucostoma*. The fly at the innermost of all carried the egg of the wasp which was laid at the normal position of the body of the fly. It was about 3 mm in length and with the posterior end produced to the right side.

The time passed by the wasp between her last entering and leaving the nest was suggestive to the time of oviposition in this species. In the nest in the course of provisioning any fly found in the cell or the tunnel did not carry the egg of the wasp, whereas in the completed nest the egg was always found on the fly lying at the bottom of the cell that was considered to have been carried in first. From the usual knowledge on the life of the hunting wasps the latter fact appears to mean that the wasp lays her egg just after she carries in the first prey and later collects and adds the necessary amount of prey. But the former fact denies this consideration. It

shows that the wasp stores the prey provisionally in the nest and after full storing rearranges them in the cell and lays har egg on the one first taken in the larval cell. The time spent by the wasp of this nest mentioned above was probably used to rearrange the prey and to oviposit and finally to closed the tunnel.

Nest 15. September 6. This nest had a similar structure as that of nest 12, the brood cell lying 2.5 cm below the surface. The tunnel was closed only at the entrance for about 5 mm and in front of the brood-cell the wasp was at rest with her head outwards. It was before rain. The cell included no fly and it was not closed at the entrance.

Additional observations in the suburbs of Sapporo, especially on the methods of prey carriage. During my study on *Bembix niponica* I made some observations on this species. The wasps of this species living sympatric in the *Bembix* colony was generally much larger in body size and had a different mode of life as compared with the inhabitants in the Sapporo Botanical Garden. So I at first doubted that they might belong to another species. But so far as my examination went I could not find any difference in the taxonomic characters between the wasps of the two populations.

d

p

d

0

ıt

 $^{\rm id}$

ie

ct

On September 4, 1947, at about 10:30 I saw 3 wasps of this species working on the sandy area, 2 of which were digging their nests and 1 was in search of her nest with the prey. The latter wasp was obstinately digging a spot first carrying the prey, but later empty-handed. Probably the entrance to her nest was disturbed by my foot print. Finally she succeeded in finding her burrow, appeared at the entrance, but without picking up the prey that had almost been covered with the thrown sand and flew away, leaving the entrance open.

On the tenth of the same month, I was surprised to see that one of the wasps who landed on the ground caught the fly with her hind pair of legs. This seemed quite strange and I began to pay a special attention to the method of prey transportation of the wasps of this species living in the area. But I could not have a further chance of observation that day.

On the 19th I was again surprised to see another strange method of prey carriage by a wasp of this species. The entrance of her nest had been disturbed by my foot-print, so that she could not find it out easily. She repeatedly came back to a certain spot to search for the entrance. During her digging work I could observe that the prey was held by the neck with her right middle leg alone. After a vain job the wasp flew away with the prey. But soon she turned back, landed on the same spot to try to find the nest. The manoevre was several times repeated and every time I could confirm the above mentioned method of prey carriage on this wasp. Finally I caught her and dug the place where she was trying to dig. But the nest could not be find out after all.

During the course of my excavation of the nests of *Bembix* I met with 3 loosely packed tunnels of some wasps. The structure of the nests was similar to each other and to that of the *Oxybelus* in the Sapporo Botanical Garden and the contents of the larval cells were all flies. Judging from the facts and the usual inhabitants of the area there was no doubt that the constructors of the nests were the wasps of this species. The number of the prey in the cells were 1, 2 and 2, but all being covered with mould in a mass and no information could be obtained regarding the egg or the larva of the wasps. The nests must have been completed and a very small number of the prey found in the cells seemed also strange as compared with the case in the members of *O. strandi* living in the city of Sapporo.

The same day, at about 10:00 I saw a wasp of this species begin to dig her nest. During the course of digging she only pushed out the sand from within to the entrance of the burrow and never appeared outside the tunnel. Toward 14:00 I saw for the first time that a hollow was

open in the middle of the small mound of debris pushed out of the tunnel. Soon the wasp came out, closed the entrance very simply and flew away. At 15:30 when I saw the nest the wasp was again closing the entrance. I caught her and dug the nest. It was similar in structure to those given above (Fig. 5) and the tunnel was thoroughly loosely filled with sand. In the cell a lagre fly that was very similar to *Chaetotachina rustica* Meigen and almost as large as the wasp was placed and to the neck of which an egg of the wasp was attached. It was about 2.5 mm long and 0.8 mm wide and laid transverse as in the case of Crabronids. This nest must have been completed, judging from the filling state of the tunnel.

The other nest that I marked was left open for a considerable while, but was later closed. I dug it. It was closed only at the entrance and the cell was still empty.

On October 8. During my digging of the nests of *Bembix* I happened to meet with 3 nests that seemed to belong to this species. The larval cells were laid somewhat deeper than usual in this species (4, 5 and 5 cm below the surface) and the contents were all covered with mould. But I could count them as 3, 3 and 4 respectively. They were of the size of *Fannia canicularis* L.

Special attention should be paid to the strange method of prey carriage and the far smaller number of the prey to one cell in the wasps that occurred in the northern suburbs of Sapporo. As to the prey carriage, however, I could not confirm whether such a method was the usual one in the population or not.

Informations from other authors. H. Uchida recorded as prey of this species observed in Tokyo in 1938 Fannis scalaris F. and Anthomyia illocata Walk. (det. Dr. S. Kato), the number per cell being 10, 1, 0, 0, 0. The cells were located 3-4 cm below the surface and in the last 4 instances the wasp was in the nest (the time of the nest examination unrecorded). H. Masuda published the detailed observation on a number of the nests in 1939. According to him the nests are located 2.5-10.0 cm below the surface; the species of the prey were Ophyra leucostigma Meig., Fannia canicularis L., Musca stbulans Fall., Spilogaster quadrum F., Stomoxys calicitrans L., and Leskia fasciata Mats.; the nest has usually a small mound of soil at the entrance which is mostly left open during the provisioning activity and the wasp with a prey dashes into it from in the air; when the wasp is compelled to drop the prey at the entrance she drags it backing into the tunnel; the number of the prey found with the wasp's egg ranges from 5 to 12, there was a cell contained 11 prey but no egg; the egg is laid to the first provisioned prey (though he observed many cells containing 1-11 prey but no wasp's egg!); at the final closure the wasp uses the end of the abdomen to pack the soil; usually the time spent to complete a nest is one day, in the most rapid instance a nest was completed within 2 hours and included 7 flies of which 6 wese taken in within an hour. The adult wasp from the egg laid early in summer emerges in September; Enemies: Tschinid flies and some ants (Paratrechina flavipes Sm.), the Tachynid flies lay the maggots in the tunnel of the nest from the entrance; descriptions on nest, egg, and larva. As to the prey carriage he gave that it was held by the wasp with the mandibles and legs. Probably, however, this is considered not based on a careful observation,

Summary

Except for the 3 nests one of which was met with in Tokyo and the others in Sapporo (nests 4 and 5) all the nests of this species that were observed in Sapporo were very shallowly made. The ceiling of the larval cell is situated 1-5 cm below the surface of the ground and the tunnel leading to it is only 2.5-7 cm in length and in a gentle inclination. It goes in the earth first somewhat in a steep inclination, but soon curved to approach level and the larval cell is always made horizontal. Sometimes the tunnel is bent on the way, forming a distinct angle between the outer steep and the inner gentle inclinations. The larval cell is melon-shaped, measuring usually 12×6 mm. At the entrance there is, as a rule, a small mound of soil and the entrance is, as a rule, left open, but sometimes roughly or partly closed with soil.

The wasp digs the tunnel and the larval cell as a series of work without interval and then

takes a rest in front of the cell, directing her head outward and closing the entrance thinly from within. When the weather is not good and from the evening she stays in the nest in the similar manner.

Hunting is soon commenced after the nest is built and apparently promptly carried out (nest 14). The prey collected are stored either in the larval cell or in the tunnel near the cell, both provisionally. When the full provision is prepared the wasp rearranges the prey in the cell and at this time she lays her egg on the one placed first and innermost. When the prey are stored in the cell it seems most probable that the wasp loosens the packed prey to go inside, lays her egg on the bottommost one, packs again the remainder of the prey and closes the cell. She then closes the tunnel throughout, but the mode of closure is not so compact as in other fossorial wasps. Before her final departure she does not level the surface around the entrance and the entrance itself is left only half closed.

The method of provisioning and the time of oviposition above mentioned are just the same as in the allied tribe, Crabronini (Tsuneki, 1960). The egg is laid at the underside of the neck of the bottommost fly in the cell with its anterior end, crossing the area transversely, with the other end producing sideways. This mode of oviposition also is the same as in Crabronini. The egg-carrying fly is always placed venter up, but the flies later added show a distinct inclination of being so placed as to become the bodies wrapped up with their wings. This is also the inclination found in the members of the Crabronini.

When the wasp transports the prey on the wing and when she alights at the entrance it is seen that the end segment of her abdomen is strongly bent and the rear part of the fly's body is very frequently produced sideways or obliquely backward and all of her six legs are not used to hold the prey. However, it remains still unconfirmed as yet whether the sting is used in this case to support it from outside or to pierce it to carry. On the other hand, some wasps in one population were observed to carry the prey with the hind pair of legs and some held it by the neck with one of the middle legs.

When the wasp enters the nest she does not, in any case, let off the prey, either directly flying into it from in the air or penetrating into it after clearing the entrance packing. Despite the fact a maggot of the parasitic fly is sometimes found in the nest. It first destroys the egg of the wasp and then the prey one after another. How to send the maggots by the abult flies may be the same as mentioned by H. Masuda.

As to the nest exceptionally deeply made the structure is different from the others in having the tunnel wholly perpendicular. From such a structure it can be presumed that the nest may belong to the compound type. So far observed, however, such a fact has not been confirmed. On the other hand, it seems also possible to suppose that the builders of such a nest may belong to some closely resembling different species. Morphologically, however, no corresponding significant difference can be discovered between the two groups.

The prey consist of the flies of Anthomyiidae, Calliphoridae, etc. and their number to one cell ranges from 4 to 8, but in one population from 1 to 4.

OXYBELUS BIPUNCTATUS OLIVIER

This species is widely distributed over the Holoarctic region. In the Palaearctic from Europe to Japan, though in reality the occurrence in the broad intermediate zone of the Asiatic Continent except the scanty records from Turkestan and E. Siberia remains uninvestigated. In Japan this species has been found only in Hokkaido, providing us with an instance of evidence regarding

the biogeographical importance of the so-called Blackiston line lying between Hokkaido and Japan proper. In Hokkaido itself this species has been known only from Sapporo and the districts, though the researches on these insects on the Island are still left in quite an incomplete state.

On the biology of this species several papers have been published in Europe. In 1901 Ch. Ferton and in 1908 G. de Gaulle recorded respectively the prey of this species. In 1926 and 29 G. Grandi described the general nesting biology and the method of prey carriage etc in this species. He also summarized his study in his 1961 book. On the other hand, in 1929 A. Crèvecoeur dealt with the method of prey transportation, adaptive behaviour of the nest closure, the cocoon and cocoon spinning of the larva and the parasites. In 1931 he again published his detailed observations on the burrowing, the structure of the nest, the prey, the egg and oviposition, mating, emergence of the adult wasp from the cocoon and the insects parasitic on this species. Further, in 1930 P. Marèchal described the structure of the cocoon and the postembryonic development of the larva in this species. Regarding the American population K. V. Krombein (1948) recorded the prey species and F. E. Kurczewski and B. J. Harris (1968) reported a dense, gregarious pnpulation.

As to the East-Asiatic representative I published in Japanese (1951) my observations on the various aspects of the nesting biology, together with a consideration on the methods of the prey carriage in this genus.

In the northern suburbs of Sapporo a broad grassland that was derived from the sand dunes and then used as pasture was extended. On the area there were scattered patches of ground where the grass was removed for various purposes during the War and abandoned after the War. This species lived in such bare sandy areas together with other sand wasps such as *Bembix niponica*, *Bembecinus hungaricus japonicus*, *Cerceris arenaria*, *Lestica alata* and several species of the spider wasps. The wasps of this species formed a comparatively flourishing colony in each area and there was no difficulty in investigating their life. In those days, however, my attention was concentrated upon the life of *Bembix niponica* and the study of other species was a rather side job.

The first observation. Angust 1, 1947. A considerable number of the wasps were nesting on one of the bare grounds and I observed various matters on this species. First I will describe them in a general way.

- 1. Nest digging. The burrow is first dug perpendicularly like a well. This is quite invariable on all the nests. But it is also invariable that it is soon turned in a right angle after reaching 5-7 mm about the length of the wasp from the surface. During the time of digging of this well-like portion of the tunnel the mode of the wasp's work is well observable. She stands always against the gentle, upward slope of the area, supporting her body with her mid and hind pairs of legs, lifting her abdomen high, thus standing almost on her head and very promptly throws away the sand grains with her front pair of legs through the underside of her thorax. The alternative movement of her front legs are very quick, as in the sand living spider wasps who are digging their burrows. After the tunnel is turned to horizoutal the working wasp becomes unobservable. But the sand thrown by her is observed to fill the well-like portion of the tunnel. After a while the wasp comes out of the filling and throws the sand pile in the well in the same manner as at first. According to the easily movable nature of the sandy ground the rate of digging is conspicuously more rapid as compared with O. strandi.
- 2. Structure of the nest. Seven nests were dug and examined. All followed the same pattern in structure. The general type is as given in Fig. 13. It is very much like that of the European representative which was given by Crévecoeur, except that the horizontal part is much gentler in inclination. This horizontal or very gently inclined part of the tunnel which follows

the first short perpendicular well-like part is from 3 to 5 cm in length, then mostly at the depth of about 2 cm from the surface (because the burrow is dug against the inclination) turns abruptly downward in a steep inclination of about $60^{\circ}-80^{\circ}$ to the horizon and goes deep into the sand for 8–13 cm. The tunnel is about 3 mm in diameter, but the perpendicular entrance part is sometimes much wider, 6–7 mm, depending upon the sand falling. The end portion of the steep part of the tunnel becomes usually somewhat gentle in inclination and is very slightly enlarged at the extreme end to about 5 mm in diameter into a cell. But it is never laid horizontal and sometimes

even without becoming gentle in inclination and used as the brood-cell. The brood-cell is, therefore, loated 10-16 cm below the surface of the ground, very much deeper than in other congeners of Japan. While the wasp is absent from the nest, the entrance is closed with sand, but the lower half of the opening is left as a small hollow. This is due to that the wasp when creeps out of the tunnel always faces downward on the slope, collects the closing material from in front of the entrance into the opening which is half filled with her abdomen

an

gh

h.

29

e-

on

b-

ıg,

er,

of

he

n.

he

ey

ıes

ere

nis

a,

of

ch

on

er

ng

be

in-

ter

ng

ds

nd

tly

he

ho

ies

el.

ne

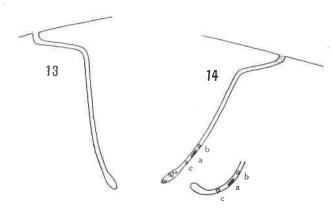
ig-

ne

he

ch

ws



Figs. 13-14. Nests of *Oxybelus bipunctatus* Olivier (lateral view, explanation in text).

and then flys away, leaving a hollow cauaed by the pulling-out of her abdomen behind her.

The nests examined this day were all in the course of provisioning. The tunnel was closed at the entrance and in front of the larval cell, both for about 5 mm and the remaining portion was left clearly open throughout. The larval cell partitioned with its entrance closure attained from 8 to 10 mm in length.

3. Method of the prey carriage. I carefully observed the mothod of prey carriage, making use of the moment when the wasp entered the nest. Some ten individuals were working under my eyes and the chance to observe such a thing was plentiful. The wasp with a prey landed in front of her nest entrance and removed the filling sand with her front pair of legs, almost in the up-turned posture, lifting her prey-holding abdomen high. In order to make the wasp long keep this posture I covered the entrance with a pebble or leveling the surface of the nest site for impeding her smooth entering. First it was ascertained on all the wasps that all the six legs were not used for holding the prey. They were, as usual, used for walking and digging. Next I could observe repeatedly that while the wasp with a prey flew above the nest site without moving like a helicopter the head of the prey was always located near the hind coxae of the wasp. On the other hand, when the wasp was on sand the body orientation of the prey was uncertain, but it never produced sideways or obliquely backward as in the case of O. strandi, but always produced straight backward in the extended direction of her body axis.

I then concentrated my attention on her method of prey-holding at the moment of her entrance clearing. The wasp stood so extremely vertical that she frequently turned over forward. So much so that the state of the end of her abdomen was well visible. According to the over-ten times observations it was not the case in this species that the caudal segment is bent ventrally to hold the neck of the fly with the aid of the sting, bacause the head of the prey was near the centre of the ventral side of the wasp's abdomen and its neck was not nipped by anything. Further,

it was also denied that the legs of the fly was held between the hind coxae of the wasp, as in some species of Cradronid. Apparently it was held by being pierced with the sting of the wasp, as was described by some authors (see p. 12, 22) with respect to some European and American species (do.).

In order to confirm the true way of the wasp I approached to one of them opening her nest with a prey and caught the fly by one of the wings with the pincette and tried to pull it off. The wasp firmly held the fly and I could not easily deprive her of the prey. I pulled it more strongly and succeeded in separating the prey somewhat from the tip of the wasp's abdomen. The result was to let me see that the sting of the wasp was inserted in the central area of the underside of the thorax of the fly. I further pulled it and completely pulled it apart from the end of the wasp's abdomen. At this moment the wasp ceased her digging, ran up to the fly that was held with my pincette, caught it, mounted on its back crosswise and turned her abdomen under the fly. I dropped the wasp and the fly on to the ground. At that moment the wasp rolled over herself, became up-side-down, holding the fly on her breast and stung it at the centre of the ventual side of its thorax. Without pulling out the sting the wasp flew up and after circling once above her nest landed by the side of the entrance and resumed the opening work.

I further tried the same technique with two other wasps with completely the same result. In these cases it must be mentioned that the end of the wasp's abdomen was always bent ventrally.

4. Prey. The prey captured by the wasps of this species were the flies of Anthomyiidae, Calliphoridae and Syrphidae in our region. Greater part of the flies obtained from the nests belonged to a species of Anthomyiidae which was later identified by the late Dr. S. Kato with Hylemyia phatura Meigen (= Chortophila cilicrura Rondani) and the Syrphid flies which were exceptional as given later were identified by Dr. T. Shiraki with Melanostoma mellinum Linné. The calliphorid flies obtained from the old nests were all fragmental remains and could not be identified.

According to the literature the flies captured by this species in Europe belonged to the genera Fannia, Chortophila, Hebecnema (Crèvecoeur, 1931), Homalomyia (Ferton, 1901), Calythea (Grandi, 1926, 28, 61) of Anthomyiidae, the genus of Chrysopila (Crèvecoeur, 1931) of Rhagionidae, the genus Onesia (de Gaulle, 1908) of Calliphoridae, etc. On the other hand, the prey of this species recorded in U. S. A. belonged to the genera, Hylemyia and Lonchaea (Krombein, 1948).

The prey of the Sapporo wasps were not killed, but only paralysed. In the fresh specimens the respiratory movement was distinctly observed. In some of the prey taken out of the nest the legs were fairly actively and the wings were vibratingly moved. These movements, however, became stopped the next day or the day after the next day. In this respect my observation was the same as those published on other species of the genus.

- 5. Activity of the wasps. I began the observation on this species from toward 14:00. At 16:30 (the weather was fine) the wasps were still very actively working. I could count more than 10 wasps that came back to their nests successively with the prey. The wasps that were digging their burrows were not less in number. They were so crowded that I could not go to one of them without destroying some of the nests by my foot-prints. At 16:50 the activity of the wasps became somewhat weakened. But from time to time some of them came back with a prey. At 17:15, I could see still a few of the wasps carrying the prey into their burrows.
- 6. Contents of the nests observed. Ten nests were dug and in 7 of them I succeedeed in following the tunnel up to the cell. They were consistent in structure with the general description given above, with a more or less variation in the relative length, inclination and curvature of the

parts of the tunnel. To my regret, all were still unaccomplished ones, including no egg of the wasp. The prey found in the cells were 1, 1, 6, 8, 2, 5 and 3 in number, of which those containing 8 and 2 prey seemed worthy of particular mention. They will separately given in the following:

- A nest suggesting the time of oviposition. In none of the above-mentioned nests could I find the egg of the wasp. This is to show that in this species also the egg is not laid simply to the first prey carried in. The nest that contained 8 prey gave me an interesting information in regard to the time of oviposition. In this nest the wasp was found inside. The tunnel was curved sideways at the apical half of the steeply sloped part and at b and c shown in Figure 14, a fly was placed separately. The wasp was at a in the Figure and in the cell 6 prey were collected, 2 being inside and pressed firmly, while the remaining 4 being near the entrance of the cell and loosely scattered. The inner 2 prey were laid side up, indicating clearly that they were not in the body orientation to receive the egg of the wasp. I supposed that in this nest the wasp had completed the work of prey collection and was just in the course of preparing for the oviposition. The prey in the tunnel must have been taken out of the cell and the 4 prey in the outer portion of the cell were either about to be done so, or simply loosened to let the wasp go inside to lay her egg on the innermost prey which would be, of course, rearranged before oviposition. Possibly the wasp rearranges all the prey that have temporarily been stored in the cell and lays her egg to the one that is first replaced in the cell, as was supposed by me in regard to the other congeners.
- 8. Exceptional prey. In the nest that contained 2 prey the prey seemed quite exceptional, though they were the Dipterous insects. The nest had the usual appearance of the nest of this species, but the owner was absent from the nest. I dug it, together with others, only to know the general structure of the nest of this species and the contents of the brood-cell. It was certainly the same in structure as in others, having the length of 5 cm at the horizontal part of the tunnel and 9 cm at the steeply inclined part. The width of the tunnel was 3 mm and that of the brood-cell about 4.5 mm. But the 2 prey provisioned in the cell were not of the Muscid, Anthomyiid, Sarcophagid, nor of Tachnid flies, but were the small hovering flies belonging to Syrphidae.

The curious kind of the prey bewildered me. But soon after my examination the wasp of this nest came back free-handed and began to make the search digging at the spot where the nest had been. According to the observation it was certain that some wasp of this species hunted sometimes such exceptional prey as food for the larva.

The second observation. Two days later, on August 3, I visited the place. I arrived at the colony toward 14:30. The weather was at first dimly fine, but gradually became overcasted.

- 9. The provisioning activity of the wasps. I took records of the return of the wasps carrying the prey to their nests (Table 1). During the course I made some observation on the spider wasps and therefore it seemed possible that some of their returns escaped my notice. Despite the fact it showed that most of the wasps considerably concentrated their provisioning activities. But, some wasps, such as Nos. 5 and 7, made provisioning only once during the time. In order to know whether this was due to the state of their nests or to my oversight I examined their burrows. In nest 5 I failed, but I obtained 1 fly from under the ground and in the cell of nest 7 I found 4 prey. As to nest 7 the question was unsolved, because I did not observe continuously from the morning. But taking into consideration of the activity of other wasps it seemed certain that the state of the nest had closer bearing upon the wasp's activity.
- 10. Nest digging and the orientation flight. At 14:40 I marked a wasp as No. 17 who was soon after the beginning of burrow-making. The frequent appearance of the wasp at the

can nest off.

in

the that men lled the once

ally.
dae,
ests
with
vere
nné.
t be

. In

thea iony of pein,

the ever, was

:00.

nens

were o to y of ith a

ed in otion f the entrance with the wet sand showed clearly the fact. She continued to dig and at 16:06 came out of the burrow, as usual with the burden of sand, and after throwing it away she, for the first time, flew above the nest. She flew about slowly at a height of about 15 cm above the ground surface over her nest site for about 5 seconds. Then she landed on sand near the opening of her nest. But at once she flew up again. This time she flew about for 10 seconds and then landed to enter the nest. She resumed the digging work, but at 16:11 again appeared out of the burrow and this time, after a few moments flights above the nest, suddenly flew far away without trying any orientation flight. About one minute later, however, she came back without going astray and after flying about low near the nest site for about 10 seconds again entered the burrow. A half minute later she appeared at the entrance, head foremost, raked together the sand grains in the opening as she slowly crowled out of it. When she left completely the entrance there remained a little hollow. The wasp flew about very slowly over the nest within the bound of 30-50 cm in diameter. Four times at some intervals she landed near the nest to take a rest. Twice she went about 2 meters far away. At 16:15 she finally and truly flew away (Fig. 15, a rough sketch).

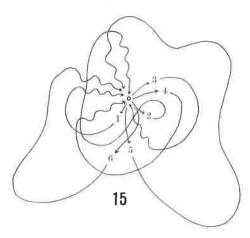


Fig. 75. Orientation flight of Oxybelus bipunctatus Olivier.

It must be mentioned that during the flight the wasp repeatedly came above the nest entrance and at that time her flight was minutely waved to the right and left. Landing was made within the bound of 3–5 cm from the nest and thence the wasp at once went to the entrance on foot, but as soon as she reached there she flew up without trying to enter. In such a case, however the wasp never landed behind the entrance. When she flew back from behind she passed over the nest, turned round and landed in front of or at the side of the nest. However, it was not always the case that the wasp landed each time of her return. More frequently the wasp flew off after approaching the entrance in the swinging movement, without landing.

It seemed to me that there was no note-worthy

land mark around the nest except myself. But I carefully changed my relative situation against the nest. Probably the wasp turned back from afar by making that bare ground in the grassland as the most important clue to go to the nest. Within the bare sandy ground, however, what becomes the cue to her to find out her nest? Is it a relative situation between the surrounding objects seen in front of her nest, as I formerly suggested in regard to the homing phenomenon of *Bembix niponica*? To solve the question, however, more analytical experiments are needed.

11. Examination of the nest. When I observed the wasps' activities two days before I left a nest mark at the side of each of 6 burrows. On August 3, I dug all of them, but succeeded in only 2 of them in reaching the brood-chamber. But this day I examined several other nests in addition. These were instructive regarding various aspects of the nesting biology of this species.

Nest 1. The tunnel was throughout closed with sand. But in the cell'I could find only 1 fly without the egg of the wasp that I observed to be carried in a couple of days before. The wasp might die by some accident and the closure was naturally done by the rain of the preceding day. Or did she miss her nest by the leveling action of the rain? The cell was found 13 cm below the surface.

Nest 2. One of the 6 nests marked by me. The tunnel was wholly closed and I could not follow it. But I succeeded in finding the larval cell 9 cm below the surface. It lay somewhat oblique as against the slope of the ground, showing that the tunnel turned as much at its steep portion. The cell was 10×5 mm in measurement, somewhat larger than usual and contained 6 prey of a small species of Anthomyiidae. The prey were placed all head in, but the innermost one was laid side up (!), with a just hatched small larva on the underside of its neck. Of the flies laid at the outer portion of the cell the upper placed ones were dorsum up, while the lower placed ones venter up, that is to say, the play showed an inclnation to be arranged so as to be wrapped with their own wings.

An old nest. Near nest 1, 10 cm below the surface, I found another brood-cell that contained remains of 4 small (4.5 mm) metallic blue flies. Their thoraces were destroyed and the heads and the integuments of the abdomens remained together. The tunnel connected to the cell could be followed for 7 cm upward. But it was 2.5 mm in diameter and distinctly finer than the usual tunnel of this species. I at first thought that this nest was parasitised by some Tachynid fly and the tunnel might be the escaping pass of its adult. But later it came to me that such a consideration was incorrect, because the escaping pass of the fly did not remain as a tunnel. This was probably also a nest of O. bipunctatus and the builder might be an extremely small female.

Nest 3. It was the possession of wasp 3 given in the table. In this nest the horizontal part was short, only 3 cm in length, while the steep part was as usual, 9 cm and its inclination became somewhat gentle near the larval cell which was 10 cm below the surface of the ground. It was distinctly enlarged to about 5 mm in width, with the length of 10 mm and obliquely inclined as usual, containing 4 prey. The prey were loosely placed in the cell, without the egg of the wasp. After my digging the wasp came back with a fly.

Nest 4. Belonging to wasp 4. While I was digging nest 3, at 16:35, the wasp of this nest came back empty-handed and several times landed on the entrance, but she did not try to enter there. I dug it at 16:40. Horizontal part 3 cm and steep part 7 cm, from 2 cm before the cell the tunnel was turned to the right and became somewhat gentle in inclination. The nest was closed at the entrance and at the end before the cell for about 10 mm. The cell was comparatively large, 13 and 6 mm at the maximum length and width and lay 9 cm below the surface at its bottom. It contained 6 flies placed as mentioned above and to the one at the innermost was laid the egg of the wasp. The egg was comparatively small, about 2.0×0.7 mm, wax white and was attached to the underside of the neck as usual, lying nearly crosswise, with the posterior end slightly produced at a side.

In this nest the wasp had already laid her egg. Nevertheless she did not completely close the tunnel leading to the larval cell. After my examination she came back empty-handed to the nest. Was she in the intention to give the tunnel the permanent closure, or to pass the night in the nest? If the last mentioned was the case it seems probable that she was in the intention to add further prey to the provision the next day.

Nest 5. The horizontal part was only 2 cm; in the steep part the wasp was rested. But the excavation ended in failure and the larval cell could not be examined. From in sand, however, one fly was dug out. This nest showed that the nest made in the afternoon was provisioned by the wasp with few prey only, and the wasp postponed the main part of provisioning to the next day.

Nest 6. Horizontal part 3 cm, steep part 6.5 cm, nearly perpendicular and near the end somewhat gentle and the bottom of the cell 7.5 cm below the surface. In the cell, 7×5 mm and closed at the entrance, were stored 3 prey which were observed by me to be taken in (Table 1,

A s in med in rent th).

out

irst

ınd

her

ded

ow

ing

hed the ass-

not

e of

fter

ght

3-5

ent,
rthy
inst
and
what

non ded. re I eed-ests this

ly 1 The ding cm wasp 6). All the prey belonged to a single species of Anthomyiidae, *Hylemyia phatura* Meigen, without carrying the egg of the wasp. One of the flies that was placed outermost moved very actively its legs when taken out, but it became quite motionless when it was examined the next morning. This nest also shows the same fact as mentioned in regard to the provisioning of nest 5.

Nest 7. The entrance well was enlarged and lengthened by falling down of the roof of the horizontal part of the tunnel which was 2 cm in length. The steep part was almost perpendicular, gently curved leftward and became gentler by degrees and stopped 2 cm in front of the larval cell where the wasp stayed. The brood-cell lay almost horizontal and the depth to its bottom was 13 cm from the surface. It was 8 mm in length, 5 mm in width, centaining 4 flies and to the

Teble 1. Provisioning activities

Time of coming back with a prey	No. of wasps
3: 15 25 32 33 41 52 55 59 4: 04 05 10 15 16 37 5: 00 15	6 6 6 3 3 8 4, 7 5 10 9 10 10 11 3 8 8

Remarks. The wasp No. corresponds the nest No. in the text.

one at the innermost part of the cell was laid the wasp's egg. The closure at the entrance of the larval cell seemed to be somewhat thicker than usual, if it was still in the course of provisioning. It might, therefore, be in the course of closing of the tunnel by the wasp, although, according to the record of the last provisioning to the cell (Table 1), there was too much time between them. If I had failed to notice the time of the last provisioning during my observation the above-mentioned supposition would become reasonable.

Nest 8. In this nest the horizontal part of the tunnel was only 1 cm and the steep part only 6 cm. There the tunnel was slightly curved, became gentle in inclination and somewhat enlarged at the end, without closure in front of the place. I found there 3 prey without the wasp's egg. During my excavation the mother wasp (No. 8) came back with a fly (17:15). I tried to enlarge the excavation and

happened to find another cell which lay in the first direction of the steep part of the tunnel and below 8 cm from the surface. It was 10×6 mm in size, contained 6 flies and the innermost one carried the egg of the wasp.

Whether this was the other cell of this nest, or belonged to another separate nest that was made close to it I could not definitely say. If the former was the case it becomes that the wasp of this species builds occasionally the compound nest. I had frequently tried the similar enlargement of the excavation, but this was the first that I met with the other cell.

Nest 9. Horizontal part was only 1.5 cm, the steep part was perpendicular, then it was inclined in the reverse direction and finally curved rightward and ended in the enlarged cell, without any closure throughout the tunnel. In the tunnel I found the wasp and in the cell I found 6 flies provisionally stored, without the egg of the wasp. The cell was very steep in inclination, 13 mm in length and 5 mm in width and its bottom was 9 cm below the surface.

I left alone nests 10 and 11 in order to obtain the cocoon of this species.

Nest 12. 5 flies of Anthomyiidae in the cell, no egg.

Growth of the larva. The larva and the eggs observed on August 3 were brought to my laboratory, each with its prey in a small tube bottle and were reared. The fine sand of their habitat was moistened and packed in Petri-dishes. A hollow of their cell size was made on sand of each dish and the larva and the three eggs were separately put in each cell with each prey. It was done the next morning and until that time they were kept in each tube bottle.

When I observed them in the evening that day the larva was healthy and was eating the prey, while the two of the eggs had already been shrunk and the remaining one showed the symptom of hatching.

August 5, at 8:00, the larva was eating the prey and the egg showed more clearly the segmented structure. But, in the evening the egg had heen shrunk without showing the further development.

On the 6th at 8:00 the larva continued to eat, but the prey in its cell began to be covered by mould. So I removed them and gave it other flies from other cell.

On the 7th, it continued to eat. In the evening it had already stopped eating and laid quietly in the cell.

August 8. Throughout the day I was occupied and forgot to observe the waspling and in the evening when I observed the larva was spinning the cocoon. Apparently the cocoon was formed except for the upperside where there was no support. But it was uncertain whether the cocoon was silky one or sandy one, because of the attachment of remains of food. I put a cover glass on the hollow. The larva at once began to stick the silk thread to the glass.

The next morning the underside of the glass was covered with a sand layer and I could not see the movement of the larva.

In this rearing it could not definitely be confirmed whether the larva span the cocoon by following the *Tachysphex*-method or by means of the *Bembix*-way. But to me it seemed that the first case was true.

The third observation. August 8, in the afternoon when I reached the habitat a number of the wasps of this species were seen coming back with their prey. The main object of my visit was to make experiments with the spider wasp (Etizenia, 36) and I did not concentrate my attention on this species. But I dug 4 nests, of which 2 were the ones marked previously.

Nests 10 and 11. From 10 and 12 cm respectively below the surface I could find out the cocoons which were wrapped with remains of the prey. The cocoons were made of sand grains, slightly elongated egg-shaped, about 7 and 4 mm in the maxim length and width.

Nest 12. The horizontal part 2.5 cm, steep part 10 cm, near the end the tunnel fairly gentle in inclination and the cell was located 10 cm below the surface. In the cell only one fly, of course without the wasp's egg. In this nest the tunnel at the entrance and in front of the larval cell was simply (less than 1 cm in thickness) closed.

Nest 13. The horizontal part 2 cm, steep part first nearly perpendicular, then inclined in the inverse direction and finally became considerably gentle, but not horizontal even at the end cell. The tunnel in front of the larval cell was fairly thickly (about 10 mm) packed with sand. In the cell 5 prey of small fly, Fannia canicularis L., were stored, without the egg of the wasp.

That day, numerous wasps were provisioning their nests. The prey, so far as ascertained, were all Anthomyiid-formed flies. Two houses with barns and pigpens of the cultivators were near that observation place and the wasps that hunt the Dipterous insects were considered to make the human domiciles as their hunting ground.

Summary.

This species lives in sandy area and the nest has a certain pattern — the entrance well, horizontal tunnel, steep tunnel that finally becomes more or less gentle and the larval cell which is also inclined as a rule and 8–13 mm long, 5–6 mm wide and 8–13 cm below the surface. The compound nest, if any, is exceptional. During the provisioning the entrance and the front of the larval cell are simply closed with sand. The wasp carries the prey by supporting it with her impailing sting alone and even when clears the filling sand she never lets it off. The prey collected

o the vasp's semed in the course ording

eigen,

very

next

f nest

of the

cular,

larval

ı was

le 1), ed to servae rea-

unnel

n and ont of egg. back

el and

st one

t was

withund 6 ation,

their sand

are mainly stored in the cell, but sometimes in the tunnel provisionally, therefore without being laid the egg of the wasp. Oviposition is considered to be done after the full provisioning is completed as a rule, in some cases, however, the wasp adds a few prey to the egg-laid cell. Before the oviposition the wasp rearranges the stored prey in the cell and lays her egg on the one placed first.

In digging the nest the movement of the wasp is very rapid and she needs about 2 hours to complete the nest building. Toward the end of nest digging the wasp begins the so-called orientation flight and when the nest is completed it is very elaborately carried out. At night the wasp stays in the nest. Apparently the wasp spends 2 days to finish full provisioning to a nest.

The egg hatches out about 24-30 hours after being laid and the larva finishes its growth after 7 days and spins the cocoon. The cocoon is made of sand; apparently it is formed by sticking together the sand grains with silk thread. However, it remains unknown from what part of the cocoon the work is commenced and whether the silk ring or silk pouch is made or not prior to the sand-inlaying work.

The prey collected by the wasps in Japan belongs mainly to the flies of Anthomyiidae, but rarely those of Calliphoridae and Syrphidae are captured.

OXYBELUS LEWISI SMITH (= Oxybelus sakuranus Tsuneki)

This species is also the inhabitant of the sandy area. I captured a female of this species in my native village when she came out of her burrow. It was about 40 years ago. Recently Mr. T. Tano collected some ten specimens of this species on the sand area sparsely covered with grass at the seaside of Neagari, near Fukui. I also captured 2 specimens on a sand area in the river bed of Tanshui-Ho, N. Formosa. These data shows that the species makes habitually the nest in sand.

The nest I saw when I was young was open on sand plain of a river bed to which the wasp entered with a fly. I covered the entrance with a bottle and captured the wasp. I at once dug it out. The tunnel went perpendicularly into the sand, but I missed it about 7 cm below the surface and I failed to discover the cell or the prey. Since that time no one has discovered the nest of this species.

OXYBELUS LATRO OLIVIER

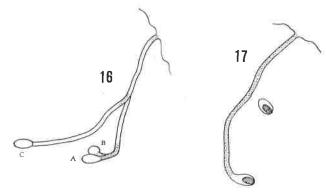
This species widely distributed over the Palaearctic region and in Europe two brief reports on the prey have been published by Giraud (1879) and Ferton (1901). The prey were the flies belonging to the genera *Sarcophaga*, *Lucilia* and *Pollenia*. While I stayed in Inner Mongolia I had a chance of observing a nest of this species.

At the upper portion of the slope, facing the south of a dried rain ditch between hills near Beizu-miao, Apaka, I found a crowded village of wild bees and wasps. The nest of this species was also found in this village. It was late in the season, on September 27, 1939, that I found a tunnel of the burrow of this species while I was investigating a nest of Agnosicrabro mongolicus. I followed the tunnel and could make out the structure of the nest as given in Figure 16.

At the entrance and in front of the larval cells, A and B, the tunnel was closed, in the former loosely and in the latter fairly compactly. Also at the branch point of the tunnel leading to cell C it was closed for about 5 mm and in front of this closure the mother wasp was found

died, probably of the coldness at night.

In cells A and B a cocoon was found respectively which was elongated egg-shaped, 8.5 mm in length and 3.7 mm in width, consisted of (earth) grains as in other species of Oxybelus. The cocoon was hung at the front part of the cell, with the rounded end directed toward the tunnel and in the rear part the remains of food were left. In cell C were con-



Figs. 16-17. Nests of Oxybelus latro Olivier.

tained 2 small flies of probably Anthomyiidae, but the egg or the larva of the wasp could not be discovered. The cells were 13-14 mm in length and 6-7 mm in width.

In the same place, on the 21st of the same month, I obtained 2 similar cocoons from a nest having the structure as given in Figure 17. As to this nest the owner was unknown and the adult wasp did not come out of the cocoons. Judging from the structure of the nest and the cocoons it seemed probable that it belonged to this species, or at least to some near relatives of Oxybelus.

COMPARISON BETWEEN SPECIES

1. Nesting place. The ground that consists of fine grains of sand is beloved by O. bipunctatus and O. lewisi. Apparently they do not make their nests in the ground of soil. On the other hand, O. venustus, so far observed, is an inhabitant of the clayey soil. O. nipponicus and O. latro also make their nests in the soil, but the soil they nest is mixed with a considerable amount of sand. While O. strandi sometimes nest in the ground of hard soil and sometimes in the sandy ground.

Thus, these species show a distinct cline with respect to the character of the ground. If we consider a case at the shore of the river or the sea, *bipunctatus* and *lewisi* will live on the sandy zone nearest to water. The next adjacent zone which consists of sand and soil will be inhabited by *nipponicus* and *latro*. While on the farthest zone of soil we shall find *O. venustus*. As for *O. strandi* this species is rich in adaptability. It will live both in sandy as well as in clayey ground. But it probably prefers the ground of hard soil to the sandy area.

- 2. Leveling. The debris dug out of the tunnel of the nest are elaborately leveled by O. venustus, hence in this species there is no mound of soil at the entrance to the nest. The case in O. strandi is quite contrary. The entrance of the nest of this species is always accompanied with the mound of soil. O. bipunctatus also does not try to level the ground. But in this case, together with that of O. strandi living in the sandy area, the sand heap is soon dried up and crambled, without keeping the mound as it was at the entrance. The nest of O. lewisi observed by me had not the mound at the entrance. As to O. nipponicus and O. latro my note books do not touch on this point.
- 3. Orientation flight. In O. bipunctatus the manoevre is very elaborately carried out and in O. venustus it is very simply performed. It does not make any particular flight above and around the nest, but to level the nesting site it frequently turns back to the nesting site. In other species no observation has been made in this regard.
 - 4. Structure of the nest. When the wasp is in the nest it is a rule that the entrance is

Mr.
grass
river
st in

eing com-

efore

aced

rs to

enta-

wasp

after

king

f the

or to

but

wasp ug it surnest

flies golia

near

nd a ngol16.
the ding ound

loosely closed with soil or sand pushed out from within. When the wasp is out, however, the state of the entrance is varied with the species. It is, as a rule, left open in *O. strandi* and loosely or half closed in *venustus* and *bipunctatus*. When it is left open in *bipunctatus* the tunnel is closed at the beginning of the horizontal part. In *strandi* also the tunnel is at some place always closed. According to my note books *lewisi* and *nipponicus* apparently belong to the *strandi*-group in this respect.

5. Method of nest closure. Masuda reported that O. strandi uses the tip of its abdomen to pack and pound the closing material at the time of the final closure. As for other species this

character remains unobserved.

- 6. Nest type. In so far as observed by me O. venustus, O. nipponicus and O. latro very frequently, if not a rule, construct the nest of the simple compound type. While in other species the simple type is the rule. In O. bipunctatus I had an instance of probable compound type of the nest. But if it is true such is quite exception in this species.
- In O. bipunctatus the form of the nest is very stereotypic, that is to say, it has a constant type in the form of the nest. When the nest is made in the hard clayey ground O. strandi is similarly has a certain type of the nest, a shallow up-turned parabolic form. While in some case of sandy ground of this species and in all other species dealt with here there is no constant type in the form of the nest, except that the tunnel nearly perpendicularly goes in the ground. As for the larval cell it must be mentioned that it is constantly inclined in O. bipunctatus, In all other species the larval cell is laid, as a rule, horizontal.
- 7. Depth of the larval cell. In most of the species dealt with in this paper the brood cell is made considerably deep in the ground, 8-13 cm below the surface of the area. Only in O. strandi when the nest is made in the hard earth the tunnel is short and runs nearly horizontal, with a result that the cell is made shallow, 1.5-3.0 cm below the surface (to its roof).
- 8. Prey. The prey of Oxybelus are, in any case, the Dipterous insects, mostly having the general appearance of the Musca-type and not large in size, with the exception of the gnat-type partly mingled by nipponicus. Hence the flies of Anthomyiidae occupy the first rank in the menu of the members of this genus. Only in bipunctatus I have a single record of observation of the Syrphid flies stored in the cell. The number of the prey per cell is usually from 3 to 8, exceptionally 1-2 and 12-15. As to O. strandi, the wasps of the Momidziyama population (the inhabitants in the northern suburbs of Sapporo) were characteristic in the small number of the prey cellected in one cell. In the extreme case it contained only a single prey of the large size and to which the egg of the wasp was laid.
- 9. Prey carriage. It has long been known that the members of Oxybelus carried the prey by impailing it on the sting. But some investigators insisted that in some species the prey is held by the hind legs. In O. venustus and strandi I observed that the end segment of the abdomen is strongly bent down and I supposed that it might held the fly by the neck with that hook-shaped curvature of the segment, although I could not confirm whether the sting is used or not, to support the fly from the underside.

At the present state of my knowledge, it seems doubtful that the prey is held by such a method alone. Probably I failed in observing the impailing sting that could not be ascertained without relying upon the special technique. This technique which was first employed by Adlerz gave definite evidence that the prey was carried by the impailing sting alone in *O. bipunctatus*.

On the other hand, O. strandi is interesting in this regard. In the Sapporo population the wasps possibly followed the ususl method of the impailing sting, while those of the Momidziyama population who captured much larger prey caught it by the neck sometimes with one of the middle

legs and sometimes with the hind pair of legs. This is probably the adaptive change of behaviour in accordance with the weight of the prey.

- 10. Provisioning and the time of oviposition. In O. venustus, strandi, nipponicus and bipunctatus there is no exception that the prey carried into the nest are provisionally stored mainly in the larval cell and sometimes in the tunnel without being laid the egg of the wasp, until the time when the necessary number of the prey is collected. Then the wasp rearranges the prey in the cell and lays her egg on the one placed first. The result is apparently the same as in the case where the egg is laid as soon as the first prey is taken in the cell and later some prey are added, as in the members of the genus Sphex. But in reality the process is utterly different from each other in both cases. In some case, however, O. bipunctatus and O. strandi at least bring a few additional prey to the larval cell in which the egg has already been laid. But this seems to be a rather exception.
- 11. Type of oviposition. The egg is attached to the underside of the neck of the prey with its anterior end, laid crosswise, with the posterior end produced sideways. This is invariably the case in the species so far observed.
- 12. Cocoon. In O. venustus the cocoon is not inlaid with grains of earth or sand. In all others the cocoon is apparently made of grains of earth or sand like those of Bembicine wasps.
- 13. Adaptability in O. strandi. The striking adaptability of O. strandi in various aspects of the nesting biology seems worthy of special mention. It can live not only in the clayey ground, but also in the sand plain. The nest is variable in form and depth according to the condition of the ground. The size of the prey and the number accordingly can change within a comparatively large extent. In the extreme case it fills the provision with a single large prey only, lays its egg on it and at once closes the nest, a primitive case of provisioning followed by such wasps as some of the members of the genus Ammophila and Sphex. In the prey carrying method this species is very adaptive. When the prey is small and light it carries it by impailing it on the sting. When it is large and heavy it catches it with the hind legs alone or with one of the middle legs. Such a broad adaptability has not been observed on any species dealt with here, in so far as observed by me.

BIOLOGICAL RELATION TO CRABRONINI

From the structural characters the tribe Oxybelini is combined with Crabronini to form the subfamily Crabroninae in the present-day taxonomy. From the biological point of view also the two groups possess a considerable number of the common characters:

- 1. Most of the Crabronini hunt the Dipterous insects and all the members of Oxybelini capture the same group of insects as their prey.
- 2. Both groups make a provisional store of the prey before oviposition and when oviposite they lay their eggs on the prey put at the bottommost part of the cell.
- 3. In both groups when the prey are arranged in the larval cell a marked tendency is observed that the inner and bottom prey are laid venter up, lateral prey side up and venter in and the outer and upper prey venter down, so as the bodies of the prey to be wrapped up as a mass with the wings of whole the prey.
- 4. The position of attachment of the egg and the manner of its placement are the same in both groups.
- 5. In some ground nesting Crabronini, for instance, *Crossocerus wesmaeli*, the cocoon is inlaid with grains of earth as in most of the Oxybelini.

unnel place o the

the,

oose-

omen s this

pecies rpe of

ıstant

adi is e case t type As for other

d cell in O. ontal,

ng the attribute menu of the exception above prey

ınd to

e prey s held lomen shaped o sup-

tained Adlerz tatus. on the tiyama

niddle

uch a

REFERENCES

- Crèvecoeur, A. 1929. Remarques éthologiques sur quelques Hyménoptères, II, Bull, Ann. Soc. Ent. Belg., 69: 358-366.
- ——— 1931. Biologie de l'Oxybelus bipunctatus Oliv. (Hym. Sphegidae). Ibid., 71: 187-192.
- Evans, H. E. 1962. The evolution of prey-carrying mechanisms in wasps. Evolution, 16 (4): 468-483.
- Ferton, C. 1901. Notes détachees sur l'instinct des Hyménoptères mellifères et ravisseurs avec la description de quelques espèces. Ann. Soc. Ent. France, 70: 83-148.
- Gaulle, G. de 1908. Catalogue systématique et biologique des Hyménoptères de France. Paris.
- Grandi, G. 1926. Contributi alla conoscenza della biologia e della morfologia degli Imenotteri melliferi et predatori. IV. Mem. Soc. Ent. Ital., 5: 187-213.
- 1961. Studi de un entomologo sugli Imenotteri superiori, Boll. Ist. Ent. Univ. Bologna, 25: 1-659 (ref. pp. 254-265, especially 263-264.).
- Hamm, A. H. and Richards, O. W. The biology of the British fossorial wasps of the families Mellinidae, Gorytidae, Philanthidae, Oxybelidae and Trypoxylonidae. Trans. Ent. Soc. London, 78: 95-131.
- Maréchal, P. 1930. Sur trois Hyménoptères se développant dans un cocon en mosaique. Mém. Soc. Ent. Belg., 23: 1-23.
- Masuda, H. 1939. Habits of *Oxybelus strandi* Yasumatsu (Hym. Oxybelidae). Trans. Kansai Ent. Soc., 8: 47-57 (in Japanese with English summary).
- Krombein, K. V. 1948. New prey records in *Oxybelus* (Hymenoptera, Sphecidae). Proc. Ent. Soc. Wash., 50 (3): 67.
- Kurczewski, F. E. and B. J. Harris. 1968. The relative abundance of two digger wasps, Oxybelus bipunctatus and Tachysphex terminatus, and their associates in a sand pit in Central New York.
 Jour. N. Y. ent. Soc., 76 (2): 81-83.
- Tsuneki, K. 1942. A Naturalist at the Front. Osaka (in Japanese).
- 1946. Further observations on the habits of Oxybelus strandi Yasumatsu (Hymenoptera). Matsumushi, 1 (2): 81-85 (in Japanese).
- 1951. Habits of Oxybelus bipunctatus Olivier observed in Japan, with notes on the method of transportation of the prey by the members of the genus Oxybelus (Hymenoptera). Ins. Ecol. (Tokyo), 3 (9): 63-74 (in Japanese with English summary).
- Uchida, H. 1938. What are hunted by Oxybelus strandi Yasum,? Kontyu, 12 (5): 182.