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

(Hymenoptera, Sphecidae)

**III. Conclusive Part**

By Katsuji TSUNEKI

(Biological Laboratory, Fukui University)

(With IV Plates and 20 Figures in the Text)

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## SUPPLEMENTS TO PART II

## 4. Learning of the sinuous pathway

(A) *A pathway with a short slope*

Apparatus: A Y-tube of glass having a diameter of 1 cm; one of the branches has a short upward slope, 2 cm in length, in the middle; the basal tube is 5 cm, the two branches are 15 cm in length; a glass cell is placed respectively at the end of the branches.

1) Wasp No. 179. Aug. 16, 1951. The nest in the vertical view was as shown in Figure 1, a. The larva was in the final instar soon after ecdysis, with 1 mouldy (probably the uneaten pedestal of the egg), 4 partly eaten and 4 intact victims. The nest was dug open from behind, leaving the first half of the tunnel as it was, and a tube bottle with the larva and one intact fly in it was connected with the cut end of the burrow (Fig. 1, b). It was at 1 o'clock p.m. Three flies were brought in on the day. The next day at 9.50 a.m., the tube bottle was replaced with the apparatus mentioned above and the larva alone was put in the left-hand cell. Whole the apparatus was covered with a sheet of red cellophane paper, and moreover, the tunnel except the bifurcation and the entrance to each cell was hidden under a layer of sand, lest the wasp should be disturbed by the stimulus of the light. The direct rays of the sun were intercepted with a wooden board stood behind the entrance to the nest.

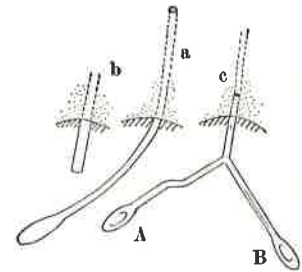


Fig. 1. The nest of wasp No. 179 (a) and its first (b) and second (c) experimental arrangements.

The behaviour of the wasp inside the apparatus at her first four times of return was diagrammatically shown in Figure 2. In the Figure the straight line represents the forward progress, the waved line the backward progress, the downward arrow shows that the wasp comes in the apparatus, while the upward arrow that she goes out of the nest, the circlet indicates touching and examining the larva, the small triangle catching the fly and the crosslet placing the fly. Therefore,  $\triangle \sim \times$  stands for the behaviour that the wasp caught the fly left in the tunnel, dragged it backing and dropped it. The numeral within a circle denotes the number of entering of the wasp to the nest within a series of behaviour at her return. Some comments will be necessary in relation to the Figure.

The repeated retransportation of the fly at the first return at 10.20 a.m. was probably resulted from the fact that the position relation between the larva and its cell was yet unestablished in the wasp's memory. Because she never examined the larva at the time when she had transported the victim. This behaviour may represents only the reflexive response to the contact with the fly during the time when the motivation of carrying food to the larva is still in action. This motivation

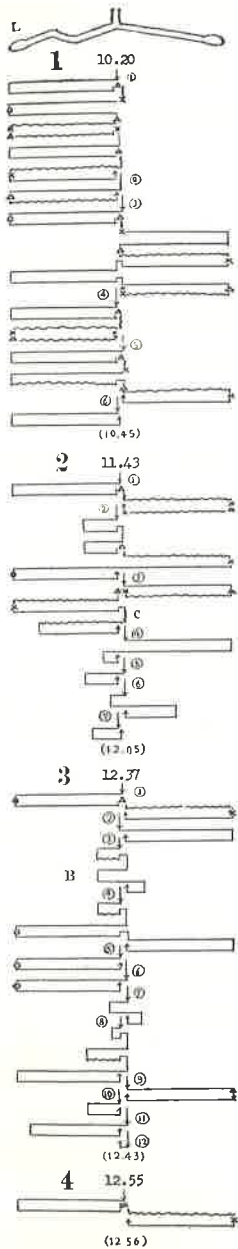


Fig. 2. A diagrammatic representation of behaviour of wasp No. 179 in the apparatus shown in Figure 1, c, in her first four times of return. Detailed explanation in the text. L denotes the larval situation.

usually disappears when the victim is transported to the side of the larva, so far as it is concerned with a single victim. In general, the behaviour of the wasp at this time is full of confusion which is probably caused by her unfamiliarity with the apparatus.

At her second return the wasp gradually became familiar with the apparatus and the positional relation between the larva and the victim was considered gradually fixated in the wasp's mind, but disturbance still continued. The behaviour marked with C represents the closing movements at the cell entrance. At the third return at 12.37, confusion did not perfectly disappear as yet. It seemed that the wasp was uncertain in her behaviour at the bifurcation and her cognition of the presence of two cells — the one the larval cell and the other the empty cell — had already broken down in her mind. The behaviour marked with B is that the wasp retreated from the slope. It seems to indicate that the wasp could not as yet respond correctly to the slope of the pathway in connection with the direction of the larval cell. The activity at the fourth return represents the automatic provisioning behaviour, utterly guided by the internal mechanism only which is usually observed towards the end of the provisioning work.

In order to test the learning effect, at her fifth return the apparatus was replaced with another having a similar slope on the right-hand pathway. At 1.31 p.m., the wasp returned with a prey. Her behaviour in the apparatus newly set was as shown in Figure 3. This result confirmed that the learning of the direction of the pathway in relation to the position of the larval cell was well established, as had previously been presumed from Figure 2. The fact shows at the same time, however, that the learning of the slope in connection with the larval cell could not be established.

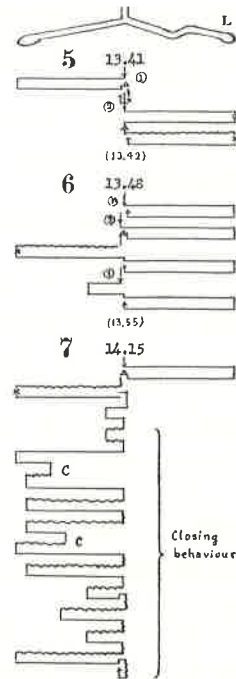


Fig. 3. The behaviour diagram of wasp No. 179 in her final three times of return.

At the subsequent two times of return the wasp well responded to the altered direction of the larval cell, but her response to the slope was quite doubtful. Behaviour at her last return is nothing but the movements for the permanent closure of the nest, only showing that the act is completely guided by the innate behavioural pattern.

(B) *A pathway with two horizontal turns*

The apparatus is similar to the above-mentioned, differing only in that the portion of the slope in one of the branches was made horizontal (Pl. I, Fig. 1).

1) Wasp No. 165. Aug. 26, 1950. The nest and the experimental arrangement were as shown in Figure 4. In bottle A a larva of the early middle stage of the

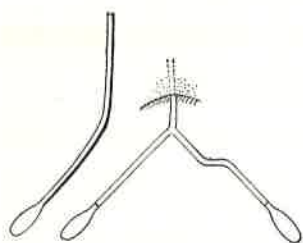


Fig. 4. The nest and the experimental apparatus of wasp No. 165.

4th instar with an intact fly was placed, while in bottle B nothing. At 11.07 a.m., the wasp came back with a fly. Her behaviour was shown in the first section of Figure 5. The result seems to show that the wasp followed her memory of the direction of her own tunnel. Therefore, the apparatus together with the bottles was turned through 180°, so as the larval cell at the end of the

straight path to come to the right. Her behaviour in the tube at her second return was given in the second section of Figure 5. According to the result, it seems that something other than the memory of the direction takes part in determining her way. So the bottles were interchanged in position, leaving the tunnel *in situ*. But in her third and fourth return the wasp in her forward progress invariably went straight to the larval cell, excepting one time when apparently she went erroneously in the other tunnel to take the victim that she had laid down in the basal tunnel.

In this case the wasp was apparently guided by some direct factor — possibly the odour of the larva — to the larval cell, without showing no concern to the character of her pathway.

2) Wasp No. 195. Aug. 23, 1951. By failure of digging the contents of the brood-cell became undiscovered. But as I had observed the wasp working since the 20th, the larva was supposed to be in the early stage of the 4th instar. A glass cell was placed for trial at the end of the entrance

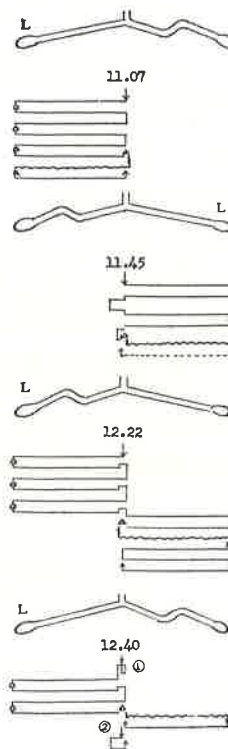


Fig. 5. The behaviour diagram of wasp No. 165. The dotted line stands for the forward progress sweeping the floor.

gallery left intact with a larva of the final instar. At 12.40, the wasp came back with a fly, normally provisioned it and went away. I replaced the bottle with the apparatus used for the preceding experiment, with the sinuous path on the left and placing the larva in the cell at the end of the right-hand straight path. The apparatus was covered with a sheet of red cellophane paper.

At 13.42, the wasp returned carrying a victim and moved about in the tunnel as shown in the first section of Figure 6. Then the larva was shifted to the left-hand bottle and the right-hand one was changed with another having the open end (Pl. I, Fig. 2). In this case, if the wasp went in the wrong way she was obliged to go out of the tunnel as a punishment. The cellophane paper was removed.

At 13.48, she came back with a fly and walked about in the tunnel as given in the second section of the same figure. At first she showed much hesitation in determining her way at the bifurcation, but finally went to the right, probably obeying her memory of the direction acquired during the course of the preceding experiment. She eventually went out of the cell, but after a short progress sweeping the floor, she began to retreat backwards and, fortunate enough, happened to reenter the tunnel again. Then she turned around and went to the left-hand tunnel head first. At the first turning point she retreated backwards three times successively. Then she passed the sinuous portion and went to the larva, touched it with her antennae and examined it carefully, holding it repeatedly between the antennae. After a while, she turned round and went to the bifurcation. Since then she visited the larva 6 times successively and finally carried the fly correctly to the

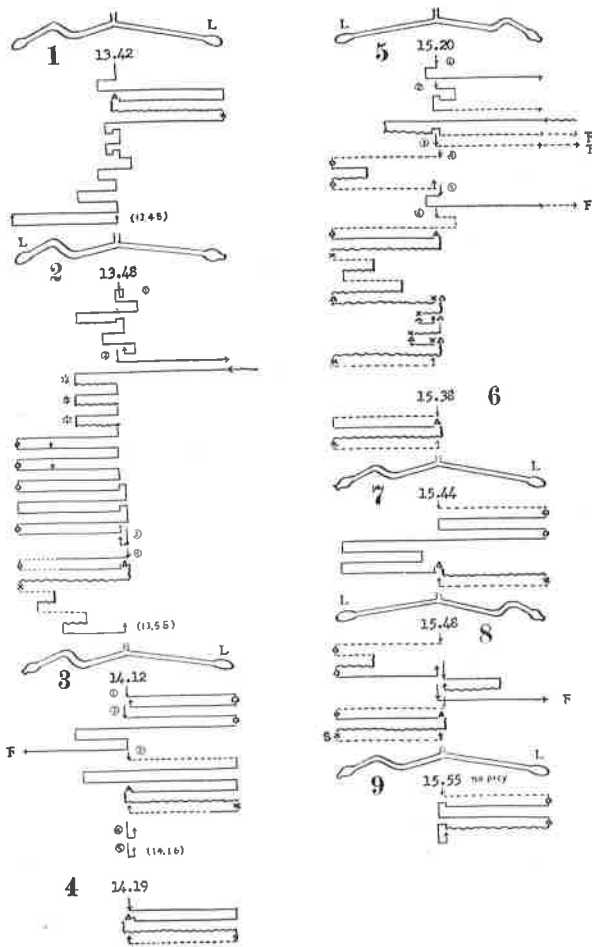


Fig. 6. The behaviour diagram of wasp No. 195. "S" and "F" — see the text.

side of it. She then showed the closing behaviour in the tunnel in front of the larval cell and normally went out of the nest.

In order to test whether or not the wasp had formed an associative memory between the sinuous path and the larval cell, the bottles on both sides were interchanged. If this had well been formed (with the memory of distance), she would turn round half way when she went in the straight pathway.

The result seems negative (Fig. 6, the third section). In this case either the wasp might follow the odour of the larva, or she might lack the sense of distance, had she not entered the way erroneously. The former consideration seems probable. In her subsequent movements in the tunnel the wasp apparently learned the way to the larval cell through the straight pathway, since, when she went in the sinuate path, she turned round at the turning point or showed her intention to turn round (only could not easily do so and eventually went on — this behaviour was denoted by  $\neq$  in the figure). The behaviour in her subsequent return at 14.19, seems to support this consideration (Fig. 6, the 4th section).

So I turned the basal axis of the apparatus through  $180^\circ$ , so as to change the position of the branch tunnels with each other and also interchanged the end bottles. The result shown by her behaviour at her fifth return at 15.20 was completely negative (Fig. 6, the 5th section. Symbol F at the apex of the arrow indicates that the wasp went out of the tunnel through the open cell, walked a short distance sweeping the sand, then flew up and went to the entrance to the nest and penetrated again). She went through the sinuous path; she went on even after going out of the tunnel. The same behaviour was repeated once more. In this case the wasp showed a search behaviour in the open cell and when went out of the cell, she soon backed and happened to enter the tunnel, turned round and went in the left-hand branch. But she returned half-way and came back in the right-hand branch again. This time she went far out of the tunnel and flew to the entrance of the nest. Subsequent behaviour can be read from the same figure.

An interesting abnormal event happened during the course. The wasp, after showing a closing movement in front of the larval cell, went backing in the chamber across the fly. Then she tried to capture a fly, but failed owing to its reverse bodily position and happened to push it forward in her attempt to catch it again. At last she pushed it up to the basal tunnel and barely recaptured it. Then she dragged it backwards towards the larval cell, but missed its hold on the way and again pushed it towards the bifurcation. The same curious manoeuvre was once more repeated. Finally she succeeded in catching it firmly and dragged it in the larval chamber.

At 15.38, the wasp normally, very smoothly and correctly took in a fly.

Then whole the apparatus was turned round  $180^\circ$ , so as the straight branch with the larval cell to come to the right. At 15.44, the *Bembix* came back carrying a booty. Her behaviour in the glass tunnel was as shown in the 7th section of Figure 6. In this case, the wasp, even when she went in the open chamber at the end of the sinuous branch, did not go out, but returned from the chamber.

She could not return, however, from the sinuous point of the tunnel.

Again the apparatus was turned through  $180^\circ$ . The wasp, when came back from her foraging excursion with a prey at 15.48, moved about in the tunnel as given in the 8th section of the same figure. This time, when she went in the sinuous branch at her third trial she returned from the turning point. But in her subsequent entering to the same branch she did not turn round at the point, but went through it and finally crept out of the open chamber to fly to the nest entrance. At the point designated by "S" the wasp caught a fly in the cell and stung it, a very strange and hitherto unobserved phenomenon.

The Y-tube was then replaced with another having a similar sinuate branch and was arranged so that the straight branch with the end larval bottle came to the right. The wasp came back at 15.55 capturing a fly and smoothly and correctly took it in the larval cell as shown in the last section of the same figure. Since this time, the wasp did not come in the glass tunnel. She dug a pocket in sand in front of the apparatus and provisioned there, without receiving stimulus from the larva.

Throughout the experiments the wasp apparently used more than one clue to select the direction to the larval cell. In her return at 13.48 and 15.20, she appears to enter the right-hand branch through the learning effect of the direction. But in all the rests of her response to the experimental change of the direction she invariably went in the direction opposite to the possible effect of her learning. Probably the wasp learned to depend on the direct guiding factor coming from the larval cell (possibly the odour) during the position change experiments so frequently repeated. In fact, at the beginning of the experiments the wasp showed not a little hesitation before she determined the way to which she went. Later, however, she showed no hesitation whatever and took the correct way from the first, despise that the direction of the larval cell was completely reversed. As for learning of the sinuous branch in connection with the empty or open cell, it appears to be negative. But no definite conclusion can be drawn from the results of the experiments here conducted, since the wasp did not frequently go in the sinuate branch.

3) Wasp No. 186. Aug. 21-23, 1951. The structure of the nest was given in Figure 7, a. The larva was at the later stage of the 3rd instar, still attaching to the pedastal fly and by the side of it were placed 3 victims of which one was half-eaten and the other intact two had been accumulated on that morning. The apparatus used and its arrangement were shown in the same

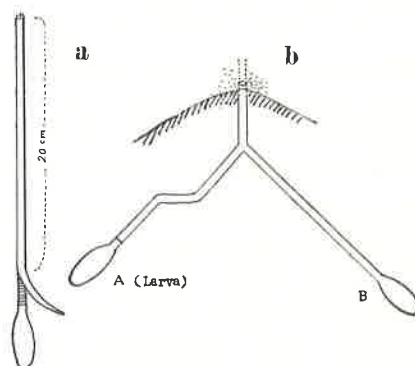


Fig. 7. The nest and the experimental arrangements of glass tubes and cells of wasp No. 186.



figure, b. In bottle A was put a larva of the early stage of the 4th instar with one half-eaten fly, while bottle B was left empty. The apparatus was protected from the direct rays of the sun by two boards of veneer, only exposing the entrance of the nest outside the shadow\*. In order to set spur on the wasp, the flies carried in the bottle were removed one after the other, leaving only one or two in the larval cell. Her behaviour in the tunnel when returned from the hunting trip was given in Figure 8 and the experimental results will briefly be accounted for below.

(1) At 13.35, the wasp came back empty-handed. She returned from the sinuous portion and went in the other branch. But she went out of the nest without meeting the larva.

(2) At 14.44, she came back with a fly. This time she found the larva, but after carrying the victim in the erroneous direction, at once flew away, without striving to retransport it to the larval cell.

(3) At 15.03, came back with a fly. Learning of any sort in relation to the larval chamber did not seem to have been established.

(4) At 15.07, with a fly. Apparently the wasp learned the larval position. But she did not try to correct the error of her transportation.

(5) During my observation of other *Bembix*, the wasp returned between 15.40-15.47. A paralyzed fly was left on the Petri-dish with which the entrance was covered during my absence.

(6) At 16.10, came back without a fly, only inspecting the interior of the nest. The wasp appeared to perceive the presence of the larva from the entrance of the brood-chamber.

(7) At 16.23, with a fly. In this case the wasp tried three times to retransport the fly that was carried in the wrong direction. But she could not correct her error to the last. Notice that the retransportation was always began from the main tunnel! Towards this time apparently the situation of the larva was fairly firmly fixed in the wasp's memory.

(8) I then turned the apparatus around the basal axis through 180° so that the sinuate branch with the larval cell might come on the right. At 17.07, the wasp came back carrying a fly. She seemed to have followed the memory of the direction to the larval cell. From her behaviour designated by  $\neq$  it appeared that she had not learn the presence of the sinuous portion in the path in connection with the larval chamber. But her movements after meeting with the larva might

\* In spite of the fact that such an arrangement completely covered the general background seen from the front of the nest-entrance, the wasp did not show any noticeable confusion in finding her nest. This is also the case when an umbrella was utilized instead of the veneer. From the fact it is presumable that the recognition of the wasp of its nest site does not depend upon the memory of the background of the nest seen from a certain definite position only, but upon the complexed general pattern of the ground seen from various positions in the air.

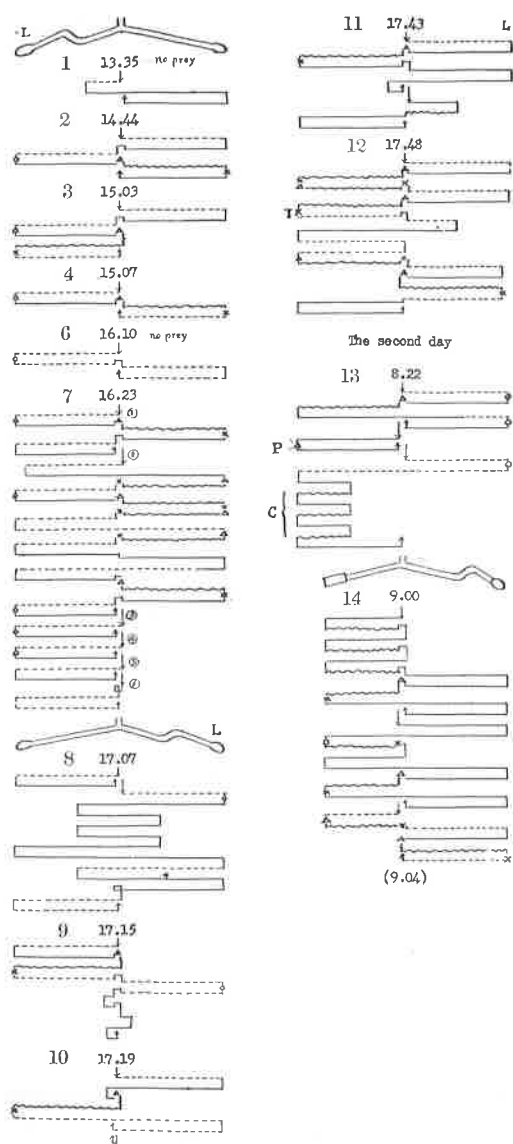


Fig. 8. The diagram of behaviour of wasp No. 186 in the experimental apparatus. Return No. 5 was omitted, since the wasp was not allowed to enter the nest.

carried the flies found there one after the other to the interior of the cell. At her last visit to the non-larval cell she caught and stung one of the flies. After the manoeuvre the wasp threw out the sand from within the basal tunnel and the

\* This fly was not transported to either of the cells in this case. But the next day (observation 14 at 9.00) it had been carried in one of the bottles.

represent behaviour searching for the prey that had been left in the basal tunnel\* If so the above presumption is not necessarily conclusive.

(9) At 17.15, with a victim. The wasp had not as yet learned the larval situation. Her behaviour at her first entrance represents only the movements governed by the intrinal automatism. Without confirming the presence of the larva she transported the fly quite mechanically to one of the cells. But the fact that she did not fly away at once but went in the other tunnel seems to show something like uncertainty in her mind.

(10) At 17.19, the wasp returned with a fly. This time learning of the way to the larva appears to have been established. But she did not correct the wrong result of her transportation of the prey.

(11) At 17.43, with a *Calliphora*. Her behaviour was similar to the preceding.

(12) At 17.48, with a flower fly. Her behaviour was similar to the above. But in this case the wasp twice tried to retransport the fly and at her second trial she succeeded in correcting her error. However, she did not try to carry away all the flies placed in the non-larval cell that had previously been transported erroneously by her. And one of the flies that were carried from the non-larval cell to the basal tunnel was left *in situ*. At T she

entrance was closed. She seemed to pass the night there. All the flies but one which was left by the side of the larva were removed from the cells.

(13) The next day at 8.22, the wasp returned with a flower fly for the first time on that day and moved about in the apparatus as given in Figure 8 (13). At P she examined and moved the fly, at C she showed the closing manoeuvre of the larval cell. In this case, too, she did not try to retransport the fly that was carried in the wrong cell.

(14) At 9.00, carrying a fly. A remarkable fact is that the wasp at her first three inspecting visits went successively in the wrong direction. According to the results, learning effect of the way to the larval chamber seems doubtful. In this case, the wasp, after two times of vain trial, succeeded in correctly retransport the fly\* to the larval cell.

(15) In order to give the wasp, when she enter the straight branch, a sufficient distance to correct her error in relation to the sinuous path (had the wasp learned the relation between the sinuation of the path and the situation of the larval cell), I attached to the end of the straight branch a 35 cm long glass tube of an equal diameter with the end closed. As a result the straight tube came to be 50 cm in length.

At 9.15, the wasp returned with a fly. At this time the wasp, when entered the wrong direction, always turned back half-way (Fig. 9).

(16) At 9.19, with a booty. She went in the wrong direction from the first (Fig. 9, (16)), without turning back on the way and showed some confusion in her behaviour (repeated forward and backward progresses). At P she caught and moved the fly she had erroneously transported. From the 4th entering onward the wasp went in the correct direction without failure. This instance is very instructive against the hasty conclusion.

(17-20) The wasp behaved fairly correctly in the glass tunnel, although she could not control her backing progress and she did not correct the results of her erroneous transportation.

(21) Test. The branches of the Y-tube with the end bottles were interchanged in position. At 10.03 the wasp entered the nest dragging a fly (Fig. 9, (21))

According to her behaviour, (a) probably the wasp followed the learning effect on the direction in her way to the cell; (b) she had not, however, learn the presence of the sinuous path in connection with the larval cell, and (c) she had not learn the absolute distance to the larval cell. From the 4th to the 12th entering the wasp invariably went in the correct direction. At her 6th and 10th entering, when she went in the straight tunnel, she turned back from the place corresponding to the situation of the sinuous portion of the opposite pathway.

(22) At 10.15, with a fly. It was clear that the renewed learning on the direction of the larval cell had not been established during the course of the

\* This was not the fly just brought in, but the one that had been left in the tunnel since 17.07 of the previous day. The fly newly carried in was laid aside in the tunnel of sand.

preceding provisioning activities, so long as it is concerned with the next return. At any rate, she could not learn the presence of the sinuous portion of the path in relation to the larval cell. From a second to a tenth entrance her movements may show the trial of new learning.

(23) At 10.35, carrying a fry. The learning effect did not appear as yet. It was considered that the wasp learned the new passage again from her second to seventh entering.

(24-26) Judging from the results it seems that a new learning has been established already at the return of the wasp at 11.15 (Fig. 9, (24)). In her subsequent return at 11.37, behaviour of the wasp was very suggestive. When she went in the wrong direction she always turned back half-way. But the same behaviour could not be observed at her subsequent return. On the contrary, she turned back from the very place of the sinuous path. The correct interpretation of the wasp's behaviour seemed very difficult.

When the wasp returned to the entrance gallery from her first visit to the larval cell, the fly left there was thrown out of the nest during her sweeping movements in the burrow. The subsequent movements of the wasp, therefore, might be a searching behaviour. If so, backing from the sinuous portion is apparently a positive proof towards her learning of the presence of such a portion on the way to the larval cell. But such may be a too anthropomorphic consideration.

(27) At 12.21, carrying a fly. At her first entering the wasp showed a hesitation at the sinuous portion of the correct way and backed to the bifurcation. The same behaviour was also observed at the first entering in the preceding return. This is probably only dependent upon the more or less difficulty of the place to pass. In this return the wasp two times transported a fly, one of which was the victim left in the tunnel. This time the wasp strived to retransport the prey to the larval cell, though ended in failure.

(28) At 12.33, with a fly. At her 2nd and 3rd visits to the larval cell, the wasp backed from the sinuous portion of the passage and flew away in confusion without closing the entrance of the nest. This seems clearly indicating that the associative memory between the larval cell and the sinuous path has not as yet been established in the wasp's mind.

(29) At 12.36, with a fly. First the wasp carried the fly left in the tunnel in her preceding return and then the fly just brought in. The former was correctly transported to the larval cell, while the latter to the end of the long tube. The confusion shown after the last transportation at the end of the tube (frequently observed) seems merely to depend on the fact that she could not easily turn round in the narrow terminal.

(30) At 13.25, without carrying a fly. When entered the straight tube, the wasp backed from a distance of 10 cm from the bifurcation.

(31) At 13.33, without a fly.

(32-37) At 13.42, 47, 53, 14.18, 22 respectively, each time with a fly. During

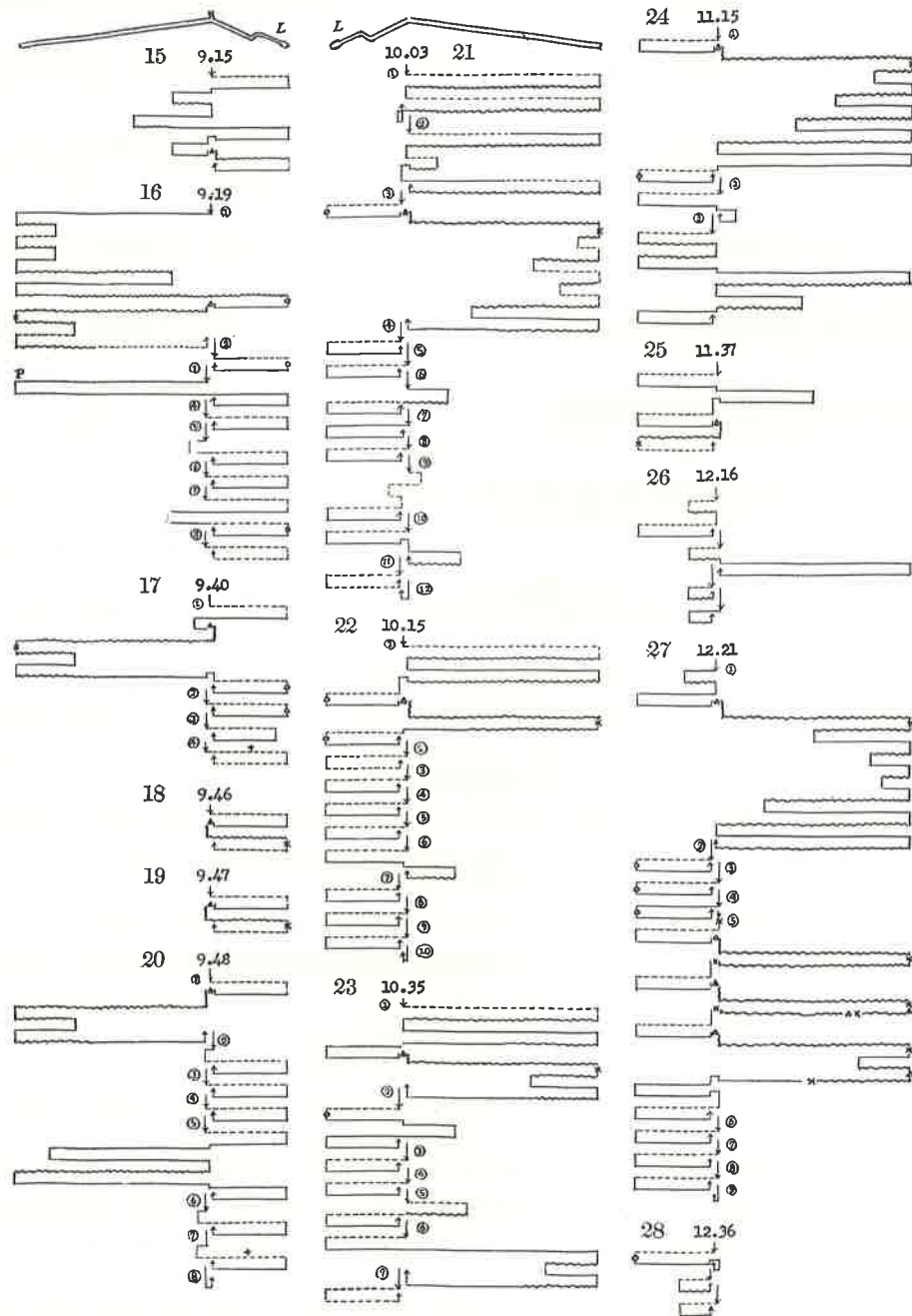


Fig. 9. The behaviour diagram of wasp No. 186 in the experimental apparatus (continued from Figure 8).

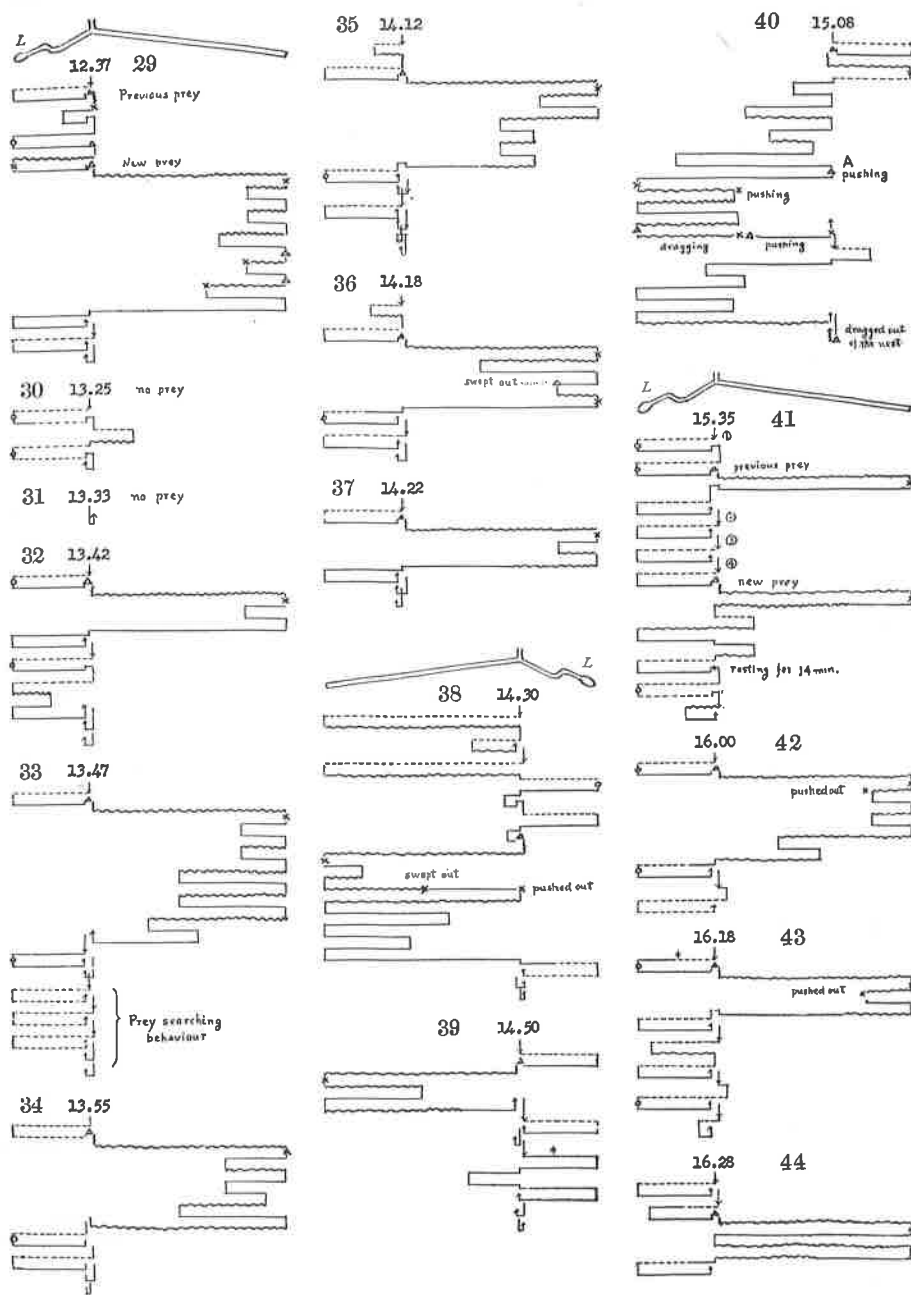


Fig. 10. The behaviour diagram of wasp No. 186 in the experimental apparatus (continued from Figure 9).

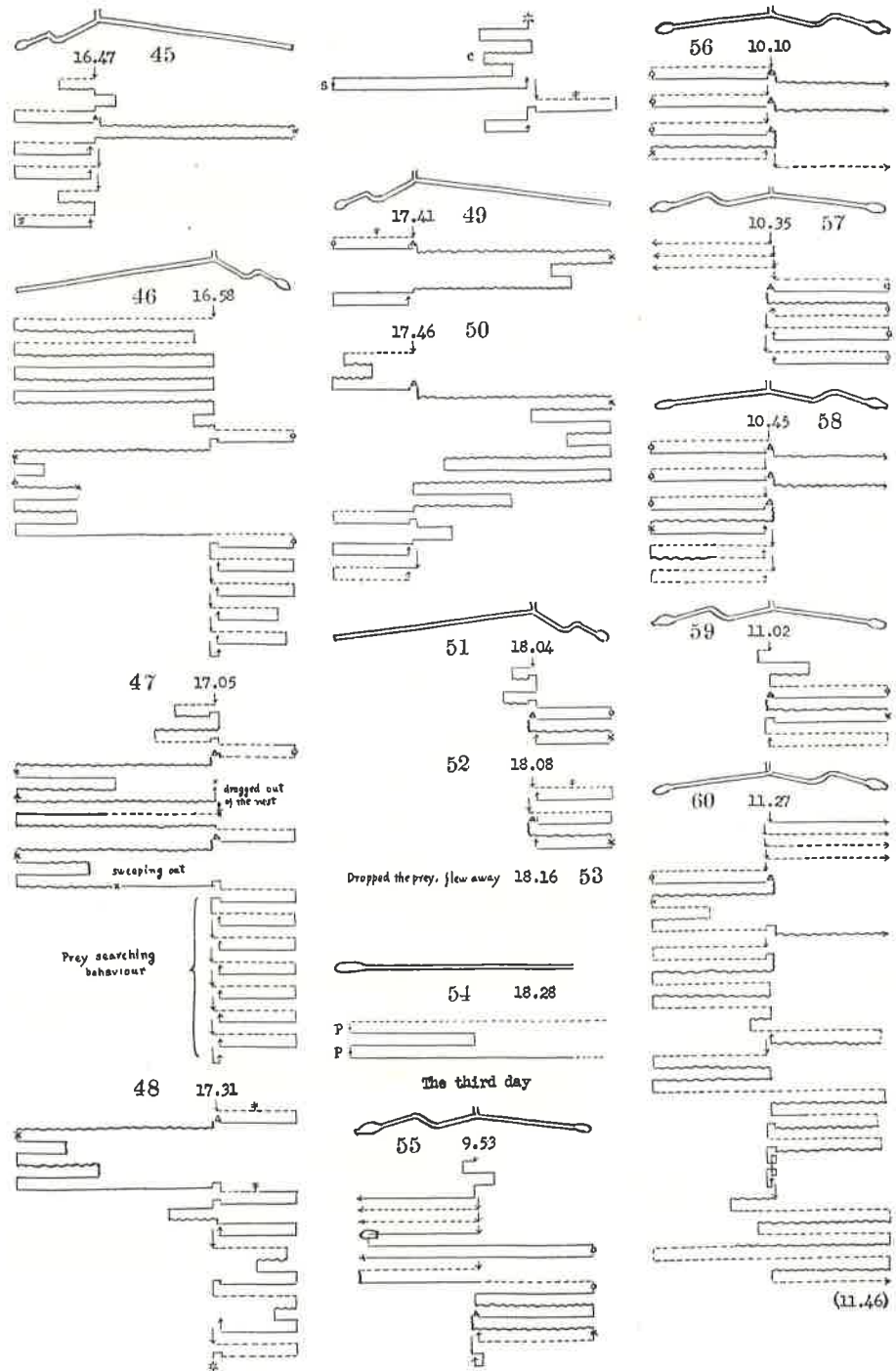


Fig. 11. The behaviour diagram of wasp No. 186 in the experimental arrangement (continued from Fig. 10).

the periods the wasp when proceeded head first invariably went in the correct direction. Strange to say, however, when backed in the tube dragging a fly, she always entered the wrong branch and after dropping the fly always showed a confusion by walking hurriedly to and fro at the end. But the retransportation of the fly did not occur excepting the incomplete one at her 36th return.

(38) Test at 14.30 by interchanging both branches with each end-cell in position. According to the result, only the same conclusion as given regarding the test made at the 20th return of the wasp was confirmed again. The wasp learned solely the direction of the pathway; apparently she could not connect the presence of the sinuous path with the situation of the larval cell.

At the point marked with A, the wasp first swept backward the transported fly. Then she turned round and apparently intended to capture it. She could not do so because of the reverse bodily orientation of the fly and eventually happened to push it forward until the forking point of the apparatus.

(39-40) At 14.50 and 15.08 the wasp took in a fly respectively. The results appeared to show that these times, the wasp learned the correct way by her single visit.

At A in the figure of the 40th return the wasp casually pushed the fly forward which had been left in the tunnel since her 36th return. At the end of the tunnel she mounted over the fly to the innermost wall and when she backed, the fly came to be pushed backward with the tip of her abdomen. Then she went forward to the end of the tube again, caught the fly that she had carried there a few seconds before and dragged it backing to the bifurcation. At this moment the fly left in the tunnel was pushed back with her abdomen. Thus the two flies were transported to the bifurcation at a time. Later, at her last entering the wasp caught one of them, dragged it out of the nest and discarded. She flew off without closing the nest entrance.

(41) The disposition of the apparatus was changed again. This time the wasp entered the larval cell directly from the first, although it was located reverse in direction. It was uncertain, however, whether she went there by chance or as a result of following the larval odour. At the point marked with an asterisk the wasp stayed in the tunnel for about 14 minutes.

(42-45) At 16.00, 16.18, 16.28 and 16.47 respectively with a fly. During the course the wasp invariably went correctly to the larval cell in her forward progress. In her backing progress, however, she always failed to go in the direction just before corroborated by her inspection and carried the victim to the empty end of the long tube. During the time she did not try to retransport the fly, though sometimes she happened to push it out some distance with her abdomen when she backed.

At her final visit to the larval cell in her 45th return (marked with S), the wasp took up a fly and stung it. Then she captured the larva and showed a posture of stinging by bending her abdomen. The larva wriggled and twisted its body and the wasp eventually dropped it.

(46) Test by position change of the branches of the Y-tube with end cells.



The result :

The wasp went in the previous direction. Probably she had been following the memory of the direction in determining her way to the larval cell. It can not be supposed that she had learned the presence of the sinuous path in connection with the direction towards the larval cell. The same seems true as to the length of the path.

(47) At 17.05, with a fly. In spite of the fact that during the preceding return the wasp repeated the trial of direct going in the correct pathway in her last four visits of the larva she could not establish the learning of the new situation of the larval cell. However, when she went in the wrong path in her first two times of trial always she stopped half way, rubbed the antennae for a while and turned back. This has apparently some significance, but it is apt to commit an error to give a hasty conclusion, since the behaviour of the wasp is still quite inconstant.

After finding the larva the wasp carried the fly in the wrong direction and tried to retransport it. At last she passed between the larval cell and the front of the nest entrance 7 times to and fro. During the time she showed a behaviour in front of the nest entrance which gave us an impression that she was searching for the prey.

(48) At 17.31, with a fly. Learning of the new direction appears to have been established. However, there remains some doubt as to the learning of the sinuous path, because at the point of turn she showed twice a posture of turning back, though she could not do so and mechanically proceeded until the end. But it seems worthy of notice that the wasp three times turned back half-way when she entered the long tube.

At C the wasp showed the closing behaviour and at S she stung the fly.

(49) Test by turning the apparatus around the basal axis through 180° together with the end bottles. Thus the larval cell with the sinuate path came on the left side. At 17.41, the wasp returned with a fly.

She went in the correct (inverse to the previous) direction from the beginning. But she showed an attitude of turning back from the sinuous portion of the pathway, though she reached the apex apparently unwillingly owing to the difficulty of turning back. According to the result, it seems that (a) she had been following the larval odour in determining the direction at the bifurcation, (b) she could not as yet establish the associative memory between the presence of the sinuous portion on the way and the location of the larval cell.

(50) At 17.46, came back carrying a fly. The wasp was allowed once more to learn the way to the larval chamber under the same condition. She went in the correct direction.

(51) To test the learning effect the apparatus was turned again. At 18.04, the wasp came back with a fly. At her first two visits to the larval cell she went in the left-hand branch — the previous direction. In both cases, however, after walking for 5 cm in the long straight way she stopped and returned backing from front of the sinuate point. This is suggestive but not conclusive, for the wasp

might stop because of the lack of the larval odour.

(52) At 18.08, carrying a fly. The wasp took the correct direction in her two visits before carrying the victim to the larval cell. In both cases, however, she showed a postuae of turning back at the sinuous portion. But she could not do so and went on eventually up to the end cell. This does not favour the view that the wasp has learned the presence of the sinuous portion in the pathway leading to the larval cell.

(53) At 18.16, the wasp returned with a fly, but dropped it in amazement in front of the nest and flew away.

(54) I removed the apparatus and placed at the end of the natural tunnel of the wasp a straight tube of 35 cm long with the larval cell at its end.

At 18.28, the wasp came home carrying a victim. She came in sweeping up to the larval cell without confusion, took up one of the flies and stung it. She then turned round, went in the glass tube, but turned back half-way to the larval cell and once more captured a fly found there and stung it. She went out of the nest, but at once hurried in, stayed a little while in her own sand tunnel and then came to the larval cell again. There she repeated that queer backward and forward progresses which were so often observed when she went to the end of the long straight tube of the previous apparatus, though in this case there was an ample space for turning round if she wanted. Then she turned back, went in the sand tunnel of her own and stayed there probably to pass the night.

The next day when I arrived at the experimental ground at 8.23 the nest had been destroyed and the glass tube had been stolen, probably by the idiotic herd-boy who had observed my behaviour from afar the previous day and who had destroyed several nests under my observation some years before. Fortunate enough, the larval cell had escaped from his curious eyes and the larva was still alive. Inside the cell there were remains of two flies, one of which must have been transported from the entrance tunnel the previous evening after my observation was stopped. But the nest had been completely destroyed from the entrance to the interior and it seemed impossible to guide the wasp to find out her missing nest again.

However, I thought of the fact that the wasp was so well trained to enter the glass tube that she might penetrate the glass tunnel from the entrance. So I buried a glass tube of 20 cm in length in the ground where the wasp had been digging and attached to its end the larval cell. I then poured the water from my water bottle in front of the glass tube so as the sand not to crumble down when dug by her and made a short canal up to the entrance to it so that the wasp might find it with ease. The wasp soon found the canal, searched and dug there, found the entrance of the tube and at once came in the apparatus. She soon appeared in the glass cell, examined the larva and went out of the nest. Once more she entered, but soon reappeared at the doorway and flew off without closing the entrance. Three minutes later (at 9.35), however, she came back holding a flower fly. At 9.42 she took in another flower fly, at 9.45 a Callipholine fly. I then replaced the tube with the apparatus used the previous day and placed at the end of the straight branch the larval cell and at the end of the other an open cell.

(55) At 9.53, the wasp came back with a fly. After a short hesitation she went in the left-hand sinuate branch 3 times successively and every time went out

of the open cell, flew to the entrance of the nest and penetrated again. At the fourth time I replaced the open cell with a closed one, lest the wasp should abandon the nest. She came in the same direction, arrived at the cell, turned back, went to the larval cell and finally found the larva. Again I replaced the left-hand end cell with the open one. The wasp came from the larval cell directly to the open cell just replaced and once more went out of the nest. But the next time when she came straight to this open chamber, she did not go out, but returned from the chamber to the larval cell and finally transported the fly to the correct cell.

It seems that the wasp clearly remembered the direction to be taken in order to meet with the larva, because in this case the odour of the larva (and the prey) did not come from the end of this branch. That the wasp showed a hesitation at her first entering seems of interest and suggestive.

(56-60) In order to test the learning procedure of the wasp the disposition of the branches and cells was every time changed. The results :

56. Only the retraining towards the left-hand larval cell.

57. The wasp did not follow the odour factor to determine the direction. She did not establish the associative memory between the sinuate path and the open cell.

58. In order to consolidate the learning effect concerning the direction, two times of the learning experience were proved insufficient for the wasp in this case. (She learned thrice more to go in the left-hand direction.)

59. At first the wasp showed a hesitation, first went a little to the left, then to the right and for the third time she went decidedly to the right — the correct way. It was uncertain, however, on what factor she was dependent during the course. But in this case she seemed to have learned and fixed to her memory the direction to the larval cell during two times of her subsequent entering. This can be supposed from the result of the following experimental treatment :

60. The wasp went in the right-hand branch 4 times successively without hesitation, despite that the odour of the larval cell did come from the left-hand branch. This may be evidence for that the wasp established the learning on the direction during the course of her movements at the previous return. However, from the result it is also clear that the wasp could not learn the open cell at the end of the left-hand branch. The behaviour of the wasp after carrying the prey in the larval cell is nothing more than the manoeuvre for the permanent closure of the nest.

#### (C) *Consideration and conclusion*

From the results of the experiments conducted with wasp Nos. 179, 165 and 195 it may be concluded that they cannot learn the presence of the sinuous portion in the passage in connection either with the larval cell or with the empty cell, no matter whether the situation may be horizontal or vertical. Judging from the

peculiar ability of the wasps to learn the topographical conditions in their natural habitat this conclusion seems almost decided. However, the states given experimentally inside the nest are quite particular and quite unfamiliar with them. Under the natural conditions they can most easily reach their larval cells only by mechanically passing through the tunnel they made, excepting for the accessory branch. Therefore, it may be a rather excessive load to them to be expected to learn the particular condition of the tunnel in connection with the larval cell. Accordingly, in order to make the wasp overcome such a difficulty a sufficient number of times of learning on the condition must be necessary. In the light of such a consideration the experiments made with the wasps mentioned must be said very inadequate. In contrast to these, the experiments carried out upon wasp No. 186 seem to satisfy fairly well the conditions required. Therefore, the conclusion drawn from the experimental results on this wasp seems more significant. According to the results :

1) The wasp could not fix the learning effect on the sinuous pathway in connection with the larval cell.

2) Interesting behaviour of the wasp was sometimes observed, however, which seems to suggest that the wasp, in some cases, might learn the presence of such a sinuous path in relation to the situation of the larval cell. This is the behaviour of backing from a certain distance (7-13 cm) away from the bifurcation at the time when she happened to enter the long straight branch-tunnel — behaviour observed at her 21st, 25th, 30th, 38th, 40th, 47th and particularly 51st return.

3) But such an effect is quite inconstant. In the preceding entrance to the long and straight tube the wasp turned back from a distance corresponding to the situation of the sinuous portion in the other branch. Whereas in her subsequent entrance to the same tube she went through the tunnel up to the end quite indifferently. It seems difficult, therefore, to appreciate properly the significance of such behaviour.

4) On this account, if such behaviour as mentioned was the true result of the learning of the character of the branch it must be considered quite uncertain and likely to be suppressed by the learning effect of another kinds such as direction and the larval odour.

#### Remarks.

(1) *Learning of the length of the pathway* Above experiments conducted with wasp No. 186. from her 14th to 50th return also suggest that the learning of the length of the path in connection with the larval cell is very similar in difficulty to the case of learning of the sinuous path. But this seems mainly dependent upon the improper technique of the experimentation. The wasp might pass through quite mechanically the pathway, because it had not a sufficient length to turn back half-way.

We have previously observed in connection with the experiments on the change of the tunnel (Pt. II of this paper) that the wasp sometimes refused to pass through a very long tube and dug her own tunnel in sand. We have also confirmed that the wasp could select

Table 1. Names and size of the prey successively brought by wasp No. 186 in her nest, together with the time of her return.

Date	Time of return	Time spent for hunting	Prey		Prey in the cell	
			Name	Size		
Aug. 18-20	?	?	<i>Calliphora</i> sp.	m	0	
	?	?	Tachinidae gen. sp.	s	1	
Aug. 21st	10.13	?	<i>Eristalis cerealis</i> F.	m	2	
	10.20	6	Tachinidae gen. sp.	s	3	
	10.28	7	<i>Eristalomyia tenax</i> L.	l	0	
	11.10	40	<i>Eristalis cerealis</i> F.	m	1	
	12.27	26	<i>Sarcophaga</i> sp.	m	2	
	13.35	-	Without a prey	-	2	
	14.44	8	<i>Olbiosyphus sapporensis</i> Mats.	m	0	
	15.03	17	<i>Sarcophaga</i> sp.	s	0	
	15.07	2	<i>Tabanus mandarinus</i> Schin.	l	1	
	15.45	38	<i>Tabanus mandarinus</i> Schin.	l	2	
	16.10	23	With no prey	-	2	
	16.23	12	<i>Ochrops fulvus</i> Meig.	m	3	
	17.07	30	<i>Eristalomyia tenax</i> L.	l	1	
	17.15	5	<i>Eristalis cerealis</i> F.	m	2	
	17.19	2	<i>Sarcophaga</i> sp.	s	2	
	17.43	22	<i>Calliphora</i> sp.	m	2	
	17.48	3	<i>Eristalis cerealis</i> F.	m	2	
	Aug. 22nd	8.22	-	<i>Eristalomyia tenax</i> L.	l	0.5
		9.00	32	<i>Eristalomyia tenax</i> L.	l	1
		9.15	11	<i>Eristalis cerealis</i> F.	m	0
9.19		2	<i>Eristalis cerealis</i> F.	m	1	
9.40		12	<i>Eristalis cerealis</i> F.	m	1	
9.46		2	<i>Eristalis cerealis</i> F.	m	1	
9.47		0.5	<i>Sarcophaga</i> sp.	s	2	
9.48		1.5	Tachinidae gen. sp.	s	2	
10.03		10	<i>Eristalis cerealis</i> F.	m	2	
10.15		9	<i>Theloria leucozona</i> Fall.	s	2	
10.35		15	<i>Eristalis cerealis</i> F.	m	2	
11.15		35	<i>Lucilia</i> sp.	s	2	
11.37		18	<i>Villa limbatus</i> Coq.	m	2	
12.16		36	Tachinidae gen. sp.	s	2	
12.21		1	<i>Eristalis cerealis</i> F.	m	2	
12.33		3	<i>Sarcophaga</i> sp.	s	2	
12.36		1	<i>Ochrops fulvus</i> Meig.	m	2	
13.25		44	No prey	-	2	
13.33	6	No prey	-	2		
13.42	9	<i>Eristalis cerealis</i> F.	m	2		



the short way. More definite evidence on the problem concerned here can be obtained under the natural condition:

The wasp, when her nest is destroyed from behind, with the entrance portion remained as it was, always search for her larval cell by digging a tunnel in the packed sand. In this case she never digs an unduely long tunnel. The burrow thus made is usually very near in length to the original one. Certainly the wasp must possess the memory of the length of her own tunnel.

(2) *The compensatory provisioning* This wasp provided us with a marked instance for the compensatory provisioning. For her own larva which was at the end of the 3rd instar the wasp had already accumulated 4 flies. For the larva newly given (at an early stage of the 4th instar) she brought indeed 62 flies for three days. Moreover, mode of her work is quite different from her usual way. Her hunting manoeuvre was continued from morning till evening, with an uniform distribution (Fig. 12). This affords proof of that the hunting behaviour was successively released each time of her return by her cognition of the presence of a scanty amount of food by the side of her larva.

(3) *Size of the prey successively captured* This is one of the rare observation instances in which the names and the order of the flies successively brought by the wasp are nearly completely recorded. According to this (Tables 1 and 2) it cannot be considered that *Bembix* brings particularly small flies to her small larva and *vice versa*, as was previously discussed in connection with the way of provisioning of this species. (cf. Pt. I, pp. 133-142).

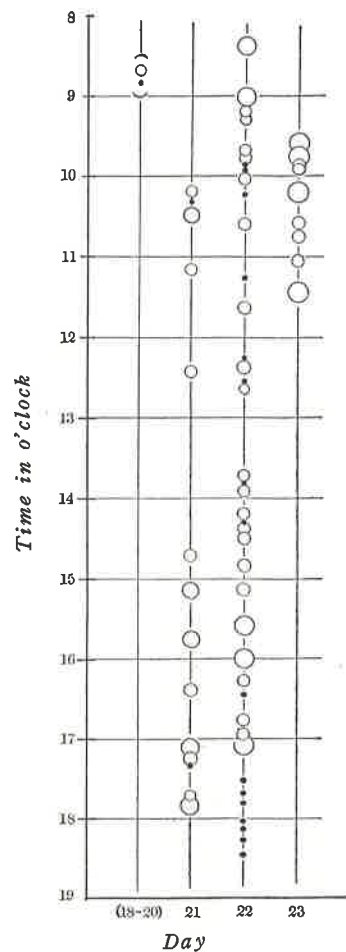


Fig. 12. The compensatory provisioning of wasp No. 186. Large circles denote the large-sized victims, middle circles the middle-sized victims and the small black spots the small victims.

## Part III

### I. BEHAVIOUR PATTERNS IN *BEMBIX NIPONICA*

#### 1. Classification of the behaviour patterns in *Bembix niponica*

Behaviour of *Bembix* exhibited during her brood-rearing activities can all be attributed to the so-called 'appetitive behaviour' in its broadest sense. According to the modern ethologists the concept incorporates in itself from rigid and stereotyped behaviour pattern to flexible and adjusting one. From the point of view of behaviour itself this may probably be true. However, viewed from the origin of behaviour the concept seems to include some qualitatively different behaviour patterns. Moreover, in order to obtain from the study of *Bembix* some significances of the behavioural evolution, it seems inconvenient to rely upon such a comprehensive concept. It is therefore, necessary to analyse the patterns from another point of view. In this respect a very convenient suggestion is afforded by the recent work of Deleurance (1957) on the activity of the nest construction in *Polistes* wasps. It is the method of classifying the behaviour in relation to the origin of the stimulating factor or factors.

According to this method somewhat modified we can divide the behaviour patterns in the brood-rearing activities of *B. niponica* into three main classes. The first is considered evoked by the innate automatism only, the second is probably released also by the internal stimulus but is governed and guided by the corresponding external stimulus (or stimuli), while the third is not only brought into appearance but also maintained by the external stimulus (or stimuli), although the internal conditions of the insect must be consistent with such activities. The first and the second, combined together, correspond to the so-called 'fixed action pattern'. As a matter of convenience for explanation the diagram of the presumed releasing mechanism of the behaviour system of *Bembix* at the time of her nesting activities has been reproduced (Fig. 13).

##### A. The first class of behaviour

In the behaviour formula of *Bembix niponica* BcHTSPOcWE{(cHST)<sup>n</sup>WET)<sup>m</sup>C, the components (or segments) of each behaviour unit are considered belonging to this innately determined pattern. These component-acts are usually combined into a system (subordinate system of a unit behaviour) like that of interlocked machines. Therefore, they can be called forth successively in an assigned order once the initial act is brought into play.

These acts (subunits or segments) excepting the initial ones are completely governed by the internal mechanism and appear in a manner innately fixed, so that they are almost completely independent upon the external conditions, although



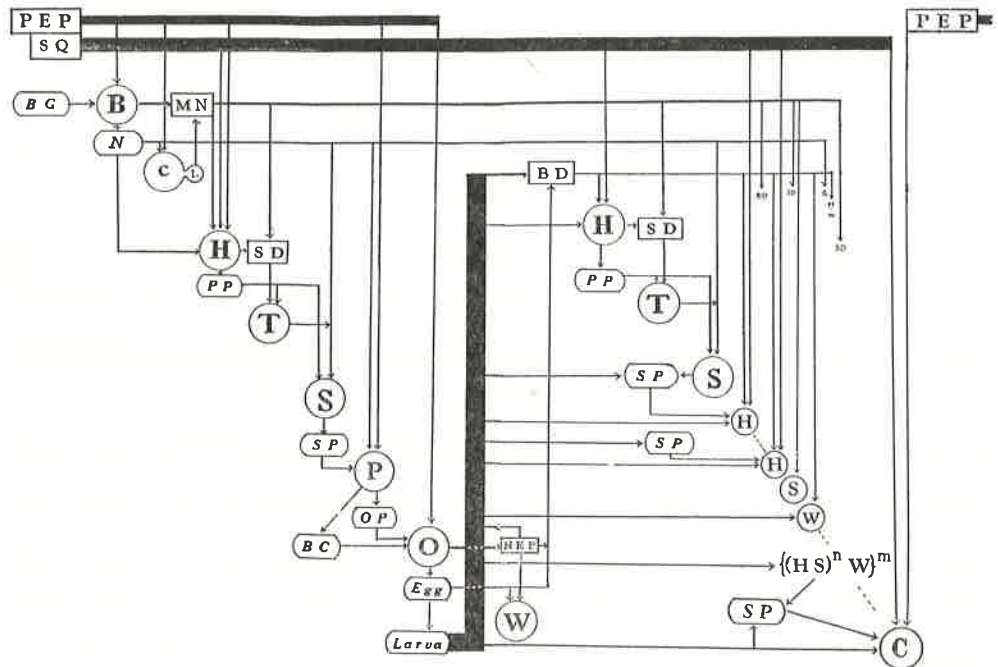


Fig. 13. The probable releasing mechanism of the behaviour system of *Bembix niponica* Smith. The rectangles represent the internal releasing factors : PEP, positive egg pressure; SQ, sense of quantity; MN, memory of the nest; SD, sense of distance; BD, breeding drive; NEP, negative egg pressure. The circles stand for the behaviour units : B, burrowing; H, hunting; T, transportation; S, storing; P, preparation for oviposition; O, oviposition; W, waiting; C, permanent closure; c, temporary closure. The ellipses denote the external releasing factors : BG, burrowing ground; N, nest; PP, paralysed prey; SP, stored prey; OP, operated prey; BC, brood-cell; The thickness of the lines shows the relative strength of the releasing power. (Somewhat emended from Fig. 3 of Part II.)

they may mechanically be impeded to roll on when some external conditions are inconsistent with them.

Some instances will most concretely interpret this mechanism.

(1) *In unit behaviour Hunting*, once the prey is discovered the succeeding procedure will be developed, as a rule, as follows :

The wasp pounces upon it from the back, captures it with her six legs, turns her abdomen aside so as to insert the tip to the underside of the thorax of the prey and then darts the sting at the anterior portion of the area. The series of acts, if the prey is lost during the course, cannot mechanically be progressed. So far as the fly is held between her legs, however, the series of acts is quite automatically, regularly and successfully evolved, irrespective of the form, size and hardness of the prey and no matter what the external conditions may be.

(2) *In unit behaviour Storing*, the acts are combined as follows :

The wasp opens the entrance closure with her front pair of legs, penetrates the burrow dragging the victim behind her, proceeds a certain distance sweeping the floor with her front legs, drops the prey, opens the closure at the entrance to the cell, goes in the brood-chamber to inspect the interior, turns back to the prey, catches it, drags it backing up to the entrance portion of the cell and finally closes the gallery just before the chamber.

In the natural conditions, these acts are very smoothly and successively developed. Each of the acts is so nicely accommodated to the respective external conditions that at first sight it appears that the environmental factors must take a part in releasing such behaviour. Experimental technique, however, reveals that such is not the case. For instance, in storing the prey in the cell, apparently the stimulus comes from the larva itself. In fact the wasp always inspects the larval chamber before carrying the prey in it. Whereas, even when the larva is removed from the cell, the wasp invariably carries the prey in it, despite of her inspection preceding to it. In this case the wasp does not necessarily fail to recognize the absence of the larva, because usually she stops her work of the nest thereafter. Only she can not adjust her behaviour against the internally originated 'action specific energy'.

For another instance, when the tunnel is replaced with a glass-tube, the wasp, when proceeds, usually sweeps the floor with her front pair of legs and when leaves the brood-cell, exhibits the vain act of gathering sand in front of the cell. Never the contact with the sand does evoke such behaviour which is apparently so closely connected with the sand.

(3) *The third good instance* is the behaviour shown when the wasp apparently intends to meet her larva. When the brood-cell is uncovered and the larva is exposed to light, the wasp that comes in the cell and flies up in amazement from the side of the larva never comes back flying directly to her larva, but always goes to the entrance to the nest and after passing through the tunnel comes to the exposed larva. The contact with the larva fatally necessitates the preceding acts of passing through the tunnel. The procedure is rigidly determined internally and the wasp can not resist such a mechanism and behaved like a puppet.

There is no doubt that these acts are released internally and governed by the internal scheme. It seems also certain that in this internal scheme the connection between the acts is so made as to ensure the occurrence of the destined order by placing the preceding act as a releaser of the subsequent act. Thus, once the initial act occurs all the others are brought into play one after the other like the chain reflex. Probably the behaviour of this type corresponds to the so-called *consummatory act* in its strict sense.

#### B. *The second class of behaviour*

The behaviour of this class is originally initiated by the internal stimulus, but is ruled and guided by the external conditions (stimuli or situation). The initial

act of each unit behaviour in the behaviour system is probably attributable to this class. But those of the hunting behaviour during the progressive provisioning and of the final closure of the nest as well as the brood-cell make usually exceptions. With regard to these, explanation will be given in connection with the following section.

The releasing mechanism of the behaviour of this type is represented in Figure 13, rectangular frames being internal stimuli and elliptic frames external releasers. Some explanation has already been given as to this Figure in Part II, but here I will reexamine it from another standpoint.

(1) *Burrowing*. The appearance of this behaviour is initiated by the innate drive, but as an actual physiological basis for it PEP (positive egg pressure including all the accompanying physiological states) is considered to play a part.\* For the actual occurrence of the burrowing behaviour (consummatory acts), optimal external condition of the nesting ground is necessary. When the drive is not as yet in a full mature state or when the nesting ground is not in a optimal condition for burrowing, the behaviour of the wasp ends in an incomplete digging or a scratching of the surface of the ground — the exploratory behaviour. Such behaviour is usually several times repeated. This corresponds probably to the 'appetitive behaviour' in a strict sense. In order to make appear completely the behaviour the minimum of coincidence (Deleurance, 1957) between the internal and external factors (releasers) is necessary.

It should be noted that in this unit behaviour the initial phase, activated by the internal drive (releaser) and the second phase, the consummatory acts, accomplished by the addition of the external condition (releaser) are involved.

(2) *The first hunting*. This unit incorporates also the initial appetitive phase and the subsequent definite behaviour phase, the consummatory acts. The initial phase is probably released by both the internal drive, which is in this case considered constituted by PEP, and the external factor derived from the preceding behaviour unit, the nest burrowed up. Driven by such factors — action potential energy? — the wasp starts for hunting. The second phase is the actual behaviour of hunting. At this time, the nest which was a direct external factor in the initial phase acts probably as an internal factor in the form of memory of the prepared nest, in addition to PEP. The actual occurrence of the behaviour (consummatory acts) necessitates a new external factor, the contact with a proper victim. Until the realization of the minimum of coincidence between the internal and external releasers the appetitive behaviour — searching for the prey — is continued.

\* In *Bembix* it is very difficult to ascertain the fact. Because when the adult female wasp emerges from her cocoon her ovary has already almost fully matured. Moreover, even when an egg is laid the next egg in her ovary is in an almost full-matured state. In this case PEP is considered to be suppressed by the working wasp, the supposed inhibitory factors are the presence of the immature larva on the one hand and the insufficient amount of provision on the other.

(3) *The first temporary closure, Transportation, Uncovering, Storing, Preparation and Oviposition.* These units, in contrast with the preceding two, always lack the initial phase. The chief internal factor is always PEP and one at least of the external factors is always the result of the preceding unit behaviour, namely, in the above described order, the nest dug up and opening (a result of burrowing), the paralysed prey, the prey at the entrance, the opened nest, the prey in the burrow and the prepared prey. Therefore, the successive development of these units of behaviour bear an appearance of the innate automatic mechanism. However, in so far as they are led and regulated by the external conditions (the presence of the operated prey, etc.), they must be assigned to the present class. In fact, each of them when the external releasers extinct always ceases its progress :

a) Transportation. The case when the prey that was imperfectly operated escapes from between the wasp's legs corresponds to the extinction of the external factor. The wasp pursues the fled prey and if not succeed in recapturing always resumes searching for a new prey. Thus, her behaviour reverses to the unit, Hunting.

b) Storing. At any step of storing, if the prey is lost either naturally or experimentally the behaviour of the wasp invariably turns back to Hunting. If the prey flees directly from her the reverse occurs directly. If it is removed from the tunnel during her inspection visit to the brood-cell reverse appears after a more or less confusion of searching behaviour. This searching behaviour is, however, obviously based on the memory of the wasp and is different from the appetitive behaviour s. str.

Similarly, when the other external factor — the nest — has been destroyed, the wasp begins at once to search for it, first holding the prey and then letting it off. In this case, too, her behaviour is not appetitive (s. str.), because it is not the reaction to the absence of obscure something, but that to the absence of the object in her memory, to the absence of the recognition of the goal! Extinction of the external factor relating to the nest sooner or later takes back the wasp to the necessary stage of the behaviour system — Burrowing in the new nest construction.

c) Preparation for oviposition. External conditions : (1) Optimal condition of the nest;\* (2) paralysed prey in it. Lack of the first factor gives rise to varied kinds of behaviour according to the conditions of the time. In the worst case occurs nest abandonment and succeeding reconstruction; if not so worse, construction or rearrangement of the brood-cell. Such a condition is brought about only by experiment. Lack of the second factor (also experimentally brought about) leads usually to nest abandonment, sometimes to reverse to hunting behaviour.

\* As described in Part I, the time of accomplishment of the brood-chamber in the unicellular nest is, in reality, after the first prey is taken in. Strictly, therefore, the unit behaviour of construction of the brood-cell is to be inserted between P and O. But from another point of view this may be considered as a phase of preparation for oviposition.

d) Oviposition. External conditions : (1) Prepared prey and (2) the optimal condition of the nest. Though unexperimented as yet, either of these external conditions is disturbed after such preparation is finished it seems most probable that the wasp will abandon the nest.

In this class of behaviour it seems worthy of special notice that there are two fundamentally different types, one having an initial appetitive phase and the other lacking such.

### C. *The third class of behaviour*

Firstly the hunting behaviour except for the initial one that is, in *B. niponica* at least, nothing but the preparation for oviposition and has essentially no significance of provisioning belongs to the third class. In this species the provisioning behaviour daily progressively carried out is, as a rule, called forth by the state of the larval cell, more strictly speaking, by the presence and the developmental degree of the larva together with the amount of food accumulated in front of it.

When the larva is still very young only a few flies are brought to it. While as soon as the larva attains the fourth (final) instar, the provisioning activity is suddenly and markedly increased. On the other hand, when the food to eat is scarce by the side of the fourth instar larva the hunting activity is strikingly accelerated accordingly. Evidence of these relations was fully exhibited in Part II of the present paper through the experiments of changing the larval size or removing the accumulated victims. In Figure 12 and Table 1 of the present Part we can also see a remarkable instance of the accelerated hunting behaviour of the wasp where the mode of provisioning was markedly changed through the successive removal of the stored flies. There is no doubt, therefore, that the hunting behaviour is released by the external stimuli — the stimuli from the larva and the amount of its food.

However, this is true only as a rule. The results of the experiments suggest that in some cases the hunting behaviour was completely governed by the internal releasing mechanism. However, this problem concerns with those centering around the variation and evolution of behaviour in *B. niponica*. Therefore, discussions regarding this question will particularly be given in another connection.

Secondly the waiting behaviour is also considerable as belonging to the same class. This is also ruled by the state of the egg or the larva together with the amount of food in the cell. There is certainly a question as to whether it is justifiable or not to treat 'waiting — doing nothing in relation to the breeding activities' as a good behaviour unit. Apparently it is nothing but an interval of the hunting behaviour. However, when we consider that it has a certain marked length of time not ruled by any climatic or daily rhythmic conditions of the external world, but governed by the wasp herself through the states of her offspring and through the amount of food in front of it, it seems better to deal with it as a unit of behaviour in order to represent more exactly the behaviour

system of *Bembix* in the behaviour formula.

As regards this waiting, especially during the period when the egg does not yet hatch out, the internal automatism seems also to take some part. But the time actually the waiting is stopped is determined by the wasp by inspecting the state of the egg.

The third instance is given by the final closure of the nest. The factors releasing this behaviour are (a) a considerably developed larva and (b) a sufficient amount of food to ensure the subsequent development of it. In some cases, however, the final closure is done quite mechanically without any connection with the external conditions and, moreover, sometimes it is considered to be compelled by the positive egg pressure in her ovary. In regard to these exceptional ones some consideration will be given later on.

## 2. Modifiability in behaviour

The modifiability in behaviour of *Bembix* is divisible into two types. One is a fluctuating modifiability and the other an adjusting modifiability. The former has nothing to do with the external conditions. It concerns only with the variability or plasticity in the innately determined, that is to say, internally released, behavioural patterns. While the latter has a close connection with the circumstantial factors. It has to do with the behaviour that is released by the external conditions. In this section the general survey of the problem and the first type of behavioural plasticity will be dealt with and the second type will be treated in the following section, since it contains varied kinds of problems and merits of special mention.

### A. Fluctuous modifiability

Fluctuous modifiability does not possess any important ecological significance in itself. But it has a latent probability of being the object of natural selection. It concerns with the behavioural patterns and not with the response to the external world. In *Bembix niponica* we can see such a modifiability in the form and structure of the nest, nature of the ground of the nesting site, mode of hunting, mode of carrying the prey in the burrow, manipulation of the pedestal prey; kind, character and number of the prey and the time of the final closure in relation to the larval development. To each of the items a brief explanation will be given below.

(1) *The form and structure of the nest.* Ample instances were already given in Part I of the present paper. The most important fact among them is that the wasps sometimes (or locally) make the compound (multicellular) nests, though they usually construct simple (unicellular) ones. According to the data obtained from the observations at Chiba where the compound type of the nests occupied the greater part this property seems to possess an inclination of fixation with the locality, just as in the morphological subspeciation in the zoogeography. While in

the observations at Sapporo where the simple type of the nests was usual there are some records wherein the same individual sometimes constructed the simple nest and sometimes the compound nest. Both the instances seem to exhibit two developmentally different stages in the behavioural evolution.

In connection with the appearance of the compound type of the nest an interesting phenomenon of simultaneous rearing of two larvae has emerged. The phenomenon, however, occurs very rare and is temporally restricted. But the very fact is also of significance in relation to the evolution of the behaviour type.

Variation in the location of the accessory branch (the spur of Evans, 1957) and in the duration of retention of it seems of next importance. It includes significances, on the one hand, of turning into the origin of the compound nest and, on the other hand, of becoming a puzzling cul-de-sac against the intruder.

(2) *Nature of the ground of the nesting stite.* Although *B. niponica* usually nests in the sandy area, she can also make her nest in the pebbly ground or in the fairly hard clay soil. In order to adjust to such different nature of the ground, the wasp has already been provided with a certain degree of modifiability in her mode of burrowing. Usually she crumbles the sand particles with her mandibles and fore legs and sweeps it out backwards through the underside of her abdomen. In this case the pair of the fore legs play a main part. In the clayey place, on the contrary, the mandibles play a leading rôle. In the pebbly ground she spends most of her digging hours by dragging pebbles backward out of the burrow. The manner is much the same as that when she dusts her nest. Usually the pebbles are dragged several to about half a meter away from the entrance and discarded.

(3) *Mode of Stinging.* After capturing a fly *Bembix* usually carries it to the near-by grass or near-by ground and stings it on the anterior portion of the underside of the thorax. Sometimes, however, she stings the prey in the air while she is flying a stationary flight. Usually the wasp grasps the prey by the thorax, but sometime she does so by the abdomen — especially under the experimental condition. In the latter case, she does not bend her abdomen, but stretches it and stings the prey exactly at the same place as selected in the usual case.

(4) *Mode of carrying in the prey.* Being taken in the tunnel, the prey is dropped in front of the stoppage of the larval cell. Sometimes, however, it is left aside in the outer part of the entrance tunnel and remains visible from outside. Probably this is a trace of the old habit as at present still observed in many members of Sphecidae wherein the prey is placed in front of the entrance of the nest during the inspection visit of the wasp of the interior. When the wasp enters the brood-chamber she usually touches the larva. Sometimes, however, especially when the provisioning is actively carried out, she does not enter the interior, only turning back from the entrance of the cell. In such a case the partition wall before the brood-cell is also very roughly constructed. The wasp gathers only 3 or 4 armfuls of sand. She does not pack them down and hurries away with the entrance

of the nest left half-opening.

(5) *Manipulation given to the pedestal fly.* The fly first hunt and used as the pedestal for the wasp's egg is usually killed. Rarely, however, it is fairly vivid, showing the active visceral, respiratory and proboscean movements. From such a condition to almost dead state various grades can be observed, though the instances increase in number towards the latter side. One of the middle legs of the fly, locating on the same side as the egg is laid is usually dislocated by twisting half a round and is placed on the half-opened wing as if to press it down from above. Sometimes this manipulation can not surely be observed, the leg being only feebly dislocated and pushed forwards\* The manipulation of the fore legs is much more variable, sometimes they are pushed forwards, sometimes one of them is manipulated and in another case they are left *in situ*.

(6) *Prey.* With regard to the variety of species, size and number of prey captured by the wasp for one larva sufficient descriptions were already given in Part I of this paper. As for the number of the prey there seems to exist something like a rule of constant quantity in relation to the size of it. But the rule is quite rough, having a considerable amplitude of variation. In respect of the species of the prey it is also a wonderful fact, though common in the world of the hunting wasps, that the prey is strictly limited to the Dipterous insects, despite that the form, size and coloration of the victims are very markedly varied. However, it is utterly unknown here also by what character the wasp can select the Dipterous insects, or to use the prevailing word, what is the sign stimulus in the wasp's selection.

(7) *The time of the final closure.* There is no exception whatever as to the rule that the final closure of the nest takes place after the larva reaches the last instar of its development. However, the critical moment of the closure is markedly variable in relation to the growth degree of the larva. Some individuals give their nests the final closure at the time when the larva has not yet attained to the middle of its growth in the final instar. Others continue to care for their larvae until they reach almost full-maturity. It should be noticed that in the latter case there is no inhibitory factor or factors considerable against their provisioning activities, such as bad weather, low temperature, strong wind, etc. The time of the final closure of the nest is considered determined by the wasp through the perception of the external conditions — the developmental degree of the larva and the amount of food provisioned. But the variation exists as to the mode or time of perception of the wasps which is utterly innate.

#### B. *Adjusting modifiability*

The innate automatism or the hereditarily determined rigid pattern of behaviour

\* Some of such instances may be the case wherein the twist was casually recovered, for such is more frequently observed in the flies comparatively stoutly built such as the members of flower flies.



which forms the back bone of the brood-rearing habits of *Bembix* is itself already quite adaptive. As it has been adaptive *Bembix* has been able to exist until now. However, it is not always adjusting. It can be adjusting only within the limit of its modifiability. Moreover, as modifiability itself has originally nothing to do with adjustment it must be determined through detailed observations whether it is adjusting or not. On the other hand, such behaviour as is released by the external stimulus is by far the more adjusting. This is quite natural, since such behaviour is nothing but an immediate response to the given stimulus. There is little doubt that in the history of behavioural evolution of the higher Hymenoptera the adjusting behaviour is the later borne and more developed one as compared with the behaviour governed by the internal stimulus only. Because of the wide scope of the problem it will be dealt with separately in the following section.

### 3. Abjument in behaviour

We can consider the adjusting behaviour under two different headings, one of which is actually observed in the activity of the wasp under the natural condition, while the other is a potential character that can be detected only by means of experiment.

#### A. *Adjustment under the natural condition*

The behaviour under consideration is so well adaptive (not only adjusting) to the circumstantial condition in nature that it appears as if governed by the innate automatism only. But through the experimental means it can easily be elucidated that it is not the case. The behavioural adjustments assigned to this type are as follows :

(1) *Adjusting behaviour to the growth degree of the larva.* Our *Bembix* brings a small quantity of food to the earlier instar larva and a large amount to the final instar one. The fact that this is the actual response of the wasp to the growth degree of the larva and is not the result of the parallel phenomenon automatically brought about between the larval growth and the innate schedule of provisioning of the wasp was clearly proved in Part II of this paper by the experiments changing the larval dimension. The wasp, as a rule, in response to the size of the larva newly replaced, sometimes reversed the procedure of her provisioning activity and repeated the schedule from a certain point of the earlier stage of her work, or sometimes she omitted a certain range of the schedule prearranged to her and changed her behaviour into what is usually observed at the later stage of her provisioning work.

The adjusting modifiability brought into appearance through the experimental technique must similarly be in action under the natural condition, only regulating the normal course of the progressive provisioning.

(2) *Adjusting behaviour to the amount of food.* *Bembix* brings a proper

amount of food to her larva in accordance with its developmental degrees. This is utterly the result of the appropriate response of the wasp to the standing amount of food in the larval cell. The fact was satisfactorily made evident by the experiments removing food from the brood-chamber.

The adjusting modifiability in behaviour of this kind, though very important under the experimental conditions, plays usually a very trifling part under normal natural conditions. It may be of use at most when a large number of maggots of the parasitic fly invades the brood-chamber. But the fact does not justify the view that such behaviour has developed in response to the invasion of the parasites.

(3) *Final closure of the nest.* As mentioned in the foregoing page, the time of the final closure in relation to the larval growth is more or less varied from one instance to another. This has been considered due to the variation of the internal pattern of behaviour. Notwithstanding which, the time of stopping the provisioning and the time of beginning the final closure is by no means indifferently determined to the states of the larval cell. As a rule, a certain degree of growth of the larva (in this respect there can be admitted a variation) and the amount of provisionment sufficient to ensure the successive development of the larva release the behaviour of the final closure upon the wasp. In some cases, however, the internal automatism appears to have a more or less share in this procedure. But even in such instances it seems doubtless that the initial stimulus of stopping the provisioning activity must originate from the above-mentioned external conditions. Only it must be perceived precedently to the final mass provisioning which is usually done just before the permanent closure.

*B. Adjustment under the experimental condition.*

Under this heading I confine the adjusting behaviour that seems not to appear usually under the natural condition, but can be revealed only by means of experiments. Such latent adjustable behaviour is considered important in connection with the evolution of behaviour, since it shows that the behavioural ability is potentially established before it is needed in the face of the actual event.

Under this item we can cite the following behaviour of *Bembix* :

(1) *Behaviour of protecting the larva from the light.* We have repeatedly observed that the wasp, when the glass brood-cell is exposed to light, shows an unusual behaviour that makes one think of the psychic unquietness and at last carries the larva in the dark portion of the tunnel. This behaviour is very much like that of the ant reared in the artificial nest. In the ant, however, such behaviour has vaguely been considered to have developed through the natural selection, since in this group of insects the nest destruction by other animals (including the human beings, especially the farmer) is not a rare occurrence. It is apparently not a strange fact, therefore, that the adaptive protective behaviour in relation to such an event has developed among them. To my knowledge, however, no particular opinion in regard to this problem has ever appeared in the literature. Probably it

has been considered as a self-evident adaptive phenomenon which was established as a result of natural selection. Under such a consideration there is certainly concealed a thought that event first occurred and the adaptive character emerged next to it, destroying those that could not develop such a character.

The case under consideration in *Bembix*, however, has presented an important counterevidence against such a consideration. In this wasp there seems to be no probability of such a chance of nest destruction as is the case in ants. To this wasp the fact that the brood-cell is dug open, if such an event truly occurred, means the complete destruction of the nest. Because the wasp can not recognize her larva directly by sight or by touch. In order to do this she must first enter and pass through the tunnel. Without the remains of the burrow that can be penetrated the wasp cannot protect her larva from the deadly light. She can not utilize the shadow of a stone or a grass. She can not dig a new tunnel to receive the exposed larva. When we thus consider, the character of protecting the larva from the light has no significance whatever to the actual life of the wasp. Despite the fact, without any connection with the development of relating behaviour, such a character has already emerged and remains latent in the behaviour of the wasp. We must put a particular stress upon this interesting discovery.

(2) *Behaviour of searching for larva in the maze.* Under the natural condition there is no need of searching for the larva in the nest. Because even in the wasp that constructs a compound nest the way to the larval cell under her care is always a straight course. If the larva is not present in the end cell it means that it has already been devoured by some invading insect. It is not a matter of probability of rediscovery to search for the missing larva in the nest. In spite of the fact, the character has already developed in the wasp. Under the experimental condition using a maze of glass-tube, especially when the situation of the larva is changed this latent character is most clearly revealed.

Under the natural condition when the entrance to the nest is disturbed by cattle or passers-by and can not easily be rediscovered the wasp always continues persistently to dig the place. In this case she is searching for the entrance to the tunnel or remains of the tunnel and not the larva itself. This behaviour is, therefore, different from the behaviour of searching for the larva in the glass maze.

(3) *Behaviour of searching for the prey in the nest.* In the normal states it is a sufficient work to the wasp that inspects the brood-cell empty-handed to go back in the entrance tunnel to take a fly. Infallibly it can be found there. It is by no means a search. And when she drags it backing to the end of the tunnel it can always reach the brood-chamber without failure. Whereas in the branched tunnel of the experimental device it occurs very frequently that the prey is carried erroneously to the non-larval cell. Under such a condition, if the wasp reinspects the larval cell, vigorous movement in search of the prey is sometimes commenced. Such instances are very abundant, but we can find the most striking case in wasp No. 74, the behaviour of which was described in detail in Part II (pp. 21-24).

*Remarks.* Among the instances concerning the searching behaviour some can not be considered as representing a latent character, but only as a result of learning of the situation. In order to estimate correctly the result detailed observation of the procedure is required.

(4) *Behaviour of retransporting the fly to the larval cell.* The mode of appearance of this behaviour is considerably different with the individual. In some cases (for instance, wasp No. 114 under triple-Y maze experiments. Pt. II, pp. 92-100) this behaviour is especially remarkable, while in others not so striking. However, in spite of the individual difference, the latent ability of this behaviour is widely distributed among the members of this species. The psychic process of this behaviour is not always one and the same, but is fairly complicated as was explained at some length elsewhere in this paper. At any rate, in the wasp that can exhibit this behaviour under the experimental condition the latent character that the releasers of the unit behaviour, Storing, can not be dissolved until the prey is brought to the side of the larva must have been developed. This is, of course, possible only on the basis of the ability of cognition of the wasp on various objects and relation in the nest. Under the natural condition the behaviour of this kind is utterly unnecessary to the wasp. Because the mechanic behaviour like that of innate automatism is sufficient to ensure the successful result. Notwithstanding, latent character of such behaviour is developed in many individuals of this species.

*Remarks.* some individuals at times retransport the prey from the larval cell. This is probably the behaviour based on the confusion of the wasp. The movements of the wasp preceding to such behaviour give evidence to this conclusion.

(5) *Behaviour apparently preventing to drop in the broader glass tube.* During the course of experiments using a Y-tube of glass having the branches of different diameters, this particular behaviour was frequently observed upon the wasp. In the case when the larval cell is connected with the end of the finer branch the wasp, not only in her backing progress but also in her forward proceeding, is very apt to drop in the broader branch at the bifurcation. Because the broader tube is more easily entered owing to the mechanical result of jointing. During the earlier part of the learning process of the direction the wasp usually enters the erroneous tube, sometimes even keeping her head toward the narrow one. In such a case, the wasp usually turns back to the entrance tunnel and resumes the inspecting trip from the first, with usually the same result. After one or several such failed trials the wasp at last becomes to enter the narrow (correct) tube directly from the broader, without turning back to the entrance gallery. This is probably done in her movements in search of her larva. After discovering the larva the wasp usually repeats once or twice her inspecting visit to the larval cell from the entrance tunnel. In such a case the attitude taken by the wasp is very interesting and suggestive. She comes from the entrance portion somewhat slowly towards the bifurcation, keeping her body as closely as possible to the lateral wall of the side of the narrow branch. This is clearly perceived from the different

stretch of her legs of both sides. Once learned such a mode of progress the wasp when returned from the hunting journey shows from time to time the same sort of posture at the bifurcation with frequent success (cf. Pt. II, p. 103-). Strange to say, however, although she shows the apparently ingenious mode of progress above mentioned at the bifurcation, once she happened to drop in the broader branch, she cannot correct her failure to the last, proceeding on in the wrong direction and in the different broadness.

So far as has been observed, it is still uncertain whether or not the occurrence of such behaviour truly describes a learning curve. However, it is certain that the acquisition of such a habit is not established by a single success or two, contrary to the case of the learning of the direction.

(6) *One stop transportation.* During the course of the observations of the above-mentioned experiment when the wasp carried the prey from the entrance tunnel to the larval cell she was very apt to drop in the broader branch, because of her backing progress as well as of the structure at the bifurcation. At that time a special mode of transportation was from time to time observed. Usually the wasp, when she returns to the prey from her inspection of the larval cell, carries the prey backing to the larval cell at a stretch, viz. by means of the non-stop transportation. While in the particular mode of transportation she stops once at the bifurcation, letting the prey off there, inspects the larval cell once more and returns to the prey; there she captures it without making her body go out of the tunnel, keeping the tip of her abdomen in the narrow correct tube, and carries it to the larval cell without failure.

This one stop transportation is not observed in the normal condition. But it occurs also in the experiments using a simple-Y maze. Judging from this result it is only adjusting to the branched tunnel and not always to the difference of the broadness of the Y-maze. Moreover, according to the observations it seems that the appearance of this apparently ingenuous mode of transportation is not effected purposively as a direct response to the difficulty of taking the correct way in the transportation. Because, if so, the learning effect must appear during the succeeding behaviour of the wasp. Whereas, in reality, this very effective mode of transportation appears only from time to time, with apparently no connection with each other (cf. Figs. 57-61 in Pt. II and Figs. 8-11 of this Part).

The mode of appearance of such behaviour may be a type of emergence of a new behavioural character in this wasp.

(7) *Adjusting behaviour against the enemy at the door.* This means the behaviour of the wasp when the large ant lion (the larva of *Acanthaclisis japonica* MacLachlan) occupies the front ground of her nest (Pt. I, pp. 125-127). Therefore, it belongs originally to the event observed under the natural condition. However, such is never observed as an usual event and, therefore, the adjusting behaviour of the wasp in such an occasion represents the same sort of responses as seen to the unusual happenings brought about by the experimental technique. Accordingly

the behaviour is dealt with here.

Adjustment in behaviour on this occasion is very striking :

a) After being attacked once or twice *Bembix* becomes very cautious. She does not alight on the ground at once.

b) While flying about very slowly above the front ground of the nest the wasp stretches her legs downwards and almost skims the surface of the earth. By this means she can easily avoid the capture of the assaulter.

c) In the case when she does not drop the fly at the first attack of the ant lion the wasp, after several vain attempts of landing, comes to try to enter the nest directly from the air.

Remarks. Adjustment in behaviour dealt with in the above-cited items is not the one that is established as a result of trial-and-error learning, but is the one that shows decided tendency of adjusting from the beginning of behaviour, sometime in a fairly complicated form.

#### 4. Habituation in behaviour

*Bimbix* when subjected to the experimental condition usually shows a marked tendency of habituation. This is particularly the case when her feeding drive is heightened. The wasp promptly habituates to the unnatural conditions such as the glass tubes and cells, branched maze, broad tunnel, the large chamber, etc. and comes to indicate not the least confusion about such strange environmental conditions.

Habituation under these conditions seems, however, not dependent upon such a simple physiological mechanism as the fatigue of the sensory or muscular organs, but upon the result of learning of the new situation. This is easily proved by the fact that the wasp once habituated to the glass instruments does not show any confusion in behaviour when she was subjected to the similar instrument at a considerable interval (from several hours to several days).

With regard to habituation one of the most interesting problems seems to be its relation to the internal automatic behaviour patterns. Among such patterns the best observed by me is that concerning the unit behaviour, Storing. With this behaviour, therefore, the relation above mentioned will be examined.

(1) The wasp when proceeds slowly in the tunnel always shows the sweeping movements with the front pair of legs. The behaviour is never omitted under the normal condition. However, when she proceeds fast in the tunnel, especially when she is in search of the prey or the larva under the experimental condition, this behaviour is almost completely suppressed. The fact seems somewhat different from the usual sense of habituation. But it is an adaptive omission of the unnecessary and complicated part of a behaviour segment in response to the environmental conditions and is considered as a special case of habituation.

(2) The series of the behaviour segment (subunits), " — letting the prey off

in the entrance tunnel — opening the closure of the brood-cell — inspecting the interior — turning back to the prey —”, is also never omitted under both the normal and the experimental conditions. However, when the provisioning is very actively and with short intervals carried out, the wasp comes to omit the inspection of the interior of the chamber (the larva and the prey) and turns back at once from the entrance\*.

This is obviously a sort of habituation. In this case, however, there is a question whether the behaviour of inspecting the larva as well as the prey can be assigned to the internal automatic mechanism or not. Rather it may be the innate automatism to turn back from the entrance, and the behaviour of detailed inspection may belong to the adjustment to the external conditions.

(3) Under the above mentioned condition, the temporary closure of the brood-cell as well as of the nest is very roughly carried out.

According to the results above described we may be concluded as follows :

Habituation does not occur, as a rule, in the behaviour belong to the innate automatism. However, a certain part of it, when very frequently repeated, is so simplified that it seems to lose almost completely the original significance.

##### 5. Purposiveness in behaviour

All insects that make their nests have their goals at the end of the series of their behaviour. Each unit of the series has also the respective goal within the minor series. Hence all of them can be designated as purposive.

To speak it in the concrete as to an instance, the ultimate goal of the nesting spider wasp is to rear her young safely at the place. Burrowing has its goal in the acquisition of the optimal depth, humidity, darkness, cell broadness, etc. The goal of hunting is to capture the favorite prey in a proper condition. Transportation, storing, oviposition and closure have similarly each goal at the end of the series of behaviour segments or subunits. However, all such purposive behaviour is innately designed, only requiring some proper external stimuli in order to be called forth. What plays a chief rôle is always the innate scheme which is the origin of the internal stimuli of the releasing mechanism. Therefore, the goal is such a situation as is hereditarily and automatically determined, and the activity to reach this is quite mechanic. There is no perception of the goal on the part of the wasp and there is no special effort in her behaviour to approach this. Accordingly if she is led in the erroneous way by the experimental technique the end of the way is nothing else than the goal to her.

In *Bembix* also the general organization of the behaviour system in nesting and brood-rearing activities follows the same general rule. However, there is in this wasp something that lacks in the behaviour system in the burrowing spider wasp. That is the behaviour assigned in the foregoing section to the third class,

\* Sometimes the wasp shows the same kind of behaviour at the entrance of the empty cell.

namely the behaviour released and ruled in the main by the external stimuli-complex, although the detailed pattern in each act follows the innately determined type. Food gathering and brood-feeding behaviour belongs to the typical case of this kind. Here, I will concern with the food-gathering behaviour only. This behaviour consists of three units, — hunting, transporting and storing, the goal being to place the captured prey in the larval cell. In the present state of our knowledge it is hardly possible to analyse this releasing system in terms of the simple stimulus-response mechanism, since at present each of the stimuli concerned can not be designated by means of a sign stimulus. For instance, the dimension of the larva has a close connection with the frequency of the hunting behaviour. But it is so only in relation to the amount of food in front of the larva, and *vice versa*. In these cases it seems better to deal with each of the stimuli-complex as a situation and the behaviour of the wasp as released on the basis of cognition of the situations. Accordingly the releasing stimuli come to be dissolved only by the cognition of the wasp of the situation fully satisfied, that is to say, by her cognition of arriving at the goal. Hence, the wasp that has failed to bring the prey correctly in the larval cell in the artificial maze repeatedly tries to retransport it until it is placed in the brood-chamber. Probably the wasp perceives the error of her transportation when she carries the prey to the empty cell and she perceives also the unsatisfied state of the brood-chamber when she goes in it in search of the larva. Both the perceptions combined together will evoke in her the drive of retransportation.

However, the above is the rule. There are many exceptions not only among individuals but also within the behaviour of the same individual\*. The fact may paradoxically prove that the retransportation is not the innately predetermined reflexive mechanism, but is the behaviour as a response to the perception of the situations.

Such purposive, or rather perceptive, behaviour as mentioned, therefore, incorporates in its procedure an effort to reach the goal. The repeated inspection of the larval cell and the repeated attempts of retransportation of the prey are

\* When the retransportation ends in the renewed failure the number of times of the repetition of the behaviour varies not only from individual to individual, but also within a single individual. Some individuals show the behaviour almost every time of their failure, while others only from time to time. Usually the retransportation is made after inspecting the cell and searching about in the tunnel, but sometimes it is commenced as soon as the wasp reaches the empty cell without any behaviour preceding to it. At times the first erroneous transportation passed without being perceived by the wasp. But when she goes to the larval cell soon after from the entrance tunnel in a satisfactory manner (walking slowly, sweeping the floor) the wasp perceives the situation (probably she finds that the prey is not present in it, and it is not that she find the insufficient provision of the cell independently of the first transportation) and the retransportation occurs after the succeeding searching movements. Further, there is also a case rarely wherein the prey correctly carried in the larval cell is erroneously retransported. But such a case usually occurs at the time when the wasp is in confusion after repeated failure of retransportation.



certainly the appearance of active states of the drive emerged from the perception of situations.

It seems of interest to see in such a case a marked variation of the manner (or type) of the act. In the transportation usually the fly is caught by the neck and dragged backwards. At the onset of the retransportation, it lies in the reverse bodily orientation to the direction in which it should be carried. When the end of the incorrect tunnel has a sufficient broadness to allow the wasp to turn round with the prey, *Bembix*, after more or less difficulty and more or less effort, is able to drag it in the usual posture. But when the place is narrow it is impossible to her to turn round with the prey. In such a case she catches it either by one of the legs, by the tip of the abdomen or by the apex of one of the wings and pulls it backwards. It is a very difficult work to carry a fly under such a condition owing to the bodily structure of the insect. The wings and the legs are expanded and bar the tunnel. When the wasp fails to grasp a steady hold the body of the fly is very apt to slip inwards (cf. Pt. II, p. 93 and 106). In one particular instance a wasp even tried to carry the fly by means of the forward progress (Pt. II, p. 106).

Usually the solitary hunting wasps refuse to carry the prey and abandon it at the time when they are prevented to grasp it in the usual manner of capture, for instance, by cutting off the antennae or the legs. In contrast to these, the response shown by *Bembix* is very surprising. The reason for this seems to lie in that the former is a sort of mere mechanic behaviour driven by the innate mechanism without perception of the situation, while the latter is the behaviour evoked and stimulated by the perception of the situation, although both are attributed, in a broad sense, to the purposive behaviour.

The above seems an interesting illustration of one of the cases in insects in which the motivation originated from the external stimuli overcomes an instinctive pattern of behaviour and changed the innate type of action so firmly, hereditarily fixated, in order to approach the goal and to adjust the movements to the immediate external situation.

## 6. Individual variations of the latent behavioural characters

The behavioural characters, on the existence of which the light can be thrown only by the experimental technique, belong chiefly to those which are separable from the inherent behavioural pattern as the adjusting behavioural type responding to the external stimuli-complex.

As in non-adjusting fluctuating characters, in these responsive abilities also the individual variations are fairly large. In the case when the food of the larva is steadily removed from the larval cell some wasps finely respond to the new situation and work hard for several days in compensating the missing food, some wasps also gather food anew in response to the removal of the flies accumulated, but their

work which is considered excessive to their predetermined schedule is ceased after several to twenty-four hours and they close the nests permanently, while others are quite indifferent to the altered situations and stop the provisioning activity according to the program innately determined.

With regard to the experimental use of the substitute having a different body dimension individual variations in the response of the wasps are similarly marked. Some show an adjusting response to the changed larva and altered the mode of their work, changing the food-furnishing pace in concordance with the developmental degree of the newly given larvae, others do so in a lesser but varying extent and still others exhibit not the least response to the situation brought about\*.

The above characters are usually latent, because their effect does not appear externally under the natural condition. Only in the cases of frequent bad weather and of invasion of a comparatively large number of maggots of the parasitic flies they might play a rôle in regulating the progress of the behaviour system.

On the other hand, the response of the wasp to the experimental instruments or to the experimental situations is similarly remarkably varied with individuals. As for the experimental instrument a good instance is furnished from the varied responses of the wasps to the brood-cell replaced with a inverted Petri-dish. In this case, however, differences of the stage of the behaviour system at which the experiment was carried out probably play a certain rôle in determining the re-

\* Professor G. P. Baerends kindly suggested in regard to Part II of this paper that there might exist 'phases' in the activity of my *Bembix* also, just as was the case in his *Ammophila campestris*, and some of the apparent inconsistencies in the results of my experiments might be explained according to his phase theory. I feel, however, some difficulties in the complete acceptance of his opinion, since our *Bembix* does not make her nest (or cell) more than one at a time. If we search in the brood-rearing activity of my *Bembix* for some phenomena that appear to merit the term 'phase', those corresponding to such may be the external and the internal releasing stages. Viewed from such a point, it can be divided into three phases: The first is the internal and ranges from burrowing to oviposition; the second is the external and includes inspection of the state of the egg and care of the hatching larva; while the third is again internal and occupies the final automatic provisionment and the subsequent definite closure. The question concerned here centers around the second and the third phases. The releasing mechanism of the hunting behaviour of the second phase is changed at a certain later stage of the provisioning activities into that of the third phase, that is, from external to internal, and after this bordering point *Bembix* apparently becomes incapable of reacting to the external situations. Insofar as this occurs regularly, the provisioning behaviour of *Bembix* may be accounted for by the theory of the phase. However, the point of this switching over in the behaviour patterns is markedly varied from one individual to another. In some wasps the second phase is almost none, while in others it has periods of a considerable length. Therefore, if we explained those vaguely definable two periods in the provisioning activities of *Bembix* in terms of the phase, we cannot overlook that striking variation which occurs in the time of its switching over. And the inconsistencies in the results of my experiments, I believe, is rather more dependent upon this individual variation than upon the difference in the phase of activity.

sponse. Similarly, some wasps easily become familiar with the T- or Y-tube of glass, while others show more or less confusion for a longer period. The behaviour of the wasps shown in response to the two or more larvae placed in a nest presents also instances of very interesting variations (Pt. II, p. 73 and 79). Some wasps dragged one of the larvae out of the nest, some killed one of them, some separated one of them from the others and fed it only, while others indifferently brought food to each of them.

Still further, the individual variations are also observed as to whether the retransportation of the prey is executed or not when it was erroneously carried to the non-larval cell in the course of the Y-maze experiments, and when it is executed, also in the degree of persistence of the behaviour.

The wasps having such individual variations of the latent behavioural characters are considered, when the chance of their appearance is given, to react differently to the external conditions and, just as in the morphological distinctions, to have probability of taking different evolutionary courses, had their behavioural tendencies been genotypic.

#### 7. Externally originated behaviour as a new character

Apart from the initial stage of the evolutionary sequence, the behaviour system of the brood-rearing activities of *Bembix*, at the time when it has already assumed a definite feature, is considered an innately relieved automatic mechanism. The system might be so arranged as to release the initial unit of behaviour by the internal stimulus (or stimuli) and as to call out the subsequent unit of behaviour by the result of behaviour preceding to it and the whole course of the system is regarded as being governed by some internal stimuli of higher grade. Therefore, in the natural states of affairs the procedure might arouse quite mechanically and smoothly. Apparently the present states of the brood-rearing activities of *Bembix* can be assigned to the same category of the behaviour system. Apparent consistency between the behaviour system of the adult wasp and the progress of growth of the larval wasp may be attributed to the concordance of progresses of two different courses of events placed in parallel which are originally independent of each other.

It has, however, been discovered through the experimental technique that in reality this is not the case. Among others ruled by the internal mechanism, the greater part of the brood-feeding activities at least belongs to the behaviour which is released and maintained by the externally originated stimuli — the states of the larva and its food. This part of behaviour is believed to have emerged from the internally determined automatic mechanism along with the evolution of brood-rearing habits of *Bembix* — from the mass provisionment to the progressive provisionment. We can presume the fact above mentioned from the occasional appearance of the innate mechanism during the course of the behaviour which is

externally originated.

(1) When the stored food was steadily removed from the nest, sometimes the wasp restored the food in compensation to a certain amount which was considered proper for the provisioning of the day and ceased the work, despite that the prey carried in were continuously eliminated one after the other. In this case the behaviour of prompt compensation due to the lack of food by the side of the larva is obviously released by the perception of the external situation. Nevertheless, the effective external stimuli are confined to that moment only, in spite of the fact that the wasp subsequently executed the inspective behaviour every time of her return. The work of the wasp which follows is completely governed internally through the perception at the initial encounter with the situation.

(2) At the final course of provisioning, this tendency becomes most striking, so much so that we may call such different periods, as has been remarked elsewhere, in terms of the phase. This fact, together with evidence that the exact moment of entering this final automatic course is considerably varied with the individuals seems to give an important suggestion as to the emergence of the adjusting behaviour from the non-adjusting.

(3) In the case of retransportation of the prey, sometimes it is ceased by a single trial without success. Here the behaviour of the wasp is considered to have become ruled by the internal mechanism from a certain moment during the transportation.

(4) In the case of retransportation of the prey in the Y-maze, the wasp, as a rule, carries it back to the entrance tunnel and after the renewed inspection of the brood-cell, tries to drag it to the cell again. In this behaviour habituation can hardly be observed. She does not try to transport the fly directly from the incorrect tube to the correct one, omitting the transportation to the entrance gallery. At times, however, such a direct retransportation certainly occurs, especially when T-maze is used. But in this case it remains doubtful whether the wasp truly selected the correct course directly by her perception of situation, or she fell in the way by mistake\*. At any rate, even if such a direct retransportation once occurred, it could not apparently exert any noticeable influence upon her subsequent behaviour.

The wasp, despite that the behaviour of her retransportation was released by the external stimuli, must have obeyed the innately determined sequence of the transportation.

The above described instances seem to incorporate the following significances :

a) In the externally adjusting behaviour the influence of the motivation is weaker as compared with the internally originated one and is likely to be broken

\* In the case of wasp No. 94 (cf. Pt. II, p. 76 & 77, Figs. 40 & 41) we saw fairly frequently the direct retransportation of the prey between cell C and cell D, rarely between cell A and cell D. Most of the instances, however, seem to have occurred by mistake of taking cell D as the entrance tunnel.

down by the pressure of the internal motivation.

b) This means that the adjusting behaviour has not as yet attained, in general, the state of fixation wherein the behaviour can be maintained completely in mechanic in accordance with the external situation, although in some more advanced individuals the state seems to have approximately been reached already. In such individuals the adjusting behaviour seems released rather reflexively.

c) In some cases (for instance, the retransportation) behaviour of the wasp is not adjusting throughout the whole course, but only in part, or only in motivation. It can be adjusting, rather within the scope of the internal mechanism.

Judging from the facts above mentioned and from the individual variation of its manifestation, the adjusting behaviour is a newly emerged character and is still in the course of active evolution.

#### 8. Mode of appearance of a new adjusting behavioural character

In the Y-maze having the branches of different diameters the wasp frequently shows the behaviour apparently to avoid dropping in the broader branch. She also shows the one stop transportation and retransportation of the prey in the Y-maze. At times the direct retransportation of the prey between cells of the artificial multicellular nest is observed. All these are doubtless the behaviour new to the wasp and all these are apparently adjusting to the respective situation.

The mode of their appearance, however, is by no means dependent upon the progressive improvement. They are not accomplished through the trial-and-error learning in its common sense. When they appear they appear as an accomplished behaviour from the beginning. However, even when they appear once, they are not usually followed by similar tendency of behaviour, since they do not appear as a result of learning. These new behavioural characters appear occasionally, always with the appearance of complete adjustment. Hence, the mode of their appearance seems deserved of the term, 'emergence'. If such behaviour is by any means fixated — by frequent repetition or rather by mutational fixation — it will become a new character of the individual. In the case above mentioned, however, the environment was artificially made for experimentation. On this account the behaviour had not a chance of permanent fixation. However, the result indicates that *Bembix* has an ability of creating a new behavioural character when confronted with a strange environmental conditions and that the mode of appearance of such a character is quite complete from the beginning, although it is not always fixated from the initial appearance. The facts seem of significance in relation to the evolution of behaviour in *Bembix*.

#### 9. Origin of the maternal affection in *Bembix*.

The mutual relationship between the mother and her young in *Bembix* is

completely a social relationship (sens str.), as it is so in ants, termites and honey bees. It can also be considered as a sort of symbiosis, since the young obtains the necessary nutrition from the mother and the latter the satisfaction of its maternal drive by caring of the former. According to the observations the mode of caring of the young in *Bembix* is indeed very much like that of the ants, in particular those having the habits of rearing their young with intact prey. However, there is an important difference between them. It lies in that while the trophallactic relationship, or the phenomenon of mutual exchange of food between adults and young is universally observed in ants, no such a relation can be observed in *Bembix*.

Trophallaxis, since the discovery by R. du Buysson and C. Janet in social wasps and the later development by E. Roubaud and W. M. Wheeler among solitary (subsocial) Diplopterous wasps, ants and termites, is widely considered as an important material bond in the social relationships between adults and young as well as between members of the same colony. Indeed Wheeler (1923) described: "This (trophallactic relationship) explains much of the behavior which has been attributed to maternal affection on the part of the queen for the workers ..... In other words, a decidedly egoistic appetite, and not a purely altruistic maternal anxiety for the welfare of the young constitutes the potent 'drive' that initiates and sustains the intimate relations of the adult ants to the larvae, ....." But this is only a diversion of the Roubaud's concept (1908) on the origin of the nursing instinct in the African solitary Diplopterous wasps, *Synagris* spp. to ants in general, who considered that the nursing instinct have evolved through the trophallactic (his oecotrophobiotic) relationship between the mother wasp and her young. Among the social or subsocial insects that give their larvae masticated food this relationship seems most naturally applicable. But can we confine the origin of the maternal care among higher predatory Hymenoptera to this category alone? The development of the social relations among anthophilous bees seems to give a suggestion regarding this problem and, moreover, the maternal affection for the young in *Bembix* throws a bit of doubt on the exclusive application of the trophallactic evolution theory of the social life to the predatory insects in general.

*Bembix* is originally carnivorous. Therefore, according to the trophallactic theory it seems natural to develop the social relations through the procedure similar to the ant or the diplopterous wasp. Whereas in *Bembix*, inasmuch as has been observed, the larva is never furnished with the masticated food and there is no mutual exchange of food between mother and her larva. Nevertheless, maternal affection much like that of ants has been developed in the adult wasp. The fact obviously indicates at least that the social relationship between the adult and the young can emerge from the non-social life through some course other than the trophallactic means. Accordingly it seems also possible in the other carnivorous insects to develop the maternal affection for the larva through the same process

as in *Bembix*. Trophallactic relationship may be a result of the social life and not the origin of the mutual affection.

Now, what initiates the social relationship between adult and larval *Bembix*? As for the external factor we can consider, from the experiments conducted, no more than the larva or the egg placed in the nest of the mother *Bembix*. Then how did the maternal drive for caring of the young emerge in the mother wasp? I can consider only that *Bembix* has an ability of bringing forth such a drive — externally it will appear as a new behavioural pattern.

We have seen in the foregoing pages that *Bembix* has an ability of creating new behavioural patterns in response to the new situations. To me it seems that one and the same ability made the new behavioural character of maternal care emerge at the time when the wasp happened to pass some time with her egg or her young, owing to the lengthened provisioning activities depending probably upon the unfavourable climatic conditions.

## II. MENTAL ABILITY IN *BEMBIX NIPONICA*

In Part II of this paper I described the behaviour of *B. niponica* under various experimental conditions mainly from the viewpoint of response of the wasp to different situations. Here I will deal with the same problem from the ability of perception on the part of the wasp.

### 1. Recognition of the internal structure of the nest

When the tunnel or the cell of the wasp was replaced with the instrument of glass having the similar size and form the wasp at her first entering invariably showed a more or less confusion in behaviour. In general, the more the change in size or in form is striking, the larger and the longer is the confusion she shows. Judging from such results it seems that the confusion is provoked not only by her perception of the qualitative difference of the interior structure of the nest — sand and glass —, but also by her perception of the morphological difference of the internal structure. This is also proved by the fact that sometimes the wasp refuses to enter the glass tube after once examining the interior, and then digs anew tunnel in sand.

In relation to the perception of the structural difference of the nest, it is an interesting problem whether the wasp remembers the curvature of her own tunnel. In the learning experiments concerning the direction of the Y-tube one of the branches that is placed in the same direction as the curvature of the original tunnel is usually adopted by the wasp at her first return. The result suggests that the wasp might possess some sort of memory pertaining to the curvature of her own burrow. Under the natural condition, however, the wasp is only to follow

mechanically the tunnel, with no need whatever of selection of this or that way. Accordingly, the apparent selection, in reality, may be nothing but the mechanical result of her muscular locomotion that seems to have some tendency of progress drawing the same curvature as the tunnel. In order to test whether such is the case or not, I have conducted several observations as follows :

In some nests the tunnel curves at a rounded angle of more than 90° and frequently goes in the opposite direction. These nests, when dug open from behind, are apt to be cut off in the middle of the curved tunnel. In such cases, the cut portion of the tunnel was packed with sand for several to some ten centimeters, leaving *in situ* the straight portion of the entrance gallery and the end portion of the curved tunnel, to see whether or not the wasp can dig a new tunnel in the same direction as her own and rediscover the end portion of the missing burrow.

Out of four instances of such an experiment, in no case did the wasps find their missing burrow. Always they dug the new tunnel straight from the end of the entrance gallery. Even if the beginning of the curved portion was more or less left as it was, the result was the same.

Judging from such results it seems conclusive that the memory of the wasp as to the curvature of the tunnel of her nest is by no means a concrete one. More frequent selection of a branch of the Y-tube lying in the same direction as the original tunnel may be resulted rather from the locomotive habit than from the determination based on the memory\*. Accordingly, the confusion shown by the wasp at her first entrance to the experimental device of glass-tubes and cells may chiefly be caused simply by the unnatural condition.

Another evidence obtained from the field observations is that the wasp has an exact memory as to the location and the direction of the entrance to the nest, but not as to its internal structure, because when two nests are made side by side and in the same direction, if one of them is destroyed and the surface is evened, the owner of the nest is very likely to enter the other nest and sometimes (when the larval condition is similar) even provisions for it, so far as she does not meet with the true owner of the nest.

However, as for the wasps trained under the experimental condition the matter is quite different.

Firstly the wasp learns the nest of glass. The excellent evidence concerning this came from the instances of wasp Nos. 74 and 186. The nests under experiment of these wasps were completely destroyed during my absence by an idiotic herdboy and when I found the accident each of the wasps was digging in search of its nest. I arranged a new glass-tube in sand and induced the wasps to enter. Especially in wasp No. 186, the nest was completely — from the entrance to the

\* When *Bembix* refuses to enter the glass tube set for experiment and digs her own burrow in sand from in front of the arrangement, sometimes the direction well agrees with that of her original tunnel. This is probably by the same character of her muscular movements as mentioned here.



cell — made of glass. The wasp soon found the entrance to the glass tube, entered it with a very familiar attitude and when met with the larva placed in it, at once began the provisioning activities. There was no doubt that the wasps accepted the glass nests set anew as their own. Such can not be expected of the untrained wasp.

Secondly, the wasp already habituated to the glass nest shows a more or less (usually a noticeable) disturbance when the apparatus is replaced with that of another pattern.

Thirdly the wasps subjected to the maze experiment, no doubt, became to learn the internal structure of the nest. Such an excellent wasp as No. 114 is considered even to obtain the general survey of the structure, but in general, such is quite doubtful. Many of them seem to learn only that the tunnel is divided and that in one of the branches can be found the larva. The latter is probably remembered in connection with the direction.

## 2. Recognition of the larva

### (1) *Discrimination between the larvae of different insects*

As described in Part II of this paper, the mother wasp can discriminate the larvae of various kinds of insects from her own and eventually abandons the nest to which such a substitute was introduced in place of her true larva. Amongst the substitutes used, some such as cabbage caterpillars and larvae of the honey bee were very easily discriminated, while others such as larvae of a Crabronid with more less difficulty. What is the clue of discrimination? What is the sign stimulus of her own larva? Under the natural condition, there seems to be no opportunity to the wasp under which such a discrimination is needed. Therefore, even if she continues to provision quite mechanically, everything must go well without any trouble. However, in order to continue the provisioning activities, the presence of the larva in the cell is an indispensable condition to the wasp. On this account, the wasp must have some means for perceiving the presence of the larva in the cell. The discrimination of the larvae of other insects from her own must be done on the basis of such an usual method of perceiving the presence of her own larva.

According to the direct observations, the wasp when she meets with the larva, touches it with her antennae, sometimes holding it between them. From such behaviour of the wasp we can suppose that the contact and olfactory senses (or the so-called contact-chemical sense) must play a chief rôle in recognizing her own larva.

The different responses of the wasp to the larvae of various other insects seem to favour the opinion above mentioned :

Those larvae which are considered markedly different from the larval *Bembix*

in the world of tactile and olfactory sensation, namely the larva of the honey bee and the cabbage-caterpillar, are easily distinguished by the mother wasp. While the larva of a Crabronid that is considered similar in odour (since it also eats the same kind of prey) as well as in contact of the integument to the larva of her own is discriminated by the wasp with much more difficulty. Indeed, in one instance, the larva of this species remained indiscriminated almost to the last. Nevertheless, most of the wasps tested could finally distinguish the substitute from her own larva.

I will reexamine what is the final cue of discrimination under such a difficult situation. In this case a slight difference of the larval form can not be considered sufficient to explain the result, since the young larva of *Bembix* also possesses a cylindrical body form similar to that of the Crabronid, and indeed, when her grown, more or less dorso-ventrally flattened larva is replaced with such a cylindrical young larva, she does not brutally deal with it. The remainder of the differences considerable are: (1) Somewhat harder body, but it is not considered important. (2) The supposed pure body odour characteristic of the species. In reality, the usual body odour of larval *Bembix* must be constituted with its inborn body odour plus the odour derived from the prey devoured. According to the human sensation, the latter is distinctly stronger than the former and, moreover, it is considerably different from one prey to another, since some prey are nectar and pollen feeders and others are saprofeeders or blood-suckers. In spite of such mingled smell, *Bembix* is considered capable of perceiving the pure odour of the larva. Probably this is the ultimate standard of odour of her own larva and the key to distinguish it from closely resembling other ones.

In this connection it seems worthy of mention that *Bembix* is much higher in this discriminating ability than those birds which can not distinguish the replaced egg of the parasite from their own.

#### (2) *Discrimination between the larvae of its own species*

In spite of the fact that the individual difference is very great as to the ability concerned here, we can say that, as a rule, the wasp of *B. niponica* is able to distinguish its own larva from another of the same species that is different in body dimension. Because most of them show more or less disturbance in behaviour at their first touching with the replaced larva and some of them even changed their feeding behaviour in response to the altered condition (Pt. II, pp. 42-55). The clue of discrimination in this case must be tactile in nature, and probably the relative dimension of the larva. The behaviour of touching the larva between the antennae is considered of much use to *Bembix* in perceiving the larval dimension and the tactile image thus obtained must become a standard of her provisioning activity.

### 3. Relation between perception of and response to the external condition

When the accumulation of food is experimentally removed from the brood-cell of the final instar larva, some wasps do not respond to the altered condition and after collecting a certain amount of food, give the tunnel the final closure, although they examine the interior of the brood-chamber, sometimes showing a more or less confusion and are obviously supposed to have perceived the event occurred. Under the same condition other wasps clearly change their mode of activity in accordance with the new situation and gather further food more actively in compensation. Among the latter group, some excellent wasps continue successively the provisioning work if the gathered food is successively removed from the cell. On the other hand some others ceased their hunting work after bringing together a certain number of flies in compensation and close the nest by means of the permanent closure.

Similar variation in response is also observed when the larva was replaced with another of different body dimension.

How should we understand such a difference of response among individuals? To me it seems to depend, on the one hand, upon the individual variation in the moment of entering the final mechanic course of provisioning activity and, on the other hand, upon the individual variation in the ability of response to the external condition. Generally in the final course of provisioning work the wasp is completely governed by the internal mechanism. The amount of food to be collected further by her is determined by the inborn sense of quantity based on the food quantity so far gathered and on the developmental degree of the larva she perceived at the last moment of her externally originated provisioning activities. Once the wasp steps in this internally ruled course of her breeding behaviour she is considered unable to respond to the external condition, although she may perceive the condition altered (this is easily presumed from the change of behaviour of the wasp). The moment of entering this course is, however, settled by the wasp, basing on her perception of the larval development and possibly in part also on the pressure from the matured egg. This moment may vary with the individuals, partly hereditarily and partly by the difference of influence of the positive egg pressure.

According to this view, we can give explanation to the greater part of the inconsistencies of responses among the wasps. However, by this opinion only, we can not fully understand the behaviour of some wasps which, in concordance with the changed condition of the larva as well as the prey, sometimes repeat the feeding procedure more than once and sometimes omit a part of the feeding schedule, markedly lengthening or abbreviating the feeding periods, sometimes even powerfully suppressing the positive egg pressure. I think this is dependent upon the individual variation in the ability of response to the external condition. The

greater the ability, the greater the power of suppressing the internal stimuli, accordingly the longer the feeding period. The wasp that has the highly developed ability of response, will have, under the natural condition, the longer period of caring of her larva and will show, under the experimental condition, well adjusted behaviour to the external conditions artificially changed.

According to this view the behaviour of *Bembix* shows two interesting steps of behavioural evolution. One is the stage wherein the ability to respond to the external stimuli has just emerged from the internally ruled mechanism of behaviour, but it is still restricted only to a part of the feeding activity. In this stage the ability is considered still so weak that it manages to fulfil the least quantity of response required in the behaviour of the progressive provisioning. While the other is the stage in which the ability to respond to the external condition is considerably large. It governs the greater part of the provisioning activity and is able, to a certain extent, to resist the internal stimuli. These stages, however, are not considered to represent the successively developed two steps, but are supposed to have emerged independently at the same time, just as various other abilities of response emerge as entity. Therefore, in reality, they are not the two stages in the procedure of behavioural evolution. Only in view of the functional height or complexity they are divisible into two evolutionary grades.

However, the grade in the ability of response is considered to have nothing to do with the grade in the ability of perception, since even in the lower grade the wasps obviously perceive the event occurred, only they can not correctly respond. Probably the ability of perception of the external condition emerged also independently of the ability of response.

#### 4. Perception of and response to the presence of more than one larva in the nest and their evolutionary significance

As discussed in Part II of this paper (pp. 79-80), *Bembix* can, with some difficulty, perceive the presence of more than one larva in a nest in the case when such a condition is provided in a multicellular glass nest. The final responses of the wasps to such a condition :

- 1) Two larvae are brought together in one of the cells.
- 2) One of the two larvae is discarded out of the nest.
- 3) One of them is killed.
- 4) One of many is separated from others by making a partition between them.

Besides the above, the following two cases were also observed, but in these instances it is quite doubtful whether the wasp perceiving them as two or more than one :

- 5) Two larvae placed in separate cells are separately provisioned. But the provisionment to each larva and the behaviour of the wasp at that time is most

reasonably understood when we consider that the wasp works under the perception of the two larvae as one and the same.

6) Two larvae placed in a large chamber (such as a Petri-dish) are fed *in situ*. In this case, too, the relation seems similar to the above.

Now, judging by the results above-mentioned, it seems conclusive at least in the present state that our *Bembix* has not even a latent ability to respond correctly to two larvae placed separately in a nest, though the wasp has a latent ability of perceiving them, with some difficulty, as two or more than one. According to this conclusion there seems to be no probability in our *Bembix* of developing their habits to such a higher state that they construct multicellular nests to rear many larvae at a time.

##### 5. Explanation to the instance of simultaneous rearing of two larvae

In Part I of this paper, I described an interesting instance observed at Chiba where the nests of *Bembix* are usually of the compound (multicellular) structure. In the instance concerned the wasp was working at the last provisioning to one of the cells, while her next cell had already been made in the same nest and contained an egg attached to the pedestal fly.

This instance shows an overlapping of parts of two behaviour systems that make their appearance, as a rule, successively but separately one after the other. However, in this colony the partly overlapped behaviour systems were not rare, so far as they are concerned with the behaviour unit, burrowing. Therefore, in this case, the matter pertains only to a little further progress. Probably the wasp was stimulated by the behaviour of burrowing and the next units of behaviour were successively released up to the unit, waiting. Sometime in the colony it was discovered that the next cell had casually been formed before the provisioning of the previous cell is finished, probably converted from the accessory branch, the digging work of which is usually involved in the unit, waiting. So far as is included in unit waiting, burrowing is not an independent unit behaviour, accordingly it is not progressed further beyond its limit.

Therefore, the instance concerned here is utterly a case of exception. In this case the matter might subsequently proceed as follows :

The wasp when reached unit waiting, turned back to the same unit (waiting) of the previous behaviour system and opened the temporary closure of the previous cell. Then her behaviour returned to the normal procedure of the cell in response to the state of the larva. The process is not unlike that of *Ammophila* investigated by Baerends (1941).

However, it is somewhat questionable whether or not the wasp could turn back to her egg already laid, or it might hatch out by the time, after she finished perfectly the work of her previous cell.

## 6. Learning ability in *Bembix*

Under the natural condition *Bembix* learns the location of its nest. The result of the learning is very exact, and there is no error nor hesitation in the recognition of the nest site. The procedure of learning is not of the trial-and-error in its common sense. Always keeping the certainty of recognition of the nest, trials of return are repeatedly carried out from a distance which is little by little lengthened above and around the nest. This learning procedure is a method in which vaguely known area is gradually taken in the well known domain, in other words, it is rather a process of ascertaining and it passes during the burrowing work of the wasp. After preparing the nest the wasp usually makes the orientation flight. But the process seems only a concentrated extension of the preceding ascertaining flight rather than that of the special learning flight. Therefore, her tests of frequent trials of return from various directions never fail. Judging from such behaviour of return to the nest *Bembix* is supposed to have a special ability of learning under the similar but experimental conditions. The theme was dealt with in Part II of this paper and the results obtained can be summarized as follows :

### A. Learning of the direction

(1) In the maze experiments using a Y- (simple or triple) or T-tube, the factors that guide the wasp at the bifurcation to the brood-cell (goal) are considered two, namely the odour emanating from the larval cell and the result of learning (memory) of the direction which are never separated under the natural condition, the former being external and direct and the latter internal and indirect.

(2) Learning of the direction is, as a rule, achieved by a single trial, never through the trial-and-error procedure.

(3) At the bifurcation the wasp first follows the memory of direction, but if it is separated from odour factor for test, she corrects her movements on the way and follows the direct leading element, the odour.

(4) However, after she is allowed to go to the goal several times without confusion (without separating the two factors for test), she comes to follow decidedly her memory of direction at the moment of the test experiment.

(5) On the other hand, frequent changes of the goal, that is to say, frequent separation of the two factors for tests, renders the wasp follow the direct factor only. Even under such a condition, however, if the wasp is liberated several times from the test, the state described in (4) is easily recovered.

(6) Retention of the effect of learning (in this respects experiments are as yet quite inadequate) continues at least for 18 hours.

(7) In the case when the direction is changed, a new learning process is at once begun and the effect of the previous learning exerts almost no noteworthy influence upon the procedure of the new learning.

### B. Learning of the short way

Under the experimental condition in which two sorts of the ways that lead respectively to the same larval cell, one the long way and the other short way, *Bembix* shows a marked tendency to learn to pass through the short way.

In this case learning is not achieved by a single trial to each way, but gradually effected with intermittent errors, namely, through trial-and-error process. Once it has been established, however, it seems to be fixated in combination with the direction.

### C. Learning of the broadness of the path

In the experiments to make the wasp learn the relative broadness of the passage in connection with the correct way to her larval cell, by using a Y-tube having branches of different width, the results were as follows :

(1) In this case three factors participate, namely, direction, odour and broadness of the path. The dominance order among them is direction → odour → broadness (cf. learning of the direction).

(2) Amongst them the first two can set to act as soon as the wasp reaches the bifurcation, while the last-mentioned must be affirmed by passing a certain distance. On this account in the experiments adopting relatively short branches, learning of the broadness of the path in connection with the larval cell always fails in the end.

(3) While, in the experiments using a Y-tube having relatively long branches of different broadness the wasp when entered the broader path that was wrong turned back half-way in most of the occasions.

(4) Judging by the results obtained, it can be concluded that under a favourable experimental condition *Bembix* has an ability to learn the relative broadness of the path in connection with the situation of her larval cell.

(5) Even when the branches of Y-maze are short, the fact that *Bembix* can distinguish between the different broadness of the paths can be presumed from other behaviour of the wasp, although the result cannot appear in her selection or correction of the path to be followed. That is her particular passing manner at the bifurcation. However, the behaviour can not be considered as a reasonable result of anticipation, but only as an instinctive adjustment. But such an adjustment can emerge only upon the basis of perception and discrimination of the external conditions. Hence the instances seem to prove the presence of such an ability in the wasp.

### D. Learning of the sinuate path

All the experiments so far conducted could not afford us any positive evidence of the presence of the learning ability of the sinuous path in connection with either the larval or non-larval cell. In some tests, however, the wasp showed behaviour that might be the result of learning of the relation. But such was very fragile and

momentary and could not be distinguished from the casual happenings.

*E. Relation between the direction and the odour in learning*

As pointed out elsewhere, during the course of the learning experiments on the direction of the pathway using a Y-maze, frequent changes (for test) of the direction of the larval cell drive the wasp to rely upon the direct clue of the larval odour only. Under such a condition, therefore, the wasp almost always selects the correct way to the larval cell, irrespective of the repeated changes of the location of the brood-cell. Apparently it is the result of habituation against the change of the direction of the goal. It seems to me, however, rather the result of that the wasp has learned either to neglect the direction or to follow the odour only, in order to reach correctly the larval cell. If so, it is an utterly new type of learning. Strange to say, however, the effect of this learning is very apt to be broken down. If the larval cell is several times left *in situ* at the successive entrances of the wasp to the nest, she comes at once to follow first the learned effect of the direction.

**7. Individual variation in the ability of learning**

In the learning experiments on the direction of the pathway using a triple-Y-maze (cf. Pt. II, Fig. 44), we obtained an astonishing result that wasp No. 114 learned the correct way, as a rule, by her single visit. Tests by changing the location of the larval cell proved that the memory of the direction acted more strongly than the direct stimulus of the larval smell. At the same time, however, frequent changes of the larval location might lead the wasp to follow first the larval smell. In order to confirm whether such is the general rule or not, I have made the same sort of experiments with wasp Nos. 180, 190 and 196.

(1) Wasp No. 190. Aug. 21, 1951. Simple nest having a straight tunnel of 25 cm and provided with the accessory branch just in front of the cell. The larva was in the middle stage of the final instar. The triple-Y-maze in the same arrangement as in the case of wasp No. 114 was employed (cf. Fig. 44 of Pt. II, p. 92). The larva and the fly were placed in bottle B, all other bottles remained empty. The

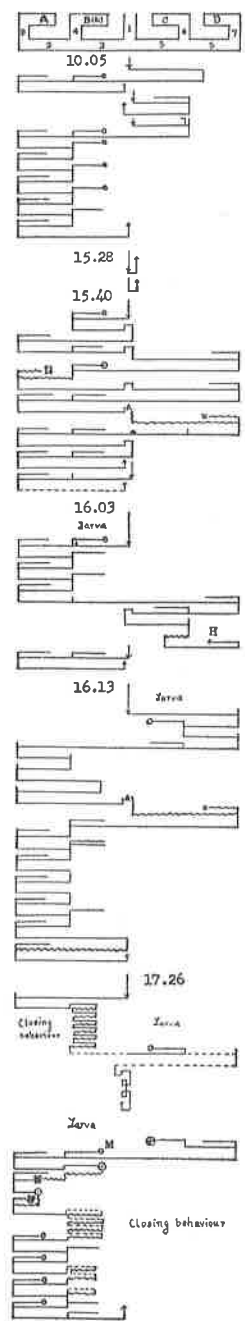


Fig. 14. The behaviour diagram of wasp No. 190 in the triple-Y maze.



movements of the wasp in the arrangement were diagrammatically shown in Figure 14.

In her first return at 13.05, learning of the direction has not been established by a single visit. In her second return at 15.40, it has already been achieved. During the course, however, the wasp transported the larva to cell A (denoted by  $\otimes$  in the figure). But her learning of the new location of the larva could not

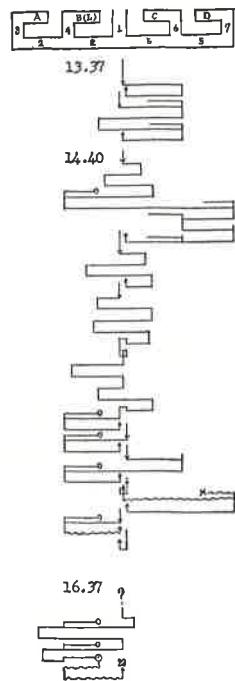


Fig. 15. The behaviour diagram of wasp No. 196 in the triple-Y maze.

In this experiment the wasp appears to learn the location of the larva with ease, but at last she carried the larva in the tunnel of her own. It was taken out from there and replaced once more in cell B. But the wasp again dragged it in the entrance tunnel.

(3) Wasp No. 180. Aug. 16, 1951. The nest and the experimental arrangement were as given in Figure 16, A. The larva was in the early stage of the fourth instar. The movements of the wasp in the apparatus were diagrammatically shown in Figures 17-18. During the course of the experiment the flies carried in by the wasp

easily be established. In her third return at 16.03, the larva was replaced in B. In her fourth return it was shifted to cell C, both by the experimenter. In these cases of return the wasp was apparently guided by the larval smell, but at the second bifurcation the mechanical easiness of the path to the outer cell seems to play some rôle. In her fifth return the wasp sealed the entrance to cell B as if it contained the larva within, probably on the basis of the memory of the previous location of the larva.

In this wasp learning of the direction could not so easily be established as in wasp No. 114. The result may partly depend upon the fact that the wasp went astray in the glass instruments as yet unfamiliar to her.

(2) Wasp No. 196. Aug. 23, 1951. Simple nest with the tunnel of 28 cm which turned near the middle at an angle of  $90^\circ$  to the right. The larva was in the early stage of the final instar. At first a short tube and a bottle of glass were placed with the larva in it and the wasp was allowed to carry a fly to the larva. Then it was replaced with the triple-Y-maze with the larva in cell B. The movements of the wasp were as given in Figure 15.

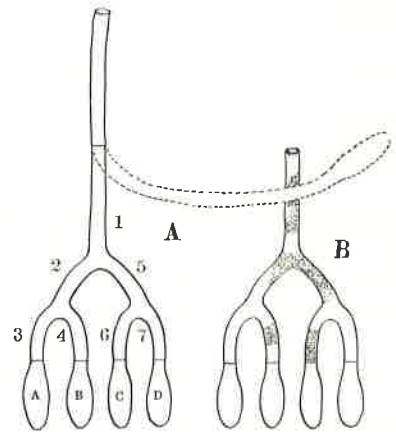


Fig. 16. The nest and the experimental equipment of wasp No. 180 (A), and the states of closure of the tunnel observed on the morning of the second day.

were always removed, leaving a single victim or two in the larval cell.

With regard to some important or interesting behaviour of the wasp observed during the course, some comments will be given below :

a) In the first return with a fly the wasp could not find the larva and the fly was swept out of the nest during her repeated ingress and egress.

b) Out of 10 times of retransportation of the fly 4 times were the cases wherein the wasp carried it directly from cell A to cell B, 3 times were the ones of retransportation from cell A or B to cell D and in the remaining 3 times the fly was carried back to the tunnel of her own.

c) Two times the wasp retransported the fly from cell B (larval cell !) to cell D. In one of the cases the wasp took the half-eaten fly from the larva by force and in the other she carried away the intact fly from the entrance of the cell. This behaviour seems to indicate that the wasp could not perceive the cell as the larval one in those moments. Probably the motivation of the retransportation of the prey was so strongly acted upon the wasp that she carried away every fly that she met with in the nest. She had been thrown into confusion in regard to the larval cell.

d) After 17 o'clock of the first day observation was stopped. According to the examination of the next morning it was made out that the wasp took in two flies further late in the previous evening. They were placed in cell D. The glass tunnel had been packed with sand at five places as shown in Figure 15, B.

e) As for the learning results :

i) This wasp had a strong tendency to take the direction in which her original tunnel was located.

ii) Towards the end of the first day it seemed that learning of the direction of the larval cell was established. But behaviour of the wasp on the next day proved that this was not the case.

iii) The wasp could not establish her learning of the direction of the larval cell till the last moment of the experiments, despite that the larval cell was never changed in position and she carried out 14 times of return including indeed 124 independent enterings to the nest.

iv) The results were analysed in Figure 19. In this figure, each of the columns stands for one time of return of the wasp carrying a fly and each of the bars shows one time of entrance of the wasp to the nest, the order being from the bottom upwards. The bars shooting out of the column to the left mean that the wasp proceeded to the left, viz. to tunnel 2, and those with a black spot at the apices represent that she went to cell B, those without indicate that she went to cell A. The bars with a spot in the middle denote that the wasp sooner or later went in cell B during her movements in the left hand tunnels. Similarly the right-hand bars shows entering of the wasp to tunnel 5, those with an apical spot to cell C, those without to cell D and those with a spot in the middle sooner or later to cell C. The solid lines denote the first visit at each entrance, while the dotted



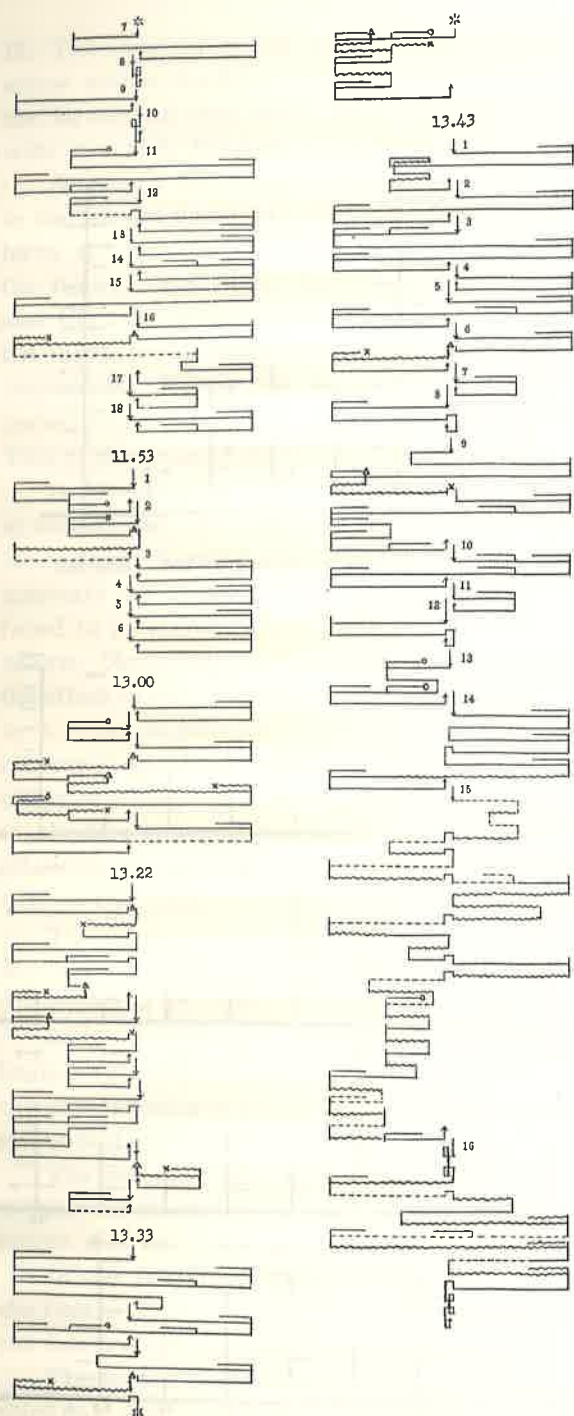


Fig. 18. The behaviour diagram of wasp No. 180 in the triple-Y maze (continued from Fig. 17).

ones the later visit during the movements in the apparatus. Therefore, the most significant bars from the point of view of the test of learning are those which occupy the lowermost position and are represented by solid lines.

According to the figure the conclusion given in (iii) of the above comments will easily be accepted.

In conclusion we may say that the ability of learning of *B. niponica* on the correct pathway in the triple-Y-maze is fairly markedly varied from one individual to another. However, judging from the results obtained from the simple Y-maze experiments such a stupid wasp as No. 180 seems rather exceptional. The instance given in the following item will afford evidence to this conclusion.

#### 8. Analysis of the learning process

Learning experiment on the sinuous pathway with wasp No. 186, viewed from another standpoint is an excellent instance of the learning of the direction. Therefore, with this material the detailed examination of the learning process of this wasp has been attempted. The movements of the wasp were diagrammatically shown in Figure 20. The method of representation is similar to Figure

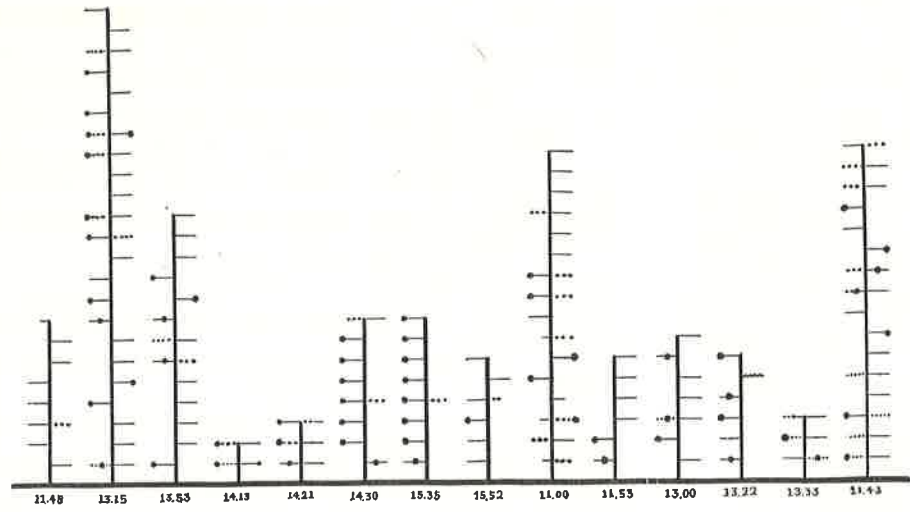


Fig. 19. Analysis of the learning process of direction of wasp No. 180. Detailed explanation is in the text.

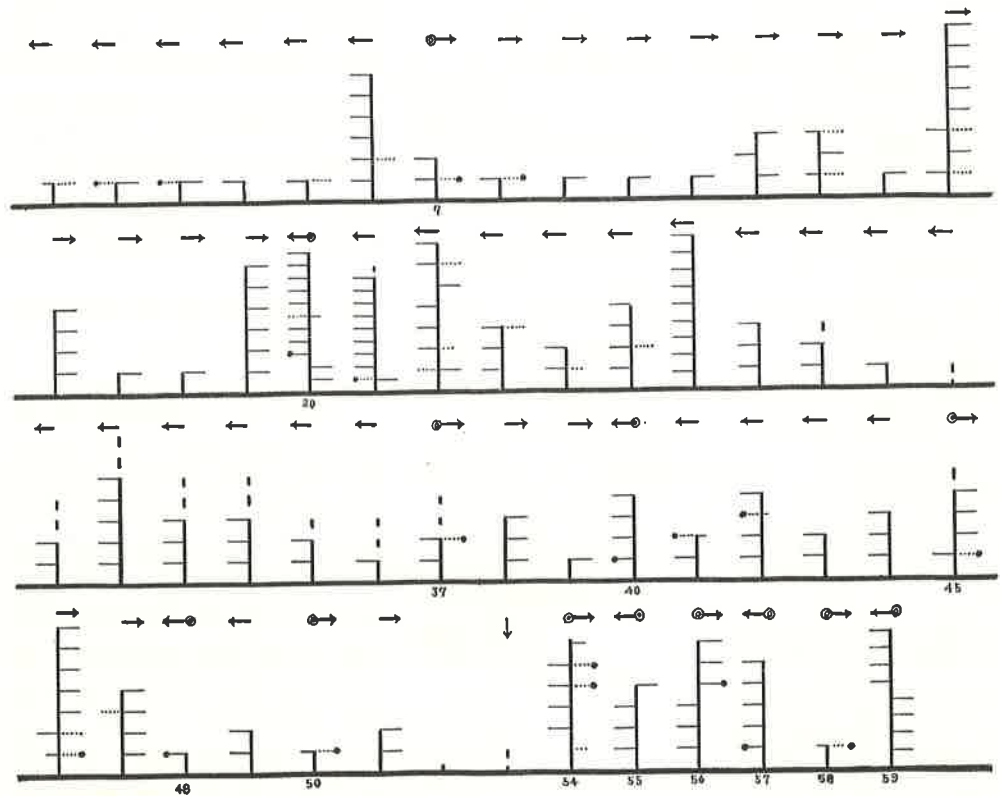


Fig. 20. Analysis of the learning process of direction of wasp No. 186.

19. The location of the larva is indicated by an arrow above each column, the arrow with a double circle at its base denotes that the change of the location of the larval cell was taken place for test. Return No. 54 was particularly dealt with as a test, because of the event occurred just preceding to it (cf. p. 17).

At return No. 7 the first test was made. At her first entrance *Bembix* went in the learned direction independently of the larval odour. Later she found out the larva at the end of the opposite branch (dotted line with a circllet at the apex in the figure). But in her second visit she followed the previous memory. This is also the case in her next return. At her second return after the test she went to the larva from the first. Thenceforth learning of the direction was established (exceptions: Return Nos. 13 and 15). According to the results two times of return (relearning) is necessary in order to extinct the effect of the previous learning. This is also proved by the second test made at her 20th return.

In the course of relearning the wasp tried to reentered the nest several times at each of her two successive returns (including the test, viz. return Nos. 20 and 21), namely 9 and 8 times respectively. In each of these, once the wasp entered correctly the larval cell, learning is apparently at once accomplished. She never failed to go correctly in her subsequent several trials within the limit of the same return. Nevertheless, she failed to go correctly at her next return and followed the effect of the previous learning. The results indicate that relearning is achieved by a single experience in the repeated trials without long intervals, but when a comparatively longer interval is inserted with the forage outside the nest, the effect of relearning is easily fallen down. Therefore, *the repeated success of the trials during stay in the nest at a single return has no important significance whatever as to the effective procedure of relearning. What is the most important is the first entrance at each of the returns.*

The correct visit to the larval cell of the wasp was continued till return No. 37, when the third test was performed. The result was positive. In this case, relearning is accomplished by a single trial.

In the fourth test at return No. 40 the wasp took the correct way from the beginning. Judging from the relatively small number of times of her return after the new learning was established the probability of her following the larval odour seems high.

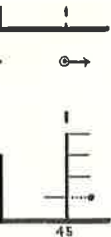
The result of the fifth test at return No. 45 was positive in relation to the memory of the direction. In this case, too, relearning was established at a second return after the change of the larval location.

In the sixth test (at return No. 48), the wasp entered the correct way from the first visit (by following the larval odour?). Whereas in the following test with the interval of one return the wasp was not guided by the larval odour.

The test at her 54th return is a particular instance. This is a first test in a third day. The wasp had been led to her larval cell through a single straight glass tube at her last return of the previous day. When I saw her on the morning of a



ailed



third day she was digging in sand in search of the larva, and the nest had completely been destroyed. Then she was led in the same Y-tube added with a simple glass tube at the base. Her behaviour represented in return No. 54 was observed at her first entrance to this replaced instruments. In this case her behaviour was rather of a sort of trial-and-error.

Thenceforth five tests were successively carried out at each of her following return, in order to confirm whether she relied upon the memory of the direction or upon the larval odour. But the results were uncertain as to the question. Apparently the wasp sometimes followed the memory of the direction (return Nos. 56, 58 and 59) and sometimes the odour of the larva (return Nos. 55 and 57). They can also be considered that her decision of the direction was made at random. But the behaviour at the 58th return seems to indicate that the wasp corrected her direction in which she began to proceed by the odour factor. In reality, however, explanation is difficult, since in this series of experiments one of the branches of the Y-tube has a sinuous portion in the middle. Moreover, behaviour of the wasp at such last portion of provisioning is considered to have already entered the final mechanical course of activities. Therefore, it seems better to take the result as done without any connection with the external condition.

In conclusion it will be said regarding wasp No. 186 that :

(1) For the establishment of relearning of the changed direction of the larval cell, a single correct visit is sufficient so far as the repeated visits withing a single return is concerned.

(2) However, the effect of this relearning has usually disappear already at her next return and new relearning is needed.

(3) In order to establish the steady effect of relearning on the direction of the first entrance of her subsequent return, the chance of correction at one or two times of subsequent return is required. Sometimes, however, relearning is accomplished by a single experience.

(4) It seems that relearning of the direction takes place at first as new learning of the larval odour to be followed and then gradually becomes connected with the direction of the pathway.

(5) The experience required to establish such a connection is considered two or three times of further return.

(6) According to this point of view, the stimulus of the larval odour gradually extincts like habituation and the memory of the direction appears as a sign of the way to the larva.

*Remarks.* The rate of progress of relearning is considered varied to a certain extent, with the individuals tested. To such an excellent wasp as No. 114 the conclusion given here can not wholly be applied.

## III. GENERAL SUMMARY

*Bembix niponica* is most closely allied to *B. rostrata* L. in its biological distinctions. It emerges once a year in summer and nests chiefly in sandy districts. In general, the nest is simple (unicellular) in structure, only rarely compound (multicellular). But a colony was found at Chiba wherein the compound type was the rule. There, though rather exceptionally, the phenomenon of simultaneous rearing of two larvae was observed. Victims given to the larva were always the Dipterous insects and more than as many as 55 species were confirmed. The number of the prey given to a larva varies with the size of the prey, usually 10-20, the maximum number being 35. The prey was stung to permanent paralysis, its longevity after carried to the nest being 1-9 days. In hunting the anterior portion of the thorax beneath is stung and sometimes thereafter the wasp imbibes syrup from the crop of such victims as flower flies.

In carrying the prey in to the nest it was first dropped in the tunnel, then the wasp opens the closure in front of the cell, inspect the interior, turns back to the prey and drags it backing to the entrance of the cell.

After carrying the first victim in the burrow the wasp digs and completes the brood-chamber. Then the special manipulation is given to the pray. One of the wings is half-opened, one of the middle legs of the same side is twisted half a round to dislocate and placed on the opened wing of the up-turned victim in a very rigid manner, as if to press it firmly in order to prevent it from recovering. Front leg is sometimes more or less distorted and stretched forwards.

Four instars are affirmed during the larval period by measuring the cranium of larvae of various developmental degrees. The duration required for the full growth varies with chiefly the temperature, being from about 6 to 14 days. Usually the larva eats into the thorax of the prey by first cutting its head off. By this means it can eat the insect with comparatively hard sclerite.

Provisioning activity is carried out according to the method of the so-called progressive provisioning. But it is not continued till the full maturity of the larva, but is stopped at a certain moment during the final instar before the full growth of the larva, with an accumulation of considerable amount of food in the cell and the nest is finally sealed up. The every day provisioning is also not carried out incessantly from morning till evening, but the greater part of the prey accumulated in a day is collected in concentration during a comparatively short period in the morning and only a prey of two are sometimes added in the evening. Therefore, the method of provisioning should be called correctly "progressive mass provisioning".

When finally the nest is closed, the tip of the abdomen of the wasp is used to pound and pack the sand taken in.

The cocoon is made of a layer of sand, lined with silk, in the equatorial zone of which the so-called respiratory pores are arranged, varying in number from 6



to 17 and constituted with three layers of silk and a crater-like projection. Encasement can be divided into six stages. First a silk pouch is woven with a funnel at an end, through which sand grains are taken in to inlay the pouch from within. The process of sand collection and inbedding is several to some ten times repeated and the cocoon is formed. Next, the construction of the respiratory pores and the lining of the interior are very slowly carried out.

*Bembix niponica* sometimes cleans the brood-cell, taking out of the nest the remains of larval food. But it occurs rather rarely.

As enemies, parasitic flies, *Solenopsis fugax* (an ant species) and the larva of *Acanthaclisis japonica* (the large ant-lion) are known. Detailed habits of these insects and the response of the wasp to such enemies were described.

Further, the remarkable persistence to the nest and the activities at the end of the season were mentioned.

In the burrow of this species an accessory branch (spur) is usually observed in front of the larval cell. The frequency of its occurrence diminishes as development of the larva proceeds. Usually the wasp uses it as a sitting room when resting in the nest, but it seems of more use as a puzzling cul-de-sac against the enemies. In the compound nest it is extended into the next cell.

Generally speaking, the size and softness of the victims supplied to the young larva are not specially different from those given to the more developed one. Therefore the popular theory that the mother wasp brings smaller and softer prey to the young larva can not be applied to this species at least. Evidence is statistically given.

The first victim used as the pedestal to the egg is (1) generally small in size, (2) usually killed or nearly killed, (3) not eaten by the larva in relatively large number. On the basis of such data a hypothesis that *B. niponica* has a tendency of using the first victim merely as a pedestal (as if an inanimate object) for the egg and not as food for the larva. This is an intermediate state between the case wherein the first victim is completely devoured as food and the case wherein the egg is laid on a pebble or a small lump of sand grains.

In homing visual cue (general pattern of the background) seems to play a chief rôle, olfactory cue has nothing to do with the discovery even of the exact place of the nest site.

Special attention was paid as to the behaviour of the wasp inside the nest using a glass tunnels and cells. Caring of the mother wasp of her young can be summarised as follows :

1. At the time of inspection of the brood-cell the wasp touches the larva with the antennae, usually holding it between them.
2. When the larva has been too near the accumulation of food at the entrance the wasp catches it with her jaws and drags it towards the middle of the cell.
3. When the prey is scarce within reach of the larva she carries a prey or two to it from the pile of food at the entrance. Thus she appears to care for the larva

not directly to take food from the provision.

4. Under the experimental condition when the larva is long exposed to light or some unfavourable event occurred upon it, she carries it to the dark portion of the tunnel.

5. Rarely she cleans the chamber, carrying the remains of food out of the nest.

6. However, trophallaxis has never been observed.

7. It is not fed with specially prepared food even in the earliest stage of development as supposed by J. B. Parker.

The following experiments were made :

First the releasing mechanism of the behaviour system of *B. niponica* is presumed from the brood rearing activities and diagrammatically presented. As introductory instances to this the behaviour systems of two other species (the burrowing spider wasp and a digger wasp, *Ammophila infesta*) were also considered and diagrammatically given.

With the aim of clarifying the external releasing factors of the hunting behaviour in *Bembix*, experiments concerning (1) removing of the egg or the larva, (2) structural change of the nest (the tunnel and the cell), (3) replacing the larva with that of various other insects (the cabbage caterpillar, the larval honey bee, the larva of a Crabronid that eats the fly), (4) replacing the larva with other of the same species, differing in body dimension, and (5) replacing the larva with a dead one, were carried out with the following results :

(1) Always the nest is abandoned, (2) when the egg or the early instar larva is dealt with, the nest is abandoned, but when the later larva is used, even a remarkable change of the structure can not lead the wasp to abandon the nest, (3) as soon as the difference is perceived, the nest is abandoned, or the substitute is dragged out of the nest and discarded, (4) when the egg is employed the nest is invariably abandoned, but when more developed larva is used some wasps changes their behaviour in accordance with the developmental degree of the given larva, some others, however, mechanically continue the work with the standard of their own larvae and seal the nest automatically, indifferent to the actual state of the substitute, (5) many of the wasps abandon the nest, but some wasps unchanged the behaviour. In this case various types of response are observed.

At the same time it was made clear that generally the wasp well responds to the amount of food in front of the larva. If the prey is removed from the larval cell many of the wasps show at once compensatory hunting activities. But sometimes there are wasps that do not show such special work and cease their work in conformity probably with their internal automatic mechanism.

In order to see whether this species is able to rear more than one larva at a time and in the same nest, experiments of various kinds were conducted with substantially negative results. But the response of the wasps considerably varied.

The following kinds of learning experiments were carried out by using simple

mazes of glass tubes and cells (T- and Y-tube, triple Y-tube), employing always the maternal drive as motivation :

(1) Learning of the direction, (2) learning of the short way, (3) learning of the broadness of the path, (4) learning of the sinuous path. The results :

(1) Positive, usually learning is achieved by a single (or two) experience, (2) positive through trial-and-error process, (3) when enough length of the path is provided, positive, (4) negative.

In these experiments the process of learning is pursued in detail and represented in figures.

On the basis of the results of observations and experiments so far conducted considerations on the behaviour pattern and mental ability of this species were made.

Basic pattern of behaviour was classified into three classes. The first is considered evoked by the innate automatism only; the second is probably released also by the internal stimulus, but is governed and guided by the corresponding external stimulus (or stimuli), while the third is released and maintained chiefly by the external stimulus (or stimuli). Evidence and instances are given. Then, modifiability, adjustment, habituation and purposiveness in behaviour were discussed. As to the latent behavioural characters which can be brought into appearance only by the experimental means, a considerable variation can be observed and which is considered the main reason of inconsistencies of the results of the experiments.

Actual and latent adjusting behaviour which is presumed to have emerged from the inborn, non-adjusting (but adaptive) and stereotyped pattern of behaviour is confined in this species chiefly to the activities of provisioning and caring of the larva. Its mode of appearance was considered. Finally in the section of behaviour pattern it was discussed that non-trophallactic origin of the maternal affection is certainly possible and *B. niponica* is doubtless a marked instance of such a behavioural evolution.

As for the mental ability the themata dealt with in the experimental part from the point of view of response were reconsidered from the standpoint of perception and recognition. It was concluded that perception and recognition of the wasp of the internal structure of the nest was under the natural condition not of a concrete one, while in the individuals trained under the experimental conditions they seemed fairly exact, and rarely even reaching such a height as having a general survey of the structure.

That there is a considerable difference of response among individuals to the removal of the prey or to the exchange of the larva is considered dependent, on the one hand, upon the variation in the moment of entering the final automatic course of provisioning activities and, on the other hand, upon the variation in the ability of responding to the external conditions.

Considerations and explanations were given to the ability of perception of

more than one larva placed in a nest and also to the phenomenon of simultaneous rearing of two larvae in a nest.

Finally, the learning ability and the individual variations of this species regarding response to various sorts of the simple maze tested were reexamined and analysis of the learning process was attempted.

## LITERATURE

- Adlerz, G. 1912. Lefnadsförhallenden och instinkter inom familjerna Pompilidae och Sphegidae IV. Kungl. Svenska Vet. Akad. Handl., 47, no. 10, pp. 269-304.
- Arens, L. E. 1948. Experiment of comparative analysis of the evolution of some innate forms of behaviour of swarming wasps, Bembicinae. Akad. Nauk. SSSR, Dok., 62, pp. 275-276 (in Russian).
- Ashmead, W. A. 1894. The habits of the Aculeate Hymenoptera. Psyche, p. 60.
- Baba, K. 1937. On some oecological observations on *Bembix niponica* Smith. Kontyu, Tokyo, 11, 1 & 2, pp. 21-27 (in Japanese).
- Baerends, G. P. 1941. Fortpflanzungsverhalten und Orientierung der Grabwespe *Ammophila campestris* Jur. Tijdschr. Ent., 84, pp. 68-275.
- . 1950. Specializations in organs and movements with a releasing function. In Physiological mechanisms in animal behaviour, pp. 337-360 (Symposia Soc. Exp. Biol., No 4.) Cambridge.
- (Bartram, J. 1763) Observation made by Mr. John Bartram, at Pennsylvania, on the yellow wasp of that country. Phil. Trans., London, 53, pp. 37-38.
- Berthoff, L. M. 1925. The moult of the honeybee, Jour. Ecol. Entom., 18, pp. 380-384.
- Bierens de Haan, I. A. 1929. Animal Psychology for Biologists. Three Lectures. London.
- . 1940. Die tierischen Instinkte und ihr Umbau durch Erfahrung. Leiden.
- . 1946. Animal Psychology. London.
- Bischoff, H. 1913. Zwei neue *Bembex* Arten aus Formosa. Deuts. Entom. Zeitschr., 6, S. 712-715.
- . 1927. Biologie der Hymenopteren. Berlin.
- Bohart, G. E. and MacSwain, J. W. 1939. The life history of the sand wasp, *Bembex occidentalis beutenmuelleri* Fox, and its parasites. Bull. Soc. Calif. Acad. Sci., 38, pp. 84-97.
- . 1940. Notes on two chrysidids parasitic on western bembicid wasps. Pan-Pac. Entom., 16, 92-93.
- Bouvier, E. L. 1900. Les retour au nid chez les Hyménoptères prédateurs du genre *Bembex*. C. R. Soc. Biol., Paris, 52, pp. 874-876.
- . 1901. Les habitudes des *Bembex*. Monogr. Biol., Ann. Psych., 7, pp. 1-68.
- . 1919. La Vie Psychique des Insectes. Paris.
- . 1919. Sur l'origine et la modification de l'instinct des Hyménoptères paralyseurs. Scientia, Boulogne. 29, pp. 449-459.
- Brethes, F. J. 1902. Notes biologiques sur trois Hyménoptères de Buenos Ayres. Rev. Mus. La Plata, 10, pp. 195-205.
- . 1918. Un Bembécido cazador de hemipteros. (*Bembidula discisa*). Physis.

- Burmeister, H. 1974. Bembecidae Argentini. Bol. Acad. Nac. Cienc. Ex. Univ. Cordova, 1, pp. 97-129.
- Buysson, R. du, 1903. Monographie des Guêpes ou Vespa (Part 1). Ann. Soc. Entom. France, 72, pp. 260-288.
- Carpenter, G. D. H. 1930. Psammocharidae and Sphecidae collected records of their different methods of filling in the stocked burrow. Trans. Entom. Soc. London, 78 (2), pp. 283-308.
- Carpenter, G. D. M. 1917. Observations on Fossors in East Afrtca. Proc. London Entom. Soc., p. 41-42.
- Chapman, R. N., Mickel, C. E., Parker, J. R., Miller, G. E. and Kelly, E. G. 1926. Studies in the ecology of sand dune insects. Ecology, 7, pp. 416-426.
- Chmurzynski, J. A. 1952. Comparative researches on the orientation in insects living on sand. I. Spacious orientation of Sphegidae on return to nest. Polsk. Pismo Entom., 22, pp. 68-68. (In Polish)
- . 1957. Preliminary notes on the colour preferences of females *Bembex rostrata* (L.) (Hymenoptera, Sphegidae). A preliminary note. Ekologia Polska, Ser. A, Tom. V, No. 2, pp. 7-13.
- Claude-Joseph, M. F. 1895. Recherches biologiques sur les prédateurs du Chili. Ann. Sci. Nat., Zool. ser. 10, 11, pp. 67-207.
- Coquillett, D. W. 1895. On the nesting habits of the digger-wasp *Bembex cinerea* Handlirsch. Proc. Ent. Soc. Wash., 3, pp. 236-237.
- Cros, A. 1922. *Bembex handlirschella* Fertou. Notes biologiques. Bull. Soc. Hist. Nat. Afr. Nord, 13, pp. 100-107.
- Deleurance, E. P. 1957. Contribution à l'étude biologique des Polistes (Hyménotères Vespides) I. L'activité de construction. Ann. Sci. Nat. Zool. Biol. Anim., Tome 19, Fasc. 1 et 2, pp. 91-222.
- Dufour, L. 1838. Observations sur le genre *Stizus*. Ann. Soc. Entom. France, 7, pp. 263-279.
- Evans, H. E. 1955. An ethological study of the digger wasp *Bembecinus neglectus*, with a review of the ethology of the genus. Behaviour, 7, pp. 287-303.
- . and Lin, C. S. 1956. Studies on the larvae of digger wasps (Hymenoptera, Sphecidae). Part II : Nyssoninae. Trans. Amer. Entom. Soc. 82, pp. 35-66.
- . 1957. Studies on the comparative ethology of digger wasp of the genus *Bembix*. New York.
- Fabre, J. H. 1856. Etude sur l'instinct et les metamorphoses des Sphegiens. Ann. Sci. nat. Zool., 4 Sér. 6. pp. 137-183.
- . 1856. Notes sur quelques points de l'histoire des *Cerceris*, des *Bembex*, des *Sitaris*, ets. Ibid., pp. 183-189.
- . 1879 Souvenirs Entomologique, T. 1. Paris.
- Fertou, C. 1899. Observations sur l'instinct des *Bembex* Fabr. Act. Soc. Linn. Bordeau, 54, pp. 331-345.
- . 1901a. Notes détachées sur l'instinct des Hyménotères mellifères et ravisseur. 1<sup>er</sup> Sér. Ann. Soc. Entom. France, 70, ref pp. 113, 125-126.
- . 1901b. Sur les moeurs de *Stizus fasciatus*. C. R. Assoc. fr. av. Sc., Ajaccio, pp. 680-683.
- . 1902. Notes détachées etc. 2<sup>e</sup> Sér. Ibid., 71, ref. pp. 514-516.
- . 1908. Notes détachées etc. 4<sup>e</sup> Sér. Ibid., 77, ref. pp. 554-557.
- . 1910. Notes détachées etc. 6<sup>e</sup> Sér. Ibid., 79, ref. pp. 147-151.

- . 1911. Notes détachées etc. 7<sup>e</sup> Ser. Ibid., 80, ref. pp. 353-358, 389-399.
- Fischel, W. 1953. Tierpsychologischen Forschung. Bonn.
- Frisch, K. von. 1950. Bees, their Vision, Chemical Senses and Language. Ithaca.
- Giraud, M. 1878. Quelques excursions entomologiques sur les dunes Normandes. Ann. Soc. entom. France, pp. 241-244.
- Grandi, G. 1926a. Contributo alla conoscenza della biologia e della morfologia degli Imenotteri melliferi e predatori. Boll. Lab. Zool. gen. agr. R. Scuola Super. Agr. Portici, 1, ref. pp. 293-306.
- . 1926b. Ibid., IV. Mem. Soc. Entom. Ital., 5, ref. pp. 189-198.
- . 1928. Ibid., VI. Boll. Lab. Entom. R. Inst. Sup. Agr. Bologna, 1, ref. pp. 14-18.
- . 1929. Contributo alla conoscenza biologica e morfologica degli Imenotteri melliferi e predatori. VII. Ibid., 1, p. 259-326.
- . 1930. Ibid., XI. Ibid., 3, ref. 309-316.
- . 1930b. Specificità ed eterogeneità della vittime degli Imenotteri predatori, specializzazione di comportamento delle femmine nidificanti e necessità dietetiche delle loro larve. Mem. Reale Acc. Sci. Istit. Bologna, Cl. Sci. Fis. Ser. VIII, 7, pp. 75-80.
- . 1931. Contributi alla conoscenza biologica e morfologica degli Imenotteri melliferi e predatori. XII. Boll. Lab. Entom. R. Inst. Sup. Agr. Bologna, 4, ref. pp. 45-46.
- . 1934. Contributi alla conoscenza degli Imenotteri melliferi e predatori. XIII. Ibid., 7, ref. pp. 53-57.
- . 1935. Contributi alla conoscenza degli Imenotteri aculeati. XV. Ibid., 8, ref. pp. 48-49.
- . 1937. Ibid., XVI. Boll. Istit. Entom. R. Univ. Bologna, 9, ref. pp. 283-290.
- . 1954. Ibid., XXVI. Ibid., ref. pp. 148-151.
- Handlirsch, A. 1889, 1890 et 1893. Monographie der mit *Nysson* und *Bembex* verwandten Grabwespen, 4, 5 und 7. Sitz. d. Akad. Wien.
- Hartman, C. 1905. Observations on the habits of some solitary wasps of Texas. Bull. Univ. Texas, 65, pp. 21-26.
- Hemmingsen, A and Nielsen, E. T. 1925. Ueber die Lebensinstinkte der dänischen *Bembix rostrata* L. Entom. Meddel., 16, pp. 14-27.
- Hine, J. S. 1906. A preliminary report on the horseflies of Louisiana, with a discussion of remedies and natural enemies. Circ. No. 6, State Crop Pest Com. pp. 7-43.
- Hingston, R. W. G. 1929. Instinct and Intelligence. New York.
- Hungerford, H. B. and Williams, F. X. 1912. Biological notes on some Kansas Hymenoptera. Ent. News, 23, pp. 241-262.
- Iersel, J. J. A. van. 1952. On the orientation of *Bembex rostrata* L. Trans. IX. Internat. Congr. Entom., Amsterdam, 1951, 1, 384-393.
- Iwata, K. 1936. On the habits of *Stizus* and *Bembix* which occur in Japan. Kontyu, Tokyo, 10 (5), pp. 233-250 (in Japanese).
- . 1942. Comparative studies on the habits of solitary wasps. Tenthredo, Kyoto, 6, pp. 1-146.
- Jacobson, E. 1909. Observations sur les habitudes du *Bembex Borrei* Handl. Lettre adressée de Batavia à M. le Prof. Bouvier. Bull. Mus. d'Hist. Nat. Paris, pp. 451-453.
- Koehler, A. 1923. Ueber die postembryonale Entwickluug der Honigbiene. Landwirts. Jahrb. Schweiz, 37, S. 183-192.
- Krombein K. V. 1936. Biological notes on some solitary wasps (Hymenoptera, Sphecidae). Ent. News, 47, 93-99.

- , et Evans, H. E. 1954. A list of wasps collected in Florida, March 29 to April 5, 1953, with biological annotations (Hymenoptera, Aculeata). Proc. Ent. Soc. Wash., 56, pp. 225-236.
- . 1955. An annotated list of wasps collected in Florida, March 20 to April 3, 1954 (Hymenoptera, Aculeata). Ibid., 57, pp. 223-235.
- Latreille, P. A. 1809. Observation nouvelles sur la manière dont plusieurs insectes de l'ordre des Hyménoptères pourvoient à la subsistance de leur postérité. Ann. Mus. d'Hist. Nat. Paris, 14, ref. p. 419.
- Lepeletier de Saint-Fargeau, A. 1841. Histoire naturelle des insectes. Hyménoptères. II, ref. pp. 339-363.
- Lorenz, K. Z. 1950. The comparative method in studying innate behaviour patterns. In Physiological mechanisms in animal behaviour, pp. 221-268.
- Lucas, H. 1877. Note sur *Bembex rostrata* et ses prois. Ann. Soc. entom. France, Bull. p. 150.
- Marchal, P. 1893. Remarques sur les *Bembex*. Ann. Soc. entom. France, 62, pp. 93-98.
- Marchand, E. 1901. Sur le retour au nid du *Bembex rostrata* Fabr. (unique observation). Bull. Soc. Sc. Nat. Ouest Nantes, 10, pp. 247-250.
- Melander, A. L. 1904. How does a wasp live at home? State Coll. Bull. Pullman, Wash., 3, 4pp.
- Minkiewicz, R. 1931. L'intéressant comportement des mâles de *Bembex* (guet-danse nuptial. Orientation. Habitudes. Rythme mnémonique). Polsk. Pismo Entom., 10, pp. 8-17.
- . 1933. Nid et prois des Sphegiens de Pologne. 3<sup>e</sup> Sér. Ibid., 12 (1-4), pp. 181-260 (ref. pp. 213-216 and Tableau synoptique 1).
- Nelson, J. A. and Sturtevant, A. P. 1924. The rate of growth of the honeybee larva. U. S. Dep. Agr. Bull., 1222, pp. 1-24.
- Nielsen, E. T. 1945. Moeurs des *Bembex*. Monographie biologique avec quelques considérations sur la variabilité des habitudes. Spolia Zool. Mus. Hauniensis, 7, pp. 1-174.
- Pantin, C. F. A. 1950. Behaviour patterns in lower invertebrates. In Physiological mechanisms in animal behaviour, pp. 175-195. Cambridge Univ. Press.
- Parker, J. B. 1910. Notes on the nesting habits of *Bembex nubilipennis*. Ohio Naturalist, pp. 163-165.
- . 1917. A Revision of the Bembicine Wasps of America North of Mexico. Proc. U. S. Nat. Mus., 52, pp. 1-155 (ref. pp. 123-141).
- . 1925. Notes on the nesting habits of *Bembex comata* Parker. Proc. Ent. Soc. Wash., 27, pp. 189-195.
- . 1929. A generic revision of the fossorial wasps of the Tribes Stizini and Bembicini with notes and descriptions of new species. Ibid., 75 (5), No. 2776, pp. 1-181.
- Peckham, G. W and E. G. 1898. The Instincts and Habits of Solitary Wasps. Wisc. Geol. Nat. Hist. Survey, Bull. no. 2, Sc. Ser. 1, ref. pp. 58-72.
- . 1900. Additional observations on the instincts and habits of the solitary wasps. Bull. Wisc. Nat. Hist. Soc., pp. 85-93.
- . 1905. Wasps, social and solitary. Westminster.
- Pichard, F. 1930. Note sur les *Stizus* et *Bembex* de l'Herault. Bull. Soc. Entom. France, pp. 41-43.
- Prell, H. 1924. Die Jugendgeschichte der Honigbiene. Märk. Bienenzeit., 14, pp. 74-78, 112-114.
- Rau, P. and N. 1918. Wasps Studies Afield. Princeton Univ. Press.

- Rau, P. 1922. Ecological and behavior notes on Missouri insects. Trans. Acad. Sci. St. Louis, 24, pp. 1-41.
- . 1935. A note on the attachment of the wasp, *Bembix nubilipennis*, to their nesting sites. Psyche, 41, pp. 243-244.
- Rabaud, E. 1928. How animals find their ways about. A study of distant orientation and place recognition (Transl. by Myers, I. M.), London.
- Roth, P. 1921. Au sujet des victimes de *Bembex mediterranea* Handl. Bull. Soc. Hist. Nat. Afr. Nord, 13, pp. 100-107.
- . 1922. A propos de l'instinct de *Bembex rostrata* L. Ann. Soc. Linn. Lyon, 64, pp. 47-52.
- Roubaud, E. 1908. Gradation et perfectionnement de l'instinct chez les Guêpes solitaires d'Afrique, de genre *Synagris*. C. R. Acad. Sc., Paris, 147, pp. 695-697.
- . 1910. *Bembex* chasseur de glossines au Dahomey. Ibid., 151, pp. 505-508.
- . 1910. Recherches sur la biologie des *Synagris*. Evolution de l'instinct chez les Guêpes solitaires. Ann. Soc. Entom. France, 79, pp. 1-21.
- Sawano, J. 1936. A collecting excursion to Gogahama. Shizen-Kenkyu (Niigata H. S.), 5, ref. pp. 41-42. (In Japanese.)
- Schneirla, T. C. 1929. Learning and orientation in ants. Studies by means of the maze method. Comp. Psychol. Monogr., VI, 1929, Art. No. 30, pp. 1-143.
- . 1933. Some important feature of ant learning. Zeitschr. f. vergl. Physiol., Bd. 19, Heft 3, S. 439-452.
- . 1943. The nature of ant learning. Jour. Comp. Psychol., 35, (2) pp. 149-176.
- . 1953. Basic problems in the nature of insect behavior. In K. D. Roeder et al., Insect Physiology, XXV, pp. 656-684.
- . 1956. Interrelationships of the innate and the acquired in instinctive behavior. In L'instinct dans le comportement des animaux et de l'homme. Paris. pp. 387-452.
- Schönichen, W. 1904. Die Lebensgewohnheiten der Wirbelwespe (*Bembex Spinolae*). Prometheus 15, pp. 761-764.
- Schuster, W. 1908. Aufzeichnungen über *Bembex rostrata*, die grösste deutsche Mordwespe. Wien Entom. Zeitg., 27, pp. 124-126.
- Sergent, E and Et. 1910. A propos d'un essai d'acclimatation des *Monedula* en Algérie. Bull. Soc. Hist. Nat. Afr. Nord, 2, pp. 81-82.
- Siebertz, C. 1903. *Bembex rostrata* L. Nerthus, 5, pp. 421-423, 449-451.
- Smith, R. H. 1923. The life history and habits of *Bicyrtes quadrifasciata* Say. Ann. Entom. Soc. Amer., 16, pp. 238-246.
- Sonan, J. 1927. On some Formosan Hymenoptera (2). Trans. Nat. Hist. Soc. Formosa, 17, pp. 359-377. (In Japanese.)
- Thorpe, W.H. 1948. The modern concept of instinctive behaviour. Bull. Anim. Behav., 7, 12 pp.
- . 1956. Learning and Instinct in Animals. London.
- Tinbergen, N. 1950. The hierarchical organization of nervous mechanisms underlying instinctive behaviour. In Physiological mechanisms in animal behaviour. Cambridge Univ. Press.
- . 1951. The Study of Instinct. London.
- Tolman, E. C. 1951. Purposive Behavior in Animals and Men. Univ. California Press.
- Torigata, T. 1930. Some observations on the habits of Hymenoptera. Mushi, Fukuoka, 3, pp. 84-88. (In Japanese.)
- Tsuneki, K. 1936. On the habits of *Bembix niponica* Smith. Trans. Kansai Entom. Soc.,



- Osaka, 7, pp. 64-69. (In Japanese.)
- , 1942. A Naturalist Amid the Battle Field. Osaka. (In Japanese.)
- , 1943. On the habits of *Stizus pulcherrimus* Smith. Mushi, Fukuoka, 15, pp. 37-47. (In Japanese.)
- , 1948. An Account of the Long Nosed Wasp, *Bembix niponica*. Sapporo. 303 pp. (Ibid.)
- , 1950. Experimental analysis of the sensory cues working in the return to the nest of the Pompilidae. Annot. Zool. Jap., 23, pp. 75-84.
- , 1956. Experimental methods on the behaviour of Invertebrates. Nakayama's Series of Experimental Methods in Biology. VIII, F2, Tokyo.
- , 1956. Ethological studies on *Bembix niponica* Smith, with emphasis on the psychological analysis of behaviour inside the nest (Hymenoptera, Sphecidae). I. Biological Part. Mem. Fac. Lib. Arts, Fukui Univ., Ser. II, Nat. Sci., No. 6, Pt. 4, pp. 77-172.
- , 1957. Ibid., II. Experimental Part. Ibid., No. 7, Pt. 1, pp. 1-116.
- , 1957. On the releasing mechanism of the behaviour system of some hunting wasps (Hymenoptera). Jour. Fac. Sci. Hokkaido Univ., Ser. VI, Zool., 13, (1-4), pp. 214-217.
- Watabe, J. 1931. *Bembix* as a means of controlling horse flies. Chuô-Juikai-Zasshi, 44, No. 10, (In Japanese)
- Verlaine, L. 1937. Qu'est-ce que l'instinct? Folia Biotheoretica, Ser. B, 11, pp. 51-66.
- Wesenberg-Lund, C. 1991. *Bembex rostrata*, dens liv og instincter. Ent. Medd., 3, pp. 19-41.
- Wheeler, W. M. 1923. Social Life Among the Insects. New York.
- Wheeler, W. M. and Richard Dow. R. 1933. Unusual prey of *Bembix*. Psyche, 15 (2), pp. 57-59.
- Yasumatsu, K. 1939. An obseration on *Bembix niponica*. Mushi, Fukuoka, 12, p. 67. (In Japanese.)

## POSTSCRIPTUM

### 1. Notes on Nielsen's *Moeurs des Bembex*

During my study on *Bembix niponica* at Sapporo I was able to know that a big work on the biology of this genus had recently been published by E. T. Nielsen. However, as the time was soon after the War and the profound confusion reigned over the Japanese people it was obliged that the work remained unaccessible to me. However, at the beginning of the description of my study on this wasp, I could enter into correspondence with the author of this work staying in U. S. A. He kindly sent me "a set of reprints of his papers", probably including the "Moeurs des Bembex". Unfortunately, however, his mail matter did not come to me after all, having possibly gone astray amid the confusion after the War. Having been compelled to write promptly my manuscript, I asked one of my acquaintances to let me know the summary of the *Moeurs des Bembex*. Looking back now, it was very regret that his answer was not sufficient, informing "this is nothing but the summarized work of the literature hitherto published; if you have adequately consulted with other papers there will be no particular necessity to refer to this paper".

When the first part of my paper had appeared I sent it to him with the letter informing that I could not directly read his paper after all. With the greatest kindness and most generous good-will he sent me again that invaluable paper which he obtained with great difficulty. Having read through the work I was greatly surprised to know that the work incorporates so many of the new findings parallel to those of my own that I have to correct some of my words in the introductory chapter. In the following I will mention about this work upon which I could not touch at the moment of description of my manuscript.

First of all I must admit that the honour of the first observation of the behaviour of *Bembix* inside the nest must no doubt be attributed to him. He used a pane of glass instead of my glass tube and cell and placed it over one side of the tunnel or of the brood-chamber which he also dug from behind just as I did. He found for the first time that the wasp (*Bembix rostrata* L.) drops the prey in the tunnel and enters the brood-cell empty-handed and head first, turns round, recaptures the fly and drags it backing to the cell. He did not, however, admit such behaviour of the wasp as an inspecting visit, but only for the purpose of turning round. It seems rather natural to arrive at such a conclusion from the observation of the nests under the natural condition only. But it seems possible to me to observe even in *B. rostrata* the relation having a inspecting significance similar to that found in *B. niponica* if the experimental technique is introduced during the provisioning activities. Despite the detailed observations on the provisioning behaviour inside the nest, he does not mention about the intimate relation between the mother wasp and her young.

He numbered the wasps by means of marking and observed their activities, to a considerable extent, successively for several days and found that the wasp, prior to "la fermeture définitive", accumulates a large number of flies during a comparatively short period within a day (wasp Nos. 3 and 4). He did not, however, observe the similar daily mass provisioning possibly carried out in the nest having a final instar larva within (he did not distinguish the larvae in their instars). Probably this is the cause of his not laying a stress on this interesting and significant phenomenon in connection with the evolution of behaviour among the Bembine wasps. According to the method above-mentioned he confirmed, moreover, that the larval period under the mother wasp's care is a week in summer in his country (Denmark). This agrees well with the results obtained in *B. niponica*.

Accordingly, I must withdraw some of my statements concerning the methods of observation in my introductory notes and would affirm that the honour of the first attempt of observing the behaviour of the numbered wasp in succession should be attributed also to him.

Generally speaking, in spite of the observations on a comparatively small number of the marked wasps (about 23, against more than 200 of mine), his results seem to cover the wide range of behaviour under the natural conditions and

fairly well agrees to those of mine with *B. niponica*. This indicates that the two species concerned here are very close to each other in phylogenetic relationships.\*

However, there can be admitted some slight differences in the habits of both the species :

1) The structure of the nest and the process of its construction

In *rostrata* the nest is always of the simple, that is to say, unicellular type, having an accessory branch (le puits, — the spur of Evans) a short distance in front of the larval cell. In *niponica* the nest is, as a rule, simple and unicellular, but occasionally it is formed in a compound and multicellular type. The ratio of its occurrence seems to be locally different.

In the simple nest, the basic type and the general tendency of its variation is considered similar in both species to each other. That the accessory branch of the tunnel is found in the early stage of the nest and tends to disappear in the later stage, and that the brood-chamber is gradually enlarged as the larval development proceeds, both the facts well agree in both species. However, a) in *rostrata* the accessory branch is first made as an end of the main burrow and then the cell burrow (le conduit de chambre, le conduit latéral) and the cell are dug; b) the nest is completely made on the previous day and the first victim is taken in on the following day; c) the brood-chamber is accomplished prior to the first hunting of the prey. In *niponica*, on the contrary, a) the accessory branch is made after the egg is laid; b) the first victim (the pedestal of the egg) is hunted and carried in as soon as the tunnel is roughly burrowed up (usually in the afternoon); c) after the first victim is taken in the roughly made tunnel, the brood-chamber is constructed\*\*.

According to his observation notes, however, the activity of his wasp No 16 (P. 80) seems utterly identical with the case in my species. The observation of wasp No. 10 (p. 126, 10-11, juillet, 1941) also affords a suggestion that the similar process might occur in this individual. With regard to this respect, therefore, further investigation with *B. rostrata* seems to be necessary.

*Remarks.* Significance of the accessory branch. Nielsen considers it as a temporary receptacle of the sand taken from the cell burrow. Contradictorily to his opinion, it is not a rare occurrence in *niponica* that the cell burrow is considerably long (10-20 cm) and the accessory branch forms the apical portion of the straight entrance burrow, far apart from the cell. Moreover, judging from the condition of its retention and its actual utilization by the wasps, as well as from its particular form (apically distinctly attenuate), I can not but hesitate to accept his opinion (cf. Pt. I, p. 129—).

2) The account on the contents of the brood-cell of wasp No. 7 (bleu)

In p. 125 Nielsen gives the following observation note :

“— 12 h. 13'; il a apporté un Diptère. Le nid fut ouvert. Dans la chambre il y avait une larve récemment éclos, longue de 6 à 7 mm, sur le Diptère porteur

\* Morphologically the structure of the male genitalia and antennae is somewhat different.

\*\* In the compound, multicellular nest in *B. niponica* the brood-cells except the initial one are completely made prior to the capture of the pedestal fly.

de l'oeuf, et 11 autre Diptères —”.

If the estimation of the larval development in this account is correctly made this instance represents an interesting exception and is very significant. To me, however, it seems highly probable that the larva in question might be in the earliest stage of the final instar.

3) The form of the cocoon.

According to his Figure 52, the cocoon of *B. rostrata* is somewhat different from that of *niponica* in that the posterior end is more acutely pointed.

4) Significance of the pedestal fly.

Nielsen (and Adlerz) observed frequently that the second fly is brought to the side of the pedestal of the egg prior to its hatching out. But they do not find the case wherein the pedestal fly is not eaten by the larva. Judging by their observations, however, the occurrence of the latter phenomenon seems to me highly probable. Further investigation will, therefore, be necessary in regard to this respect.

In the third chapter (Remarques generales) Nielsen deals with the animal behaviour in general and in order to give explanations of the mechanism of the animal actions, he distinguished among them three types, namely réflexes, émotion (et appétence) and plasticité. These seem to correspond essentially to the modern concepts of the hereditarily determined rigid behaviour patterns, the internal drive (and the appetitive behaviour) and adjusting modifiability of behaviour of the non-hereditary nature respectively. He made distinctions between the plasticity and the individual variation in behaviour. The latter shows, according to him, the uncertainty of the genetic constitution and possesses the possibility of mutation, the creator of evolution.

There is certainly a question as to the use of the term, reflex, as was pointed out by Evans (1957). As a whole, I can not always justify such standards of classification of animal behaviour.

On the basis of the action types above-mentioned Nielsen attempts to classify the behaviour in general of *B. rostrata* into four principal actions, namely, le repas, protection personnelle, la copulation et le soin du couvain. The former two concern with the existence of the individual and the latter two with the preservation of the progeny. His principal action represents essentially the same sense as the consummatory act of the modern ethologists, as also pointed out by Evans. Here I will touch on the care of young only, with which the present paper most concerns.

He divided the behaviour of care of young into three phases :

1) Le creusement du nid (le creusement même, la fermeture provisoire et l'orientation); 2) la chasse et le transport de la première proie, et la ponte; 3) les inspections du nid, le transport des proies ultérieures et la fermeture définitive du nid.

If the activities of *Bembix* in relation to her brood-rearing are divided in such

a sort, the third phase at least of his categories should be further divided into two, since the provisionment and the definitive closure represent respectively a different step of behaviour having a different significance.

He then takes up the problems of the inter- and intraspecific variation of habits and emphasizes the importance of such sorts of variation as appearing without being accompanied with any morphological characters. In this section he gives many valuable suggestions concerning the future study of the biology of the genus. Some of the questions he presented (for instance, the mechanism of provisioning and of the final closure), however, may have been solved by my experimental investigations. Further, he discussed the phylogeny of Aculeata and of *Bembix* and considered the multicellular nest in *Bembix* as a phenomenon of atavism. It seems a question to take the problem simply as such, since there can be another consideration that it shows a new evolutionary process, independent of the ancestral behavioural characters.

## 2. Notes on Evans's *Comparative Ethology of Bembix*

Recently Howard E. Evans of Cornell University has published the results of his extensive studies on thirteen species of *Bembix* occurring in North America :

Studies on the Comparative Ethology of Digger Wasps of the Genus *Bembix*. Comstock Publishing Associates (a Division of Cornell University Press), Ithaca, New York, 1957. 248 pp.

In this book stress of the author is of course laid on the comparative studies of the habits of the thirteen species dealt with, namely, *Bembix spinolae*, *comata*, *sayi*, *amoena*, *belfragei*, *cinerea*, *hinei u-scripta*, *nubilipennis*, *troglodytes*, *texana*, *pruinosa* and *occidentalis*.

After describing the general habits, especially those of nesting and brood-rearing, of each species so far investigated by previous authors and especially by himself, he attempts the interspecific comparison with regard to the following characters :

Distribution, habitat, number of generations per year, nature of colonies, mating flight of males, type of nest, number of cells per nest, leveling of mound, construction of false burrow, laying of egg, maintenance of outer closure, cell-cleaning activities, nature of final closure, aggressive flights, robbery of prey, nest dimensions (burrow length, cell depth, cell dimensions), types of flies used as prey and natural enemies.

In comparing these characters he attempts to refer to those of all the habits-known exotic species and, therefore, the work becomes as much valuable.

In Chapter V, Evans discusses the evolution of behaviour in the genus *Bembix*. Of the thirteen species dealt with by him, he takes up ten behavioural characters in which the primitive and specialized types are distinct, assigning a value of zero to the primitive characters, a value of one to the specialized and a value two to the

most specialized and obtained a rough "index of specialization" of behaviour. Upon such indices he creates very temperately a figure (p. 222), indicating a presumed phylogenetic position of each species. He then made similar "index of specialization" on the basis of morphological distinctions and obtained similar but not identical results and discusses the relation between them.

His considerations are further extended to the evolution of the manner of oviposition, evolution of nest type, significance of cell-cleaning, evolution of mound-leveling and of the false burrow, differences in nest closure and their significance, behavioural differences between subspecies, social behaviour in *Bembix* and finally enumerates the hypothetical causes of evolution of behaviour in *Bembix*.

Prior to entering into the comparison of behaviour patterns in the species studied by him, he gives "Analysis of behaviour of *Bembix*" in Chapter II. However, what is mentioned there seems very similar to Nielsen's concepts, excepting for the introduction of the behavioural formula and of the modern terms of ethology.

The extensive comparative studies of behaviour in Bembicine wasps such as shown in this book are only possible in a few blessed areas where abundant species occur. Such investigations must certainly contribute much to clarifying the evolutionary process of the behavioural patterns, especially when the characters which seem having much to do with the behavioural evolution, such as the state of the pedestal fly and the ratio of the pedestal fly of the egg that serves only as a pedestal and not as food, are more extensively studied. Nevertheless, in this group of wasps the behavioural evolution seems to be not always consistent with the phylogenetic relationship. This has already been shown by Evans and the reason for this has been suggested in my present paper in the section dealing with the mode of appearance of new behavioural characters in *Bembix*.

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**Explanation of Plate I**

1. Method of observation of behaviour of *Bembix* inside the Y-tube, the entrance is covered with a Petri-dish, lest the wasp should enter during the time of absence of the observer.
2. The same as 1. The two boards of veneer are removed. One of the branches is sinuous and one of the cells is open at the end.
3. The same as above. The wasp is dragging a fly toward the non-larval and open cell.
4. A cocoon that indicates the process of inlaying sand grains to the silken pouch. This was obtained by giving the larva insufficient amount of sand.

**Explanation of Plate II**

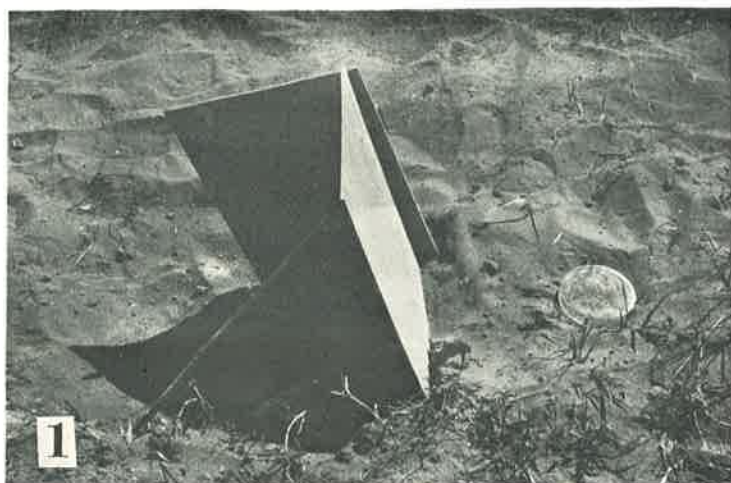
1. A larva with victims in a glass cell.
2. The same, but the mother wasp comes in it.
3. A wasp opening the entrance with a fly under her body.
4. A search digging by a wasp when the surface is confused. The fly is thrown aside in front of the entrance.
- 5, 7 A wasp dragging a fly in the glass tube.
6. A larva with the flies in a glass cell.

**Explanation of Plate III**

- 1, 2, 4, 5 and 6. *Bembix* in the glass tube. She is proceeding with sweeping movements.
3. A cocoon of *B. niponica*. The respiratory pores are observable.

**Explanation of Plate IV**

1. A cocoon of *B. niponica* after the adult wasp emerged.
- 2, 3. The form of the cocoon of *B. niponica*.
4. Method of observation of encasement of the larva using a set of the Petri-dish. The larva is protruding its anterior body from the funnel of the silken pouch to take in the sand grains.
- 5, 6, 7. Abnormal condition given for encasement. The glass larval cell is set standing without sand grains in it. Under such a condition the larva weaves the cocoon with the secretion only of the silk glands.
8. Another method of observation of encasement of the larva. The innermost portion of the tube bottle is packed with wet sand and the entrance is closed with a cotten plug. The larva is placed between them with victims.

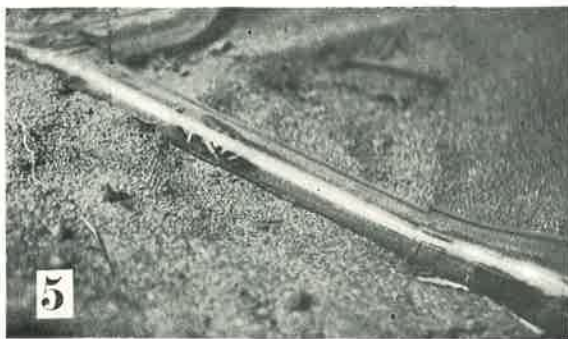


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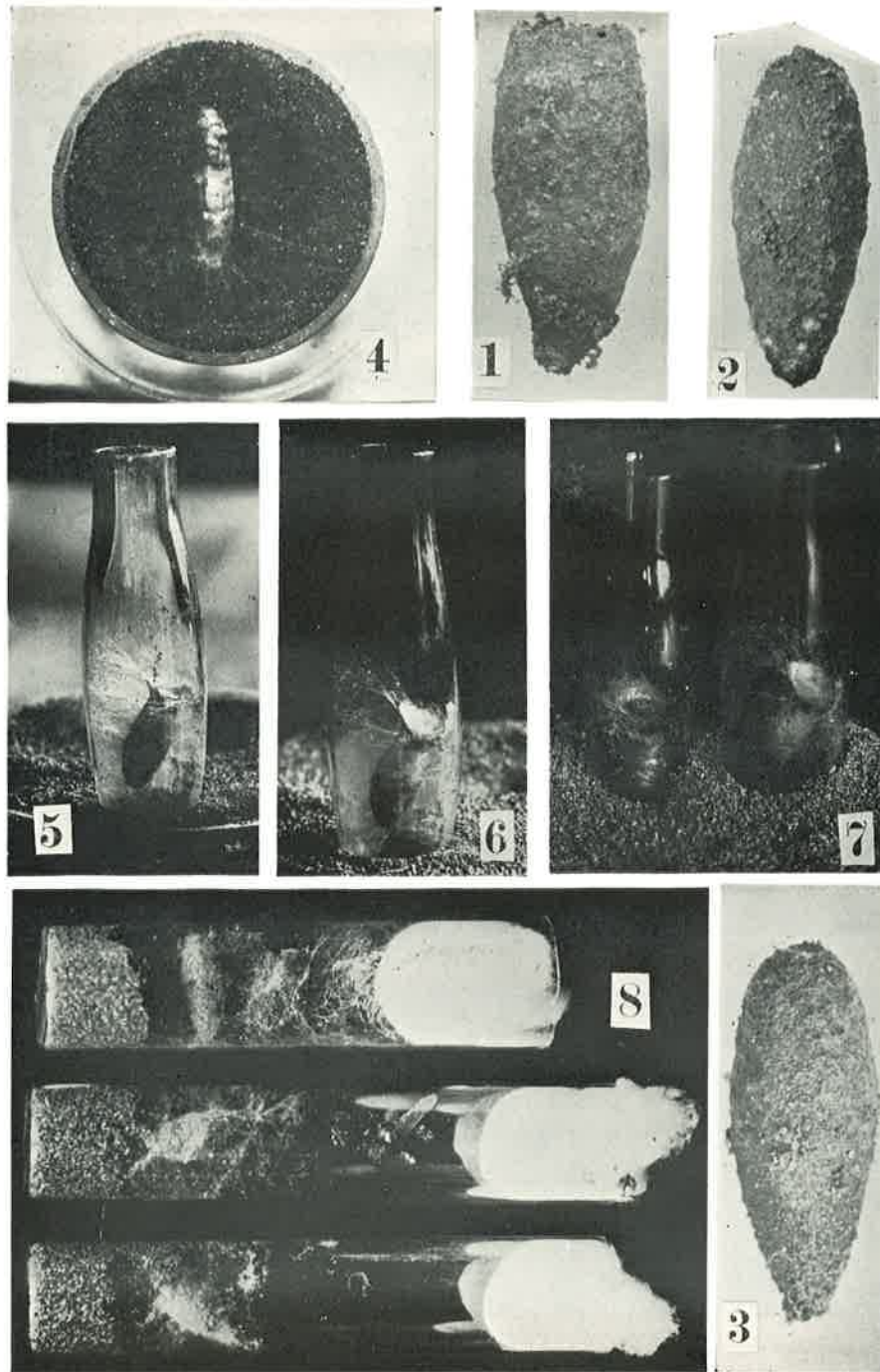




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