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

(Hymenoptera, Sphecidae)

II. Experimental Part

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(With 65 Figures in the Text)

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CONTENTS OF THE PRESENT PART

	Page
I. RELEASING MECHANISM OF THE BEHAVIOUR SYSTEM IN *BEMBIX NIPONICA* SM.	1
1. Releasing mechanism of the behaviour system in some other solitary wasps	2
a) The burrowing spider wasps	2
b) *Ammophila infesta* Smith	6
2. Releasing mechanism in *Bembix niponica* Smith	8
a) Behaviour system	8
b) Subunits within each behaviour unit and their releasors	9
c) Releasing mechanism	11
II. EXTERNAL CONDITION TO RELEASE THE HUNTING BEHAVIOUR	11
1. Presence or absence of the egg or the larva	12
2. Structural conditions of the nest	20
3. Kinds and characters of the larva	36
4. Dimension of the larva	42
5. Response of the wasp to the dead larva	56
III. RESPONSE TO THE PRESENCE OF MORE THAN ONE LARVA IN A NEST	59
1. Experiments of placing two larvae in a nest	59
2. Experiments of placing more than two larvae in a nest	73
3. Consideration and conclusion	79
IV. RESPONSE TO THE AMOUNT OF FOOD IN FRONT OF THE LARVA	81
V. LEARNING EXPERIMENTS	86
1. Learning of the direction	86
2. Learning of the short way	100
3. Learning of the broadness of the path	103

I. RELEASING MECHANISM OF THE BEHAVIOUR SYSTEM IN *BEMBIX NIPONICA* SM.

It seems rather a difficult matter to analyse the complex system of behaviour of *Bembix* in terms of the releasing mechanism, that is to say, to analyse the behaviour into units that are successively brought into appearance by some external as well as internal stimulating factors. Because in some behaviour *Bembix* is very

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plastic; moreover, her response to the same set of stimuli is sometimes markedly varied from one individual to another; and still further, even in the parts of behaviour which are considered rather mechanic in appearance, it is usually needed to call out a single unit a set of stimuli which are by no means so simple as can be represented by the so-called sign stimuli. The task is just so much difficult as to interprete the behaviour of the ant in terms of the stimulous physiology.

However the attempt to do so seems of significance in that it may not only grasp the complexity of behaviour of *Bembix* in a concrete form, but also strictly clarify the restricted range of each stimulus that will, together with others, call forth a certain unit of behaviour in this wasp.

The behaviour system of *Bembix* seems to represent one of the most advanced forms among those of the solitary hunting wasps. Before to tackle with the problem at once, therefore, we may be better to have some knowledge regarding the releasing mechanism of some more primitive hunting wasps, in particular regarding those which have close connection in their behaviour with *Bembix*.

1. Releasing mechanism of the behaviour system in some other solitary wasps

a) The burrowing spider wasps

In Japan four basic types of behaviour systems can be observed in the spider wasps. The first is represented by the members of *Pseudagenia* that construct a mud pot prior to get the prey. The second is shown by some species of *Deuteragenia* that make their brood-cell in some pre-existed hollow tubes by partitioning them with mud walls. The third is the commonest and most primitive type in which the prey is first hunt and then the nest is dug in the ground to receive it and to which the greater parts of the Pompilids of such genera as *Batozonellus*, *Cyphononyx*, *Cryptocheilus*, *Episylon*, *Priocnemis*, *Anoplius*, *Pompilus*, etc. belong. This type includes several somewhat differentiated subtypes and semi-parasitic one (for instance *Batozonellus annulatus* F.). The fourth is the true parasitic type which is represented by such genera as *Homonotus*, *Xanthampulex* and *Ceropales*.

Behaviour system The burrowing spider wasps belong to the third type. Their behaviour system can be summarised as follows :

The wasp goes in the field, captures a spider of certain species that can adjust to her innate standard and stings it into paralysis. She then carries it to her base nesting ground where the nest is made by her day by day and drags it on to a branch of a grass. Next she selects a favourable place and burrows her nest. During her work of burrowing, she frequently leaves the hole to visit and examines the spider. When the burrow is dug up, she comes to the spider and carries it into the bottom chamber of the burrow. The egg is deposited on the abdomen of the prey. After the oviposition, the burrow is tightly closed with the dirt. In many species the dirt that has been piled near the orifice of the nest during the digging work is carefully scattered away after the closure of the nest is completed. In some species, moreover, the site of the nest is deliberately camouflaged with fragments of fallen leaves, twigs and grass halms, pebbles, lumps of earth, etc. Thus the behaviour system comes to an end. We can divide this system into several units and arrange them as follows :

Hunting (H) — Transportation (T) — Burrowing (B), accompanied by several times of Examination (E) of the prey — Storing (S) of the spider in the cell — Oviposition (O) — Closing (C), including the scattering of sand or camouflaging.

According to the method of Iwata (1942) we can abbreviate this by using a symbol for each unit (as given within parentheses in the above description) into the following formula :

$$\mathbf{H\ T\ (B\ E)^{n}\ S\ O\ C}$$

Beleasing mechanism Now, in this behaviour system each unit is considered to be connected with the neighbouring ones in the interlocking system in which the result or the behaviour itself of the preceding unit is immediately the releasor of the subsequent unit. But this does not mean that the system is an indivisibly well-united one that can be driven by the innate automatism only. Indeed, it seems true that the leading factor in the external expression of this system is the internal drive on the part of the mother wasp and every plan of the procedure is prescribed innately in the nervous system of the wasp. Notwithstanding, in order to make appear each unit excepting the initial one several corresponding external releasors are always needed.

The releasor of H (hunting behaviour) is considered to be primarily an internal stimulus —— maturation of the egg together with every physiological state accompanying with it. This I will call positive egg pressure (PEP). T (transportation) seems to be called forth externally by the presence of the paralysed prey (PP) and internally by the sense of distance (SD) which is acquired during her hunting behaviour and strengthend and made accurate during her later frequent voyages between the hunting field and the nesting ground. Moreover, environmental differences between both the places seem to play some part in releasing this unit.

Experiment 1. Experiment of depriving the wasp of her spider just after hunting or during her transportation. This always results in the renewed (or rather reversed) hunting behaviour, after long continued searching movement. In this case PEP is still acting upon the wasp and can release behaviour H, while the disappearance of the spider ceases the progress of the subsequent behaviour.

Experiment 2. Experiment of inducing the wasp to come on a plate or a net while she carries the spider backward, and transporting her together with the spider to or beyond her nest. The result of this experiment is clearest when it is done after the nest has been burrowed up and the distance between the spider and her nest comes to be small. The wasp carries the spider straight after passing across the plate and stops her transportation when she walked as large a distance as had been between the nest and her situation just at the time of the displacement. This result clearly indicates how accurate the sense of distance of the wasp is.

Experiment 3. Experiment of capturing the wasp with the prey to transport her to her nesting site and to set free. The result is that the wasp shows a more or less confusion, but finally she carries the spider to some neighbouring grass and begins to search for her nesting place on the ground, omitting behaviour T which must precede this in the normal course of the behaviour system. This shows that the appearance of the base nesting ground the image of which is fixed in the memory of the wasp and the presence of the spider at the place make the sense of distance disappear from the internal releasing mechanism of the wasp.

Behaviour B (burrowing) is also guided by PEP, but externally it is chiefly released by the presence of the paralyzed spider. The memory of the base nesting ground seems also to take some part. But it does not always require the disappearance of the sense of distance as a preceding procedure. Therefore, behaviour B and T frequently appear alternately. Unit E seems to be released by the internal stimuli, the sence of time after leaving the spider and the sense of distance to it. Through the behaviour of digging the burrow, two new sources of stimuli appear, namely, the presence of the nest (N) or the favourable condition for oviposition and the negative sense of equilibrium (NSE) which serve as releasors of the subsequent units of behaviour. In order to release unit S (storing of the prey), the presence of the nest, the paralyzed prey and the sense of distance are needed, but it is also guided by the positive egg pressure.

The releasor for oviposition is considered to be the positive egg pressure and the paralyzed prey stored in the nest.

Now, viewed in the light of releasing mechanism, the process H T $(B\ E)^n$ S O is released per unit by the respective releasor or releasors. Amongst them, however, some concerns only with a single unit, some with two or three units, while another rules over the process as a whole. That is to say, amongst the various kinds of releasors there is a difference of order. The higher the oder, the greater the range ruled by it. That the positive egg pressure is of the highest order in this group of wasps and reigns the procedure from H up to O is easily proved by the following experiment :

Experiment 4. Experiment of depriving the wasp of its spider at any point within the range above described, for instances, just after hunting, during transporting or burrowing, or after storing it in the burrow but before the oviposition is over. The wasp, after searching for it long, always resumes the procedure from the first. In this case, the order of the procedure is always fixed, namely H - T - B - S, never, for instance, B preceding H, or B being omitted because of the presence of the burrow. This indicates that, so far as PEP is in action, the behaviour system can always be reversed up to any necessary point of the procedure before O.

As for PP (paralyzed prey), its presence rules from T to O under the support of PEP.

Experiment 5. When the spider is shifted far from the neighbourhood of the nest, the process of the system is reversed to T, even after the spider is stored in the cell (but of course before the egg is laid). In this case if the burrow is destroyed and the spider is placed on the ground near the nest, the behaviour of the wasp is reversed to B.

On the contrary, once the oviposition is finished, the procedure of the system can not be reversed to any necessary point before O.

Experiment 6. Just after the egg is laid, the wasp is driven out of the nest and the spider is taken out of the brood-chamber. Usually the empty burrow is carefully closed by the wasp, even when it is inspected before closing.

Experiment 7. In the above experiment, if the spider with the egg is placed near the nest, the wasp shows usually one of the following two responses :

1) The wasp, even when she meets with the spider, does not show any concern about it and continues to close the nest as usual.

2) The wasp catches the spider and carries it to a branch of a grass near-bye. But in the long run, it is discarded in situ and the closing process is continued.

By the above experiments it is evident that the change of the highest releasing factor occurs at the point of O and once the process entered within the range ruled by the second main factor, it cannot be reversed to any point of the other range beyond the bordering point, O. The so-called non-adjusting and blind successive occurrence of the instinctive behaviour is usually observed in such a case.

Then what are the releasors of the final unit of the closing behaviour ? I think them to be the negative egg pressure (NEP) emerging from the oviposition and the negative sense of equilibrium (NSE) which must be acquired during the course of digging the burrow by confusing the equilibrated ground, that is to say, by making a hollow in the ground and heaping the sand dug out on the ground. This negative sense of equilibrium seems to act as an agency requiring the re-equilibrium and restoration. This is proved by the following observation and experiment :

Observation 1. The Pompilid wasp usually abandons the half-dug burrows two or three times before finally completing the last one of them. In such a case, the abandoned burrows are, as a rule, more or less completely closed with earth.

Experiment 8. During the course of closing the burrow by the wasp, two or three holes, more or less similar in form to the true nest, are artificially made near-bye. The wasp, when took notice these holes, at once closes them. The same result is also obtained when the experiment is done after the wasp has finished the closure and is scattering the dirt to flatten the surface.

The above mentioned

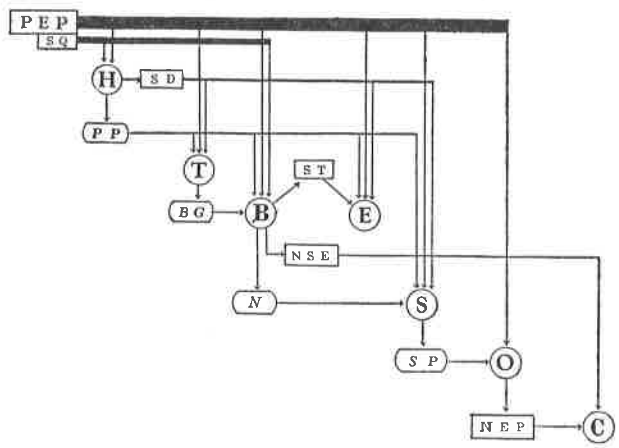


Fig. 1. A diagramatic presentation of the behaviour system in the burrowing spider wasp. The circles represent the behaviour units : H, hunting. T, transportation of the prey. B, burrowing. E, examination of the prey. S, storing. C, closing. The rectangles stand for the internal releasing factors : PEP, positivie egg pressure. SQ, sense of quantity. SD, sense of distance. ST, sense of time. NSE, negative sense of equilibrium. NEP, negative egg pressnre. The ellipses show the external releasing factors : PP, paralysed prey. BG, burrowing ground. N, nest or the environmental conditions for oviposition. SP, stored prey.

releasing procedure of the behaviour system of the burrowing spider wasps is as designated in Figure 1.

Subordinate releasing mechanism within a single unit Each unit of the behaviour system has its own releasing structure in itself. For instance, Unit Hunting consists of the following subunits : Searching for the prey, Capturing the spider and Stinging it into paralysis. The external releasor in this case except the initial one is the contact with a living spider which can adjust to the innate standard of the wasp. But the procedure of the occurrence of these subunits or segments of the behaviour is chiefly guided by the innate mechanism in which the preceding act is likely to turn to the releasor of the subsequent act. Therefore, whole the process is much more mechanically carried out. For another instance, Unit Storing consists of the following segments : Carrying the spider up to the entrance to the burrow, Penetrating the burrow head first to inspect the interior, Coming out to the entrance head first, Catching the spider by one of the legs and Dragging it in the burrow.

The successive order of this process cannot easily be altered even when the unit behaviour is forced to repeat under the experimental condition :

Experiment 9. When the wasp has entered the burrow to inspect the interior, the spider placed at the door-way is shifted 10 – 20 cm away from the orifice. The wasp, when comes back to catch the spider, is thrown into confusion, but soon finds the spider in her search, carries it to the door-way and repeats the same manoeuvre as has just been carried out. This experiment can usually be repeated as many times as pleased with the same result.

As seen in the above instance, the subordinate behaviour system within a unit behaviour is progressed like a chain reflex, once the initial segment which alone belongs to the higher order is released.

Moreover, each segment of behaviour has also its own minor system in itself. This is chiefly physiologic, except that it has a certain type of expression. For instance, in capturing the spider for transportation, the wasp grasps it by one of the legs (mainly of the 3rd or the 4th pair) at its base; in carrying the spider it proceeds backwards; in stinging the prey a certain spot under the cephalothorax is invariably selected. But all the rest of the procedure belong to the domain of the mascular physiology.

Thus the behaviour system of the burrowing spider wasp is considered to have a hierarchical organization, as N. Tinbergen pointed out in some Vertebrates.

b) *Ammophila infesta* Smith

This species is cited as a representative of the solitary wasps having the habits of digging the burrow first, prior to hunting the prey, such as the greater parts of the species of the Sphecidae (sens latr.). In this species there are two types of behaviour systems, in one of which the wasp provisions its nest with a single caterpillar, in the other it stores in its nest from two to four caterpillars. The former is rather close to the spider wasp in behaviour system excepting that the nest is burrowed before hunting. While the latter is similar to *Bembix*. Here, the description is confined to the latter type only, adopting the case in which three caterpillars are stored in the nest.

Behaviour system The behaviour system of *Ammophila infesta* Sm. in the case adopted here can be designated as follows :

Burrowing (B) — Temporary closure of the nest entrance (c) — Hunting (H) — Transporting (T) — Uncovering the entrance of the nest (U) — Storing (S) — Oviposition (O) — Temporary closure — Huting — Transporting — Uncovering the nest — Storing — Temporary closure — Hunting — Transporting — Uncovering — Storing — Permanent closure (C). Its behaviour formula is as follows :

$$\mathbf{B\,c\,H\,T\,U\,S\,O\,C\,(H\,T\,U\,S\,C)^2}$$

Releasing mechanism That the burrowing appears first is perfectly due to the innate scheme. However, by what mechanism the burrow is temporarily and very simply closed before the wasp goes for hunting is rather difficult to explain. Probably it is released by the presence of the burrow which is not or not fully stored with the prey. The presence of the burrow gives rise to the negative sense of equilibrium (NSE). This is the chief factor for the closing behaviour. But it is regulated by the not or not fully stored state of the nest which seems to act as a releasor through the sense of quantity of the prey, resulting in the simple temporary closure. This sense of quantity (SQ) seems to make its appearance with the positive egg pressure (PEP) and innately leads the wasp to accumulate the necessary quantity of food for the larva. This internal factor, therefore, must exist even when a single large prey alone is stored in the cell. Through the burrowing and the temporary closing accompanied by the locality study the memory of the nest (MN) emerges which has a close relation to the later hunting, transporting and opening units. Hunting behaviour is aroused by the positive egg pressure (PEP) and the memory of the nest. It is also accompanied by the sense of quantity. The presence of the paralysed prey and sense of distance (SD) releases Unit transportation. The prey at the entrance (PE) and the memory of the nest give rise to Unit uncovering the entrance. By the presence of the opened nest and the prey at the entrance the behaviour of storing is called forth. Oviposition occurs by the cooperation of PEP, N (nest, or the environmental condition for breeding the larva) and SP (stored prey). A second temporary closure which is somewhat more elaborate as compared with the first one seems to be accomplished by the cooperation of such releasors as the negative sense of equilibrium (NSE), the memory of the egg (ME) which emerged through the negative egg pressure (NEP), the presence of the nest opened and the sense of quantity.

The releasing mechanism mentioned above and its remaining part which follows that is given diagramatically in Figure 2. The final permanent closing behaviour seems to be released by the satisfied state of the sense of quantity (the balance between SQ_1 and $SQ_2 + SQ_3 + SQ_4$ comes to be zero), the memory of the egg, the presence of the nest that is opened and the negative sense of equilibrium which is derived from the last opening behaviour.

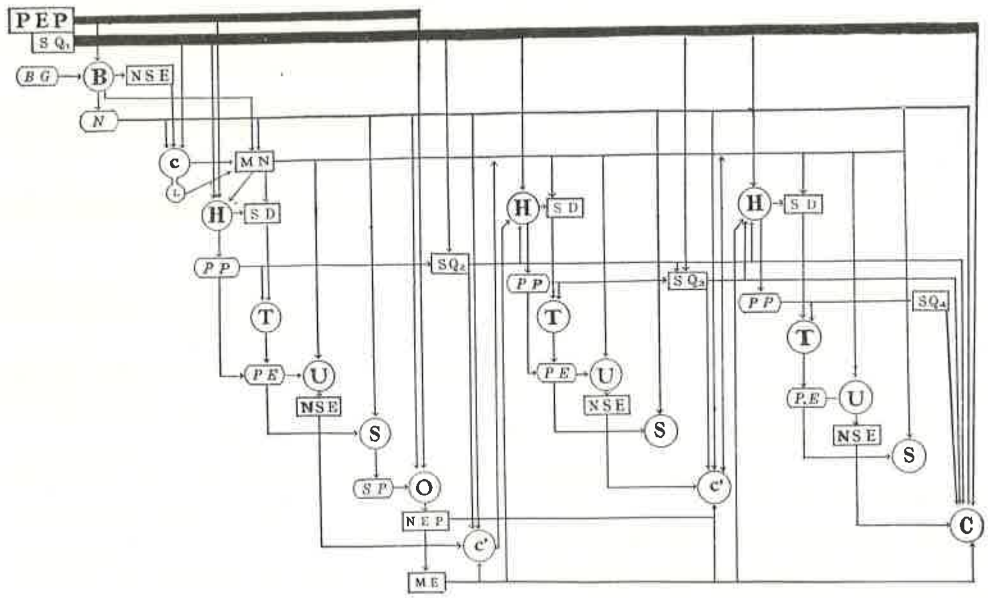


Fig. 2. A diagramatic presentation of the behaviour system in *Ammophila infesta* Sm. Symbols are as explained in Figure 1. New symbols in the circles : c, temporary closure. L, locality study. U, uncovering or opening the nest. c', temporary closure of more elaborate nature. In the rectangles : SQ_1 – SQ_4, the primary, secondary, tertiary and quaternary sense of quantity. MN, memory of the nest. ME, memory of the egg. In the ellipses : PE, prey at the entrance.

I have abundant evidence for the theory above described*. It is not the aim of the present description, however, to enter into the detailed discussion on the releasing mechanism in this species. Therefore, It must be postponed till a proper opportunity to give full description and discussion on my experiments of the behaviour system of *Ammophila infesta* Sm. But I think that it has sufficiently been described what is the releasing mechanism I would mean.

2. Releasing mechanism in *Bembix niponica* Smith

a) Behaviour system

The behaviour system in brood-rearing activities in *Bembix niponica* seems to be represented with some difficulties by the following formula :

* It was partly published in Japanese in the following book : Tsuneki, K. 1956. Fxperimental methods on the behaviour of the Invertebrata. In Nakayama's Series of Experimental Methods in Biology, Tokyo.

$$\mathrm{B\,c\,H\,T\,S\,P\,O\,c\,W\,E\,\{(c\,H\,T\,S)^{n}\ W\,E\,F\}^{m}\,C}$$

In the above formula P means preparation for oviposition, W waiting mainly in the nest, E examination of the egg or the larva and F feeding the larva. Other symbols are the same as in the case of the spider wasps and *Ammophila*. Power **n** indicates the number of times within a day and **m** the number of days necessary for rearing a larva.

b*) *Subunits within each behaviour unit and their releasors

The subunit or the segment of a unit-behaviour represents usually a simple act and is released by the internal as well as external factors as in the unit behaviour. The behaviour units in *Bembix* are considered to be composed of several subunits respectively as given below :

Burrowing. Loosening the sand with mandibles and fore legs. (Releasor : Contact with the sand of favourable condition) — Throwing the crambled sand-grains behind through the underside of its body. (Rel.: Contact with the loosened sand. Contact with a pebble awakens the act of grasping and carrying it out of the tunnel) — Clearing the tunnel, the repeated sand-throwing acts with backward progress. (Rel.: Contact with the sand piled up behind the body) — Scattering the sand and evening the surface at the entrance. (Not carefully done in this species. Rel.: The same as above, except that the pile is on the surface outside the nest. Probably this is a continuation of the preceding act). The series of acts are many times repeated. Besides the releasors described above, whole the process is guided by the internal stimulus, the positive egg pressure (PEP).

Temporary closure. Including the simple closure of the entrance only, when the wasp leaves for the firft time after burowing the nest. But later, it usually includes also the closure of the tunnel just before the brood-cell. The releasor for the external closure is the opened state of the entrance and that for the internal closure the opened state of the brood-cell. However, the latter is completely restrained by the presence of the paralysed prey in the tunnel. On the other hand, in order to release the act of closing the brood-cell, it is also necessary that the egg or the young is well going in the chamber. The negative sense of equilibrium seems to be not well developed in this species, since the wasp does not close the entrance when she abandons the half-burrowed nest, or she does not carefully evens the surface of the ground when the nest is burrowed up. However, the closure of the entrance from inside at the time when the wasp rests in the nest belongs probably to another unit. But this has nothing to do with the breeding habits of the wasp.

Hunting. Searching for the prey (Rel.: Positive egg pressure at first, but later the presence of the larva in the cell) — Capturing the prey (Rel.: An insect coming in sight which is responsible for the prey innately determined in both quality and quantity) — Stinging the prey into paralysis (Rel.: Direct contact with the prey).

Transportation. This becomes almost a segment of Hunting, or rather of

Storing in this species. But, because of the fact that the physiological mechanism of the transportation is perfectly different from both of the units mentioned, it seems better to treate it still as an independent unit. This consideration seems also supported by the state of the unit in spider wasps and in *Ammophila*. Releasors : Paralysed prey between the legs and the sense of distance.

Storing. Opening the entrance (Rel.: Closed state of the entrance and the paralysed prey between legs) — Carrying the prey in the tunnel, as a rule, up to the sand partition before the cell (Rel.: Captured fly and the opened burrow) — Dropping the prey (Rel.: Preceding act, not the contact with the sand partition, because the wasp drops the prey even when the partition wall is experimentarily removed) — Opening the closure of the brood-cell (Rel.: Contact with the sand stoppage) — Entering the cell, sometimes examining the larva (Rel.: Preceding act, sometimes perception of the larva through probably the sense of smell) — Returning to the prey (Rel.: Preceding act) — Capturing and dragging it backward in the cell (Rel.: Preceding act and the contact with the prey). When the first prey is taken in, the series of the acts comes to an end at the point of "Dropping the fly in the tunnel".

Preparation for oviposition. Some unknown act in the tunnel, probably weakening or killing the prey (Rel.: Preceding act, contact with the physical conditions in the tunnel, contact with the prey and positive egg pressure) — Completing the brood-cell (Rel.: Preceding act, PEP) — Operation on the fly (Rel.: Preceding act and PEP). Each act in this series may be a good unit in the behaviour system. But I treated them as a segment within a single unit respectively, since there can hardly be discovered the external releasor.

Oviposition. Releasors : PEP, the favourable condition for laying the egg and preceding act.

Waiting. I mean by this expression not only the quiet resting of the wasp in the nest, but also some doings performed during her waiting for the time of the next work, such as closing the entrance from within and burrowing the accessory branch.

Examination of the egg or the larva. Opening the closure of the brood-cell — Examination of the egg or the larva with the antennae — Closing the cell. The releasors of these acts are quite internal, including probably the sense of time after laying the egg or after previous examination of the larva. The releasors of the second and third acts are respectively the preceding act.

Feeding. It occurs usually after the examination of the larva. It is the behaviour of bringing a prey from the pile of food at the entrance of the brood-cell. The acts are : Catching a fly at the entrance of the cell — Dragging it backward to the side of the larva. The releasors : The presence of the larva and the lack of food about it.

Permanent closure of the nest. Gathering the sand at the bottom of the tunnel — Pounding it with the tip of the abdomen. This series of acts is repeated many times. The external releasors : An adequately grown larva in the cell and the sufficient amount of food before it. But the latter factor is sometime replaced by the preceding behaviour, that is to say, the hunting and storing behaviour repeatedly carried out. Positive pressure of the next egg takes also some part.

c) Releasing mechanism

The behaviour of *Bembix*, especially while the wasp is breeding her larva, is fairly plastic and rather difficult to represent as a concrete system. However, if it is presented in the commonest type of the procedure, it will become as shown in Figure 3.

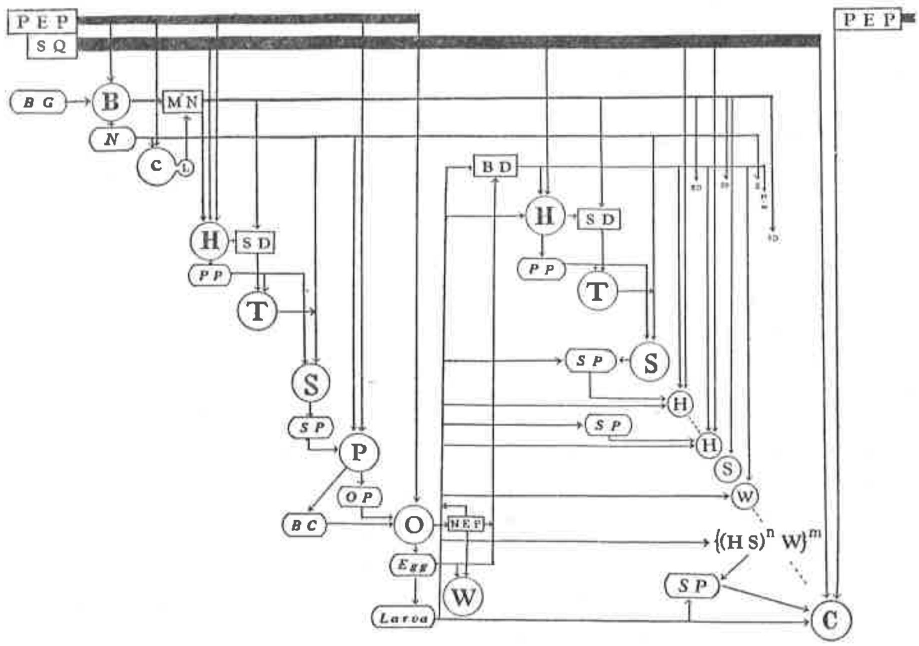


Fig. 3. A diagramatic presentation of the behaviour system in *Bembix niponica* Sm. Symbols are as in Figures 1 and 2. New symbols in the circles : P, preparation for oviposition. W, waiting, including and Examination of the egg or the larva. Temporary closure is included either in H or in W. In the rectangles : BD, breeding drive, a changed form of NEP. In the ellipses : OP, operated prey. BC, brood-cell.

II. EXTERNAL CONDITIONS TO RELEASE THE HUNTING BEHAVIOUR

Those persons who read the accounts of the maternal care of *Bembix* in Part I of this paper will have no doubt the confidence on the importance of the presence of the larva in the cell as a releasor of the hunting activities of the wasp. However, strictly there has been given no examination whatever as to the scope of the larval conditions that can release the prey-gathering activities in the wasp. It can not always definitely be denied, therefore, that such an opinion based upon the reflex theory of the instinct as that the performance of the provisioning activities of the mother *Bembix* depends solely upon the blind inner impulse derived from the innate automatism. Or, conceding for argument's sake that the presence of the larva in the cell is truly an indispensable condition for the feeding activities in *Bembix*, it is utterly unknown whether or not any larva may do so, so long as it is a larva of an insect, irrespective of its kind, form, odour and dimension. Moreover, it is also an unsolved problem whether or not the nest conditions other than the larva, such as the curvature of the tunnel, the size and form of the brood-cell can exert an influence upon breeding activities of the wasp. These problems immediately relate not only to the question on the contact between the mother and her young, but also to the question on the capacity of discrimination and recognition on the part of the mother wasp. In order to solve these questions, if any, the following experiments were carried out :

1. Presence or absence of the egg or the larva

a) *Experiments of removing all the contents from the brood-cell*

If the hunting activities are performed depending solely on the internal releasing factor alone, the work must be done most mechanically without cease, even when the brood-cell is made empty.

(1) Wasp No. 13. Aug. 20, 1946. At 9.00 a.m. Simple nest, with the tunnel of 27 cm in length. In the brood-cell was the larva of the early stage of the 4th instar with 12 victims, nearly a half of which were already eaten. The wasp was in the course of the day's provisionment. At 9.12 I removed the larva and all the victims out of the cell and covered the place with a thick layer of sand. At 10.20 I found the wasp throwing out the sand from the nest. She continued her work eagerly. At last she perforated the sand wall that I had pressed from behind and came out in the open air. At once she flew to the entrance and entered the nest again. I placed once more a thick layer of sand on the hole. The wasp continued her burrowing work without taking a least recess until 2 p.m., when I examined the nest. She was digging and lengthening her tunnel. It was presumed that she was searching for something in sand. The next day the entrance of the nest left opened and the wasp did not return to the place. It was clear that it was abandoned.

(2) Wasp No. 51. Aug. 8, 1947. At 2.30 p.m. A simple nest. The larva was in the early stage of the 4th instar. Remains of 2 victims were by the side of it and 10 intact ones at the entrance portion of the cell. Two of the intact flies were observed carried in by the wasp at 2.03 and 2.17 respectively.

I removed all the contents of the cell and put an empty bottle in place of the larval cell. At 5.00 p.m. I uncovered the bottle and knew a flesh fly (*Sarcophaga* sp.) had been placed in it. I replaced the bottle with another empty one and covered it with a thick layer of sand. The next day at 10 a.m., I examined the bottle and found a green bottle fly (*Lucilia* sp.) in it. But later until 6 p.m. no victim was brought in the nest. Two days later, at 2 p.m. I dug out the cell and knew it was abandoned by the wasp, for there was only the green bottle fly in it.

(3) Wasp No. 53. Aug. 9, 1947. The wasp was seen working eagerly from early in the morning to carry in the victims to her nest. But all her effort was made in vain. Because, the

nest was invaded at its entrance by a larva of the large ant lion. Seven victims that were brought by the wasp were discarded at the entrance until 3 p.m., when I dug the brood-cell and found a larva of the early stage of the 4th instar and 6 victims inside. Among the victims 2 were already eaten and 1 was just decapitated by the larva. I removed all the contents of the cell and placed instead an empty bottle. Also I removed the enemy from in front of the entrance.

Two days later when I uncovered the cell I found only one flower fly placed in the bottle. The next day the bottle remained as before.

(4) Wasp No. 54. Observed the same day as above. At 3.30 p.m. I dug the cell and found an egg attached to an flower fly. I removed it together with the pedestal and placed instead an empty glass-cell. I examined it on the 11th and also on the 14th, but no more victim had been carried in it.

(5) Wasp No. 67. Sept. 3, 1947. The nest was of the compound type, including 2 cells inside. In one of which was a cocoon and in the other a just moulted 4th instar larva, attaching still to the pedestal-fly. The prey were 7 in number, of which 2 were partly eaten. I removed all the contents from the chamber and put in place an empty glass-chamber. The next day at 10 a.m. a large quantity of sand had been thrown out and piled up in front of the nest. The cell remained empty and a new tunnel was dug along the bottle through the sand. Until 5 p.m. the wasp did not return and it was clear that the nest was abandoned after something was eagerly searched for.

As shown in the above experiments when the contents of the nest are entirely removed from it, the wasp, after seeking them in sand, abandons it in the end. But rarely the tendency of the automatic provisionment can still be observed, when more than one victim was brought in the empty cell (for instance No. 51).

b) Experiments of removing the larva alone

(1) Wasp No. 57. Aug. 19, 1947. Having observed a wasp bring a victim twice to her burrow I dug the nest from behind at 10.05 a.m. It was a simple nest and in the brood-cell I found a larva of the early stage of the 4th instar supplied with 8 victims of which 2 were already eaten. I put the two eaten flies alone in the glass bottle and connected it with the end of the natural tunnel. At 11.25, I uncovered the cell and knew that 2 flies had been added in it. At 11.30, I saw the wasp carry in a *Ochrops fulvus*. I hurried there and at once unearthed the cell to wait for the wasp coming in. The wasp, after spending one and a half minutes in the tunnel, showed her head at the entrance of the glass cell. But without coming in, she turned round and disappeared in the tunnel. The next moment, however, she came backing in the cell with the prey. She mounted over the victims already piled up at the entrance and left the burden on top of the pile. Then, without making an examination of the interior, she trampled over the pile of flies and went in the tunnel. Immediately, however, she returned head first, but stopped without entering the cell and began to proceed and retreat in the tunnel. keeping her head inwards. For about 3 minutes she repeated such a strange movement, making her head appear and disappear in and from the glass cell. At last she fell into confusion by the light. So I covered the cell. At 11.35 she was throwing the dirts from the burrow, but soon ceased the work and flew away. On examining the cell at 2.30 p.m., I knew that a considerable quantity of sand was thrown in the cell and covered almost entirely the heap of 5 victims. Ten days later, I examined the cell. It remained as it had been, containing 5 already rotten flies, indicating

clearly it was abandoned by the wasp. This instance seems of interest in that the wasp carried in the cell without the larva three flies automatically.

(2) Wasp No. 58. Observed at the same time as the preceding instance. The nest was of the simple form. The tunnel of about 20 cm led to the brood-cell in which were a larva of the early stage of the 4th instar and 12 flies including 4 partly eaten ones. All the intact flies showed active movemets on their proboscises and legs; especially one of which, an *Eristalis cerealis*, when taken out, beated its wings so violently that it appeared to be able to fly off. Probably they were hunted on the early hours of the day. I put one yellow horse fly alone in a glass cell and placed it at the end of the tunnel of the wasp. It was at 11.00 a.m. At 11.27, I uncovered the cell and found a *Chrysozona tristis* had been taken in. At 11.35, however, I saw the wasp throwing out the sand from the entrance. At 2.32 p.m., I reexamined the cell and knew that an flower fly had been added inside. Ten days later, however, when I dug the cell, it had been abandoned, without being added any more fly than the two.

(3) Wasp No. 65. Sept. 3, 1947. At 11.30 a.m., having failed to dig upon the brood-cell, I missed the larva in sand. But by searching in the sand dug out, I succeeded in finding 2 intact flies and 2 remains of victims. Judging from the results, the larva was supposed to be of the 3rd or, more probably, of the 4th instar. I placed the vicims and remains in a glass-cell and placed it at the end of the tunnel. Two minutes later the wasp came back with a booty and carried it in the burrow. I uncovered the cell and awaited the wasp. After spending 2 minutes in the tunnel, she came in the cell and walked about. While her walking about she caught this or that fly with her mandibles and turned them over. Her behaviour was very machine-like, without showing any such emotional appearance as a careful examination of the object with the trembling antennae or with the inclined head, nor she did make the rubbing of the antennae with a front leg, as so often seen in the behaviour of the spider wasp or *Ammophila*. However, my impression was that she was searching for her missing larva. At last she felt the light and fell into confusion. So I covered the cell with sand. Ten minutes later, I saw the wasp entering empty-handed from the entrance. At 12.30, on uncovering the cell I found a flower fly newly brought in at the entrance to the chamber. All other flies were scattered irregularly in the cell. At 4.00 p.m. no change had occurred within. At 4.20 I saw the wasp enter the burrow empty-handed. The next day at 10.40 a.m., on examining the cell, I found only one intact and one half-eaten flies. Other 3 were unknown. The entrances remained opened and there was a wing of a fly in the tunnel. Whether the result was due to the act of the wasp or to the intrusion of some carnivorous enemy I can not say. But the observation of the previous day seems to indicate that the wasp missed her interest of gathering food for the nest.

(4) Wasp No. 72. Sept. 4, 1947. A simple nest, containing an egg attached to the pedestal fly. By the side of it was placed an intact fly. I removed the egg alone from the cell, leaving two flies as they were. It was at 3.30 p.m. Two subsequent day, the weather was bad and I examined the nest on the 7th at 10.50 a.m. The surface of the sand plain was evenly smoothed by the rain, but the entrance of the nest had been already opened. Judging from the condition of the sand thrown out in front of the nest it was certain that the nest was opened on that morning. Without examining the interior of the nest, I closed the entrance and placed a pebble upon it. It was not moved throughout the day. I examined the nest on the 9th and 10th. But the pebble remained as before and no change was observed inside the cell. Probably the wasp stayed in the nest during two days of the unfavourable weather; but on the 3rd day she examined the cell before starting on her hunting excursion and knew that the egg had missed. Then she might search for it in sand and abandon the empty nest at last.

(5) Wasp No. 100. Aug. 12, 1948. The wasp was digging her burrow at about 10 a.m. At 10.30 she brought her first victim to the nest. At 1.00 p.m. I dug the nest from behind and found the wasp resting in the accessory branch. The brood-cell, however, was unfortunately dug out by my first shovelling and the egg together with the pedestal became unknown. I put a small fly in a glass-bottle and placed it at the end of the accessory branch. The next day at 12.30 I uncovered the cell. A small quantity of sand had been thrown in the cell. But the fly remained as I placed. The subsequent day, at 2.35 p.m. I saw the wasp eagerly sweeping out the sand from the entrance, but later she could not be observed at the place. In the interior of the nest, just at the place where the true cell had been, a new tunnel had been made. Probably when intended to examine the condition of the egg, she knew that it had missed and abandoned the nest after digging the original place in search of it.

The instances above given seem to indicate that the wasp would abandon the nest at last when it was deprived of the larva, though at times she brings more than one victim to the cell. It is supposed that such a blind action of the wasp is caused by her non-attending to her larva during the busy time of her provisioning work. According to the results, the hunting behaviour is sometimes released by the internal stimulus only. However, once the wasp notices the absence of her larva from the brood-cell, she usually searches for it by digging a tunnel in sand and at last, after a fruitless work of several hours, invariably abandons the nest.

c) *Experiments of removing the victim alone*

Although a considerably definite evidence seems to be collected already pertaining the mother-wasp's connection with her larva, I have performed further experiments with the aim of confirming whether, when the pre-stored food is removed from the brood-cell, she continues her provisioning activities to compensate the missing food, or ceases her work mechanically after gathering a certain amount of food prescribed in her innate schedule in the behaviour system. In order to show the results more clearly I select some experiments regarding chiefly the larvae of the 4th instar out of many that have been carried out. Because, the hunting activity of the mother wasps is most frequently conducted for the final instar larva which needs much food to eat.

(1) Wasp No. 59. Aug. 19, 1947. A simple nest, with a larva of the early stage of the 4th instar. Three eaten or partly eaten flies and seven untouched ones were in the brood-cell. I removed from the cell all the victims excepting one decapitated fly. I placed the larva and the fly in a glass cell and connected it with the end of the tunnel. It was at 11.28 a.m. At 2.30 p.m. I examined the cell and found 2 horse flies of the different species had been added in the cell. The next day I started on my journey and it was 10 days later that I reexamined the nest. In the cell there were remains of the 3 victims I had known and a rotten larva, indicating that the wasp stopped her work without doing any compensatory activiry for the lost food. But it was uncertain whether the wasp ceased her work automatically on account of the completion of the pre-determined amount of provisionment or she did so on account of noticng the death of the larva, or else whether the stop of the hunting activities depended upon the accidental death of the wasp. At any rate it was certain that the total amount of food she had collected was well fitted to her 4th instar larva.

(2) Wasp No. 60. Aug. 29, 1947. I saw the wasp carry in her burrow a booty of hunting at 11.43 and 12.00 respectively and dug the cell as usual. The larva was soon after the last moulting and was supplied with 10 prey, of which 2 were already eaten, another 2 were decapitated and the remainder were all intact. I replaced the brood-cell with a glass-bottle, putting in it the larva alone. At 0.05 p.m. the wasp was carrying out the dirts from the entrance, so I examined the cell. The larva had been supplied with one flower-fly placed by the side of it. At 1.10 I opened the sand-cover again. One further flower fly and one flesh fly had been added in the cell and the larva was feeding upon a fly. At 1.50 I knew 2 more flower flies had been taken in the cell. I removed 4 flies from the cell again, leaving only one that was being eaten by the larva. At 2.30 when I uncovered the cell, no further fly had been brought in the cell. Probably the wasp did not return since 1.50. At 5, things remained as before. It was rainy the next day (30th), but the sky was clear during a short period in the morning. On the 31st, when I arrived at the place at 9.00 a.m., the surface of the sand plain had been evened and smoothed by the rain of the previous day and no trace of the wasp's activity of the day could be observed. So I uncovered the cell to know the results of the wasp's work of the previous day. The larva grew to about 8/10 of its full mature size and was greedily devouring the remains of victims. On examining the remains, I knew that 4 flies had been added in the cell. Moreover, one bee-fly was found in the accessory branch that must have been made by the wasp after the arrangement of the bottle. I removed again all the remains and put in the cell the bee-fly. At 10.40 a wasp — probably the wasp No. 60 — was sweeping the surfane of the entrance. At noon I examined the entrance tunnel, which had already been permanently closed. In the cell no further fly had been collected.

This instance seems also to indicate that the wasp ceases her work when she has stored a certain pre-determined amount of food for the larva.

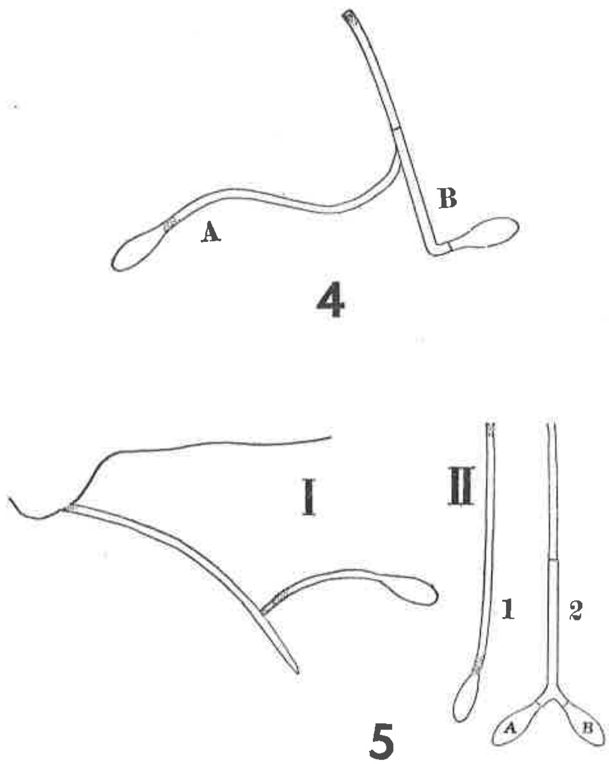
(3) Wasp No. 71. Sept. 4, 1947. I saw a wasp carry in her nest a booty at 0.50 p.m., and dug the cell from behind. The tunnel turned obliquely to the left near the brood-chamber and had an accessory branch at the turning point on the other side. In the brood-cell was a larva of the early stage of the 4th instar with a very rich store of food, namely 4 *Lucilia* of the large size, 4 *Eristalis cerealis*, 4 *Sarcophaga carnaria*, 2 some species of Muscidae of large size, 1 *Eristalomyia tenax*, 1 *Tabanus mandarinus*, 1 *Heterochrysops mlokosiewiczi* and 2 already eaten flies (*Syrphus corollae* and a species of Muscidae). Summing up the victims were 19 in number. Judging from the number and the size of the flies the provisioning activities of the wasp were supposed to be just about to complete.

I put in a glass bottle only the remains of 2 flies and the larva, and connected it with the end of the straight gallery. At 1.53, the wasp came back with another prey. After spending one and a half minutes in the tunnel, she appeared in the cell head first and empty-handed. She came straight to the larva, touched it with the antennae, turned around at once and went in the tunnel. A minute later, she came again empty-handed to the larva, touched it once more and went back. In her 3rd entrance she came backing with the prey, holding it with her mandibes by the neck, placed it at the entrance of the cell and at once went out. I covered the cell with sand. At 1.27, the wasp was observed taking in a new prey. At 3.30, the wasp carried in another prey. At 4.00, in the cell were found the three victms added, namely 2 flower flies and 1 Tachynid fly of the large size. The next day, unfortunately the nest had been invaded by a host of the small red ant, *Solenopsis fugax*.

Though still incomplete, this instance seems to show somewhat the compensatory activity of the wasp.

(4) Wasp No. 104. Aug. 14, 1948. I dug the nest at 1.30 p.m. It was as shown in Figure 4, A. I changed the disposition of the tunnel and cell by means of a glass-tube and a glass-bottle into the states shown in the same Figure, B.

The larva was in the early stage of the 4th instar. The victims were 12 intact and 5 eaten flies. I left the larva with a single decapitated fly in the artificial cell and removed all the others from the cell. At 2.55, a pebble placed on the entrance closure had been moved, showing that the wasp entered the nest. At 3.42, the same occurrence was also observed. On examining the cell, however, I could not find any other fly taken in. The next day, I saw the wasp carry in a prey at 11.58 and 12.00 respectively. At 0.05 I uncovered the cell and found 10 flies had been brought in the cell. The larva had grown larger, attaining about 6/10 of the full-mature size. I removed again the victims from the cell, excepting for a single fly that was being eaten by the larva. At 0.07 and 0.12, the wasp carried in a prey respectively. At 0.25, she was closing the tunnel by means of the permanent closure.



Figs. 4 and 5. Nests and experimental arrangements of Wasp Nos. 104 (Fig. 4) and 138.

In this instance, when the wasp entered the nest empty-handed at 2.55 and 3.42 p.m. on the 1st day, it seemed that she intended to make the permanent closure of the nest*. The number and the quantity of the prey stored in her own cell seemed to permit such a consideration. However, she is supposed to notice that the victims offered in front of the larva were too scanty to close the nest and to resume the hunting activities. Judging from the store of 17 flies in her own cell, the number of 10 flies brought in anew in the glass cell is too superfluous to be regarded as a normal course of her remaining work. On the other hand, when I deprived the larva of its prey for the 2nd time, she did not make any marked compensatory work. Probably at that time, the wasp was performing her last work of provisionment quite mechanically without attending to the larva, accordingly

* It was often observed that the wasp enters the nest empty-handed prior to the commencement of the permanent closure of her nest.

without noticing the lack of food before it.

(5) Wasp No. 115. Aug. 21, 1948. I had observed this wasp making the burrow at 0.15 p.m., on Aug. 17. When I dug the nest at 11.05, on the 21st, the nest contained a larva of the 4th instar that had just finished its moulting and 6 flies, of the latter one had already been eaten. Among the intact victims 3 were taken in on that morning at 9.05, 9.25 and 10.07 respectively. I replaced the posterior portion of the nest with a glass tube and a glass bottle and put the larva alone in the cell. While I was thus preparing, the wasp came back with a new prey. So I covered the entrance with a Petri-dish. She flew about and sometimes landed on the near-bye ground and at times on the vessel. Having finished the preparation, I removed the Petri-dish. She entered the nest at once and soon (about 15 seconds) appeared in the cell, head first. Then she touched the larva, turned around and went back in the tunnel as usual. The next moment the wasp came again backing with the prey, laid it down at the entrance porch and hurriedly returned in the tunnel. She emerged out of the entrance and showed an alarming attitude against the observer. So I covered the bottle and retreated a step backward. The wasp at once entered the nest. After she started on the next hunting excursion, I uncovered the bottle. The larva had been slightly shifted outward and placed at the centre of the cell, eating calmly the fly that had been brought by the side of it. At 0.47 p.m., one further fly was carried in and the wasp went off 3 minutes later. At 1.10 she entered the nest once more carrying a fly. At 3.40, on examining the nest only the three flies that I saw were found in the cell and the wasp was resting in the accessory branch. Two days later, on the 23rd, I dug the nest. It had been already completed and permanently closed. The larva had grown to the middle stage and 13 flies were stored in the cell, of which 4 were already eaten.

In this instance the wasp showed a tendency to the compensatory provisioning, since 13 flies are sufficient in amount as food for the 4th instar larva. The 6 flies that had been removed from the cell is considered to be placed out of account of her later activities.

(6) Wasp No. 137. Aug. 26, 1948. The wasp carried a fly in her burrow at 9.37 and 9.55 respectively. When she emerged I caught and marked her. At 10.08, she came back empty-handed. Three minutes later she went out. At 10.15, the brood-cell of the nest was opened from behind. It contained a larva of the later middle stage of the 4th instar and 19 flies (11 intact and 8 eaten). I replaced the cell with a glass bottle and put in it the larva and one fly. At 1.29, when I saw the nest the wasp was performing the permanent closure, On examining the contents of the cell, it was found that 4 flies were added, 2 of which were placed in the adjacent tunnel.

This instance shows clearly that once the wasp enters the final course of provisionment, she does not pay any attention to the states of the brood-chamber.

(7) Wasp No. 138. Aug. 26, 1948. At 11.00 a.m. when she was carrying out the sand from her burrow I caught and marked her. She did not return on that day. However, the next day at 8.20 she was at the entrance and was taking out the sand from the tunnel. During the work she pulled out remains of a fly from the inside. Meanwhile it began to rain and the wasp stayed in the nest, closing the entrance from the interior. When the shower passed she went on a foraging excursion and at 9.37 came back with a booty. At 11.29 she brought another prey to the nest. At noon I dug the nest. It was as shown in Figure 5, having a typical accessory branch. The wasp was resting in the tunnel before the accessory branch and stayed there during the work of my experimental arrangement. In the cell there

were a larva of the early stage of the 4th instar and 5 intact and 2 eaten flies. I cut off the posterior portion of the nest, including the cell and the accessoy branch and connected a Y-tube of glass with the end of the natural tunnel, putting at each end a glass-cell (Fig. 5, II, 2). In one of the glass-cells (A) I placed an *Eristalomyia* fly alone, while in the other (B) the larva and a flower fly of the same species. When I finished the arrangement the wasp came from the tunnel in the glass tube, but without entering the cell she turned round and went back. I covered the cell with sand.

The next day when I examined the cell it had already been permanently closed. Cell A remained empty and cell B contained the larva and the two flower flies that were placed the previous day. But the larva had been dead, probably owing to the slight wound given during my treatment. One of the prey must have been carried from cell A. It was uncertain whether the wasp completed her work normally and mechanically without taking into acocuut the death of the larva, or she stopped the provisioning activity according to the death of the larva, only closing the entrance tunnel automatically. However, the fact that comparatively small number of flies stored up to that time in the cell seems to support the latter consideration.

(8) Wasp No. 154. Sept. 6, 1949. At 10.00 a.m., I dug the cell. The nest was of the simple type and in the brood-chamber was a larva of the later middle stage of the 4th instar. Eaten prey were 6 in number, while the untouched ones 8. I put the larva alone in a cell of glass and placed it as usual at the end of the tunnel. At 1.50 p.m. 8 prey had been stored in the cell. I removed all the prey but one. The next day when I examined the nest it had already been premanently closed. In the cell nothing of the victim but the pre-existed one was found.

This instance, too, seems to show the automatic activity of the wasp toward the end of her work.

d) *Summary of the results*

1) When the contents of the nest are all removed, the wasp, after searching for the missing objects in sand by digging a tunnel, sooner or later abandons the nest, without gathering food further.

2) However, in case the wasp has already carried a booty in her tunnel before taking notice the event occurred in the chamber, she always continues to take the victim in the empty cell, although she examines the brood-chamber in advance.

3) Sometimes, however, there were instances in which more than one fly (at most two) was carried in the empty cell. Probably such a result is effected by the fact that the wasp works during the time without examining the contents of the brood-cell.

4) When the larva alone is removed from the brood-cell, either without touching the prey stored in it, or with the number of the prey eliminated, the results are much the same as in the above case.

5) In no case, however, the wasp utilizes such a nest as a second nest to lay her second egg, but always abandons it.

6) When the victims alone are all removed from the brood-cell, or markedly diminished in number, the wasp, as a rule, continues her provisioning activities, sometimes even compensatorily so for the missing food.

7) However, towards the end of her work, while she is gathering the last store of food, or she has finished her provisioning activity, she usually performs only the rest of her predetermined work, quite ignoring the event occurred and closes the tunnel as usual, even when she examines the interior of the nest prior to the permanent closure.

The above results will be sufficient to show that one of the most important external releasors of the hunting activities of *Bemax* is the presence of the larva in the cell.

2. Structural conditions of the nest

Even in the above experiments more or less change of the environmental conditions of the larva has been introduced not only regarding the food condition but also concerning the internal structure of the nest. In the present series of experiments the inner structure of the nest, chiefly the form, has been markedly altered. The chief aim of the experiments is to study how far can the structural conditions of the nest exert an influence upon the releasing value of the larva. From another point of view, it can also be said that it is to investigate the influence of the change of the larval environment upon the mother-wasp's recognition of her larva. Accordingly it also involves the question as to whether or not the structural condition of the nest is firmly fixed in the memory of the wasp, quite in the same manner as in the absolute location of the entrance to her nest.

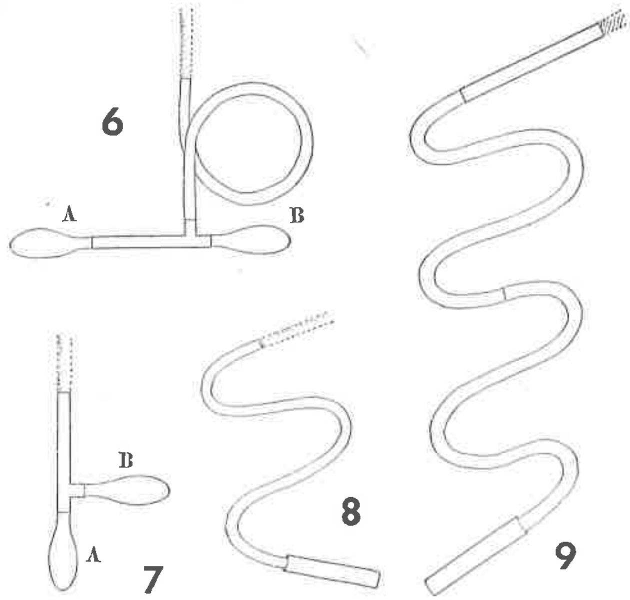
a) *Experiments on the change of the tunnel*

(1) In two of the instances mentioned in the previous section, namely in Wasp Nos. 104 and 138, a considerable change was introduced respectively in the arrangement of the tunnel and the cell. In both cases, however, judging from the final result, no decided confusion which seemed to be provoked by the change of the structure of the nest did not occur upon the behaviour of the wasps.

(2) Wasp No. 73. Sept. 7, 1947. When I found this wasp she was patiently searching for the entrance to her nest which had been disturbed by trampling of the cattle. At last at 2.40 p.m., after an effort of about 2 hours and a half, she could discover the entrance to her nest. She entered there but soon came out, closed the tunnel temporarily and went on her foraging excursion. One and a half minutes later, she returned carrying a booty. At 2.50, I dug the cell. It was situated at the end of the straight tunnel of about 30 cm in length. In the chamber were 4 victims and a larva which was probably in the 2nd inster and attached still to one of the flies. It was eating the 2nd fly that was placed by the side of it, across the thorax of the pedestal fly, without eating the latter. I shortened the tunnel into 20 cm and set at its end 1 circular and 1 branched glass-tube with two bottles attached to the apices. The arrangement was as shown in Figure 6. As a result, the tunnel leading to the cells became more than 70 cm in length. I put in both bottles a larva and 3 prey respectively. The larva in bottle A was the rightful master of this nest, while that in bottle B was derived from another nest and similarly of the 2nd instar. The next day it was rainy and cold; the inhabitants of the colony were supposed to pass the day inactive. The subsequent day the weather recovered. At noon I saw the wasp sweeping the sand at the entrance to her nest. At 2.00

p.m., I examined the nest. In the glass tube a small amount of sand had been brought in, indicating that the wasp entered it. But no change had occurred in both cells either on the larva or on the prey, with the exception that the larva in B was dead. Probably the wasp entered the glass tube, but on account of its extraordinary change she did not reach the cells. I covered the nest and left it alone.

The subsequent day, at about 11 a.m., the wasp was actively carrying out the sand from the entrance of her nest. At 1.00 p.m., she was still digging the burrow. So I dug the nest. The wasp was burrowing a tunnel just beneath the experimental instruments to search for her original cell. The circular tube was packed thickly with sand at its anterior end and the new tunnel was originated from that point. Not the least change could be observed in both cells. Probably the wasp, having felt something unusual, ceased to pass through the glass tunnel and began the search digging.



Figs. 6-9. Experimental arrangements of Wasp Nos. 73 (Figs. 6 & 7), 74 (Fig. 8) and 79.

It was made out that the extraordinary change of the tunnel rendered the wasp cease to pass through it. In other words, this is a positive evidence for the fact that the wasp has some sort of memory regarding the inner structure of her nest.

I then removed the circular tube and altered the arrangement as shown in Figure 7. The contents of the cells were unchanged. At 3.10 p.m., I uncovered the cells and knew that the wasp entered the cells. The prey had been taken in and a larva had been transported from one cell to the other. The subsequent procedure will be described in connection with other problem.

(3) Wasp No. 74. Sept. 7, 1947. At 3.20 p.m., I dug the nest from behind and found a cell at the end of the straight tunnel, 23 cm long. In the cell there were a larva of the 3rd instar and 2 intact and 1 eaten flies. The wasp was resting in front of the tampon of the cell. She was frightened at my digging and fled away from the open end of the tunnel. Soon, however, she returned, entered the burrow from the entrance and rested as before. I connected a deeply bisunuated glass-tube with the open end of the tunnel and placed at its end an usual tube bottle of 12 mm in diameter (Fig. 8). In the bottle the larva and two dried flies were placed. As a result, the tunnel was changed not only in curvature but also in length, elongated by about 30 cm. The weather became cloudy and the wasp's work was stopped. It was rainy the next day. On a third day it was fine. At 0.30, I saw the wasp carrying out the dirts from the burrow. Ten minutes later I uncovered the nest. The larva was at the

anterior end of the chamber and the prey were left at the posterior end. That is to say, no change had occurred upon the contents of the cell. Probably the larva, having been incapble of eating the drying-up flies, abandoned them and proceeded forwards in search of food. It had hardly grown any more and stayed in the 3rd instar, possibly owing to the starvation. Judging from the result it seemed doubtful that the wasp entered the cell. At 0. 40, however, when I saw the nest the wasp was struggling in confusion in the glass-cell which I happened to forget to cover. So I placed at once a handful of sand on the cell. But I left carefully a small window in the sand and through which I peeped in the cell. The wasp was about to go backing into the tunnel, capturing the larva between her legs. Thereafter she stayed in the tunnel till 0. 55, when she emerged from the entrance. But at once she turned round and went in again. Soon she came out, closed the door-way without hesitation and flew off. I uncovered the cell. The larva had been placed by the side of the uneatable victim in the cell.

I then exchanged the larva for another that was obtained from wasp No. 75, namely the larva in the 4th instar, having the body length of about 20 mm. It was about twice as large as the true larva of the nest. At 1. 07, the *Bembix* came back carrying a booty and entered the nest. She soon came in sight in the exposed cell, empty-handed and head first. She touched the larva with her antennae and went back in the tunnel. As it is usually the case that the next moment the wasp appears again dragging the prey backward in the brood-cell, I expected to see such a scene. But when she appeared again, she was empty-handed and came head first. She examined the larva with her antennae once more and returned in the tunnel. Strange to say, she then appeared outside the nest, but at once turned round and entered the nest. She came again in the cell, but this time, too, she brought nothing. There, she touched the larva, caught it between her mandibles and moved it a little. Again she hurried away in the tunnel, but, when she reappeared in the cell, she was still empty-handed. The same manoeuvre was repeated once more. During the course, the wasp invariably touched the larva every time she entered the brood-cell. The manner of her hurried return to the tunnel was sufficient enough to make us suppose how strongly stimulated she was to bring a victim the next time to the hungry larva. But, the wasp, when she returned in the tunnel, always passed through it and emerged from the entrance in the open air. There she turned round in a puzzling manner and hurriedly came back in the burrow. Despite the fact, when she appeared in the cell, always did she bring nothing. I thought that it might occur on account of the unnatural condition that the cell was exposed to the daylight; so I covered the cell with sand. The wasp stayed a while in the nest, but soon, at 1. 15, came out and this time closed the entrance and flew away. On examining the cell, however, I found that nothing had been brought in it. Where is the fly that the wasp carried in a little while ago ?

At 1. 27, the wasp came back with another victim. Uncovering the cell, I waited for her coming in. Soon she appeared head first in the cell, touched the larva as before and returned as usual. But, when she reappeared there for the second time, she again did not bring the fly. She touched the larva and hurried away. She returned once more in the cell, but again no fly was transported by her. I covered the cell with thick layer of sand and left the wasp alone. At 1. 42, the wasp dragged in a third fly to her nest. I uncovered the cell. It contained nothing except for the dried-up flies. The wasp came in, touched the larva and hurriedly returned away as before. I covered the cell again. While I was observing another nest, I kept my attention to the nest. The wasp was seen appear out of the nest, but soon entered again. Supposing that the same manoeuvre was being repeated, I went to the nest and uncovered the cell. Nothing had been added in the cell as before. Just at that moment the wasp came in and again repeated the same behaviour. At last, the wasp appeared at the entrance, closed there and flew away. In order to know whether or not the 3 victims had been laid down in the tunnel, I uncovered from behind the sinuated glass tunnel as far as possible. But not a shadow of the fly could be seen. I covered it again. At 2.30, the wasp carried in one more fly. But, she did not bring it to the brood-cell, although she repeated twice again the same queer manoeuvre as before. At 2.55, the entrance to the nest was closed. I examined the cell and found that the larva and one of the dried flies had been missing from there. However, they were discovered in the glass-tube only 5 cm in front of the cell. The hungry larva was trying to gnaw the hardened victim. At 3.00, I uncovered the glass-tube throughly, but, there was no trace of the flies newly brought in by the wasp. Finally I dug the nest from the entrance. But in her own sand tunnel, too, the 4 flies in question could not be discovered. I removed the glass-tube and dug the place from behind. In the sand I found 2 *Eristalis* which were, no doubt, the victims that I had observed carried in. At that moment, the sand fell down and it became impossible to find the remainder of the flies. But it seems clear that the wasp dug a new tunnel in sand in the same place as her own gallery had been.

In my previous work in Japanese (The study on the behaviour in Bembix, Sapporo, 1948), I have tried to interprete the procedure of the events as follows : "The wasp, after digging her new tunnel and, probably also the cell in sand in the same direction as her original tunnel, might quite mechanically gather food there, though there was no larva to be fed in her new burrow. The stimulus necessary for her provisioning activities must have been obtained from the contact with the larva placed at the end of the bisinuate tube by me. It must have been accelerated by the hungry condition of the larva. But when she entered the nest carrying the prey, she was guided by the strong memory concerning the direction of her own original tunnel and dragged it in the new burrow made by herself. But later when she entered the glass tube either in the course of her wandering in search of the larva or merely by accident, she found the larva there. She felt the impulse to bring a victim to it and returned in the tunnel with the intention of fetching the fly. However, it had already been stored in her new burrow and, in addition, the place had probably been closed mechanically at its entrance. Therefore, she could not find the fly in the tunnel and emerged eventually from the entrance in the course of her search. There she was puzzled and came back in the nest again. Her behavlour shown thereafter was nothing but the repetition of the visit to the larva and the search of the victim to be brought to it until she noticed that the victim was missng from the tunnel and it had to be hunted in the field. Then, she closed the tunnel temporarily and went on the foraging excursion. In short, this strange manoeuvre of the wasp must occur as a result of the spatial separation of the biologilcal signficance of the brood-cell — a significance as the place of the larval residence (= the source of activity of the wasp) and a significance as the place to store food. The sole factor that resulted in such a queer division must be the memory of the wasp on the direction of her original tunnel !"

According to my present knowledge, however, my previous opinion mentioned above must be corrected in some important points. This is chiefly the consideration regarding the cause of the spatial separation of the significance of the brood-cell. In reality, I do not believe at present such a consideration. The occurrence observed must be only a result of an accident. In fact, to explain the phenomenon, there is no need to demand the intervention of the memory of the wasp concerning the direction of her original tunnel. The only cause that the victims were transported in her own tunnel seems to lie merely in that the tunnel can more easily be entered by the backing wasp than the glass-tunnel. Accordingly, the procedure of the events can be accounted for as follows : "When the wasp entered the nest with a prey, she soon laid it aside in the tunnel and came straight to the brood-cell or came there after visiting her burrow. (Because in her burrow there was no larva and this stimulated her to search for it.) There she touched the larva and returned in the tunnel to bring the prey. While she dragged it backwards, however, her hind legs took the easier course to enter and led her into the tunnel of sand. This must be done quite mechanically against her intention. There she dropped the prey, but having been unable to find the larva she began to search for it in the tunnel. During the course, she came to enter the glass-tunnel and found the larva". The subsequent behaviour of the wasp will correctly be explained by the accounts given in my previous work. One question, however, remained still unsolved. Why did she not retransport the victim that she had carried to a wrong place to the rightful larval cell ? Such a retransportation of the prey to the correct postition is uually observed upon many individuals of our species under similar experimental condition.

Apart from the explanation of the behaviour of the wasp, however, this instance has brought to me two kinds of important evidence regarding the influence of the change in the nest structure. One is that the wasp continued her work inspite of the marked change occurred on the structure of the tunnel. The other is that the wasp searched for her missing chamber in sand in the same directoin as her original tunnel had been.

(4) Wasp No. 79. Sept. 10, 1947. At 1.00 p.m., I dug the nest from behind. It was simple in structure, containing a larva of the 3rd instar and 4 flies, of which 1 had already been eaten. I placed a trisinuate glass-tube at the end of the tunnel and connected with its extremity a glass bottle (Fig. 9). As a result, the tunnel was lengthened by about 80 cm. In the bottle the larva with 3 intact flies was placed.

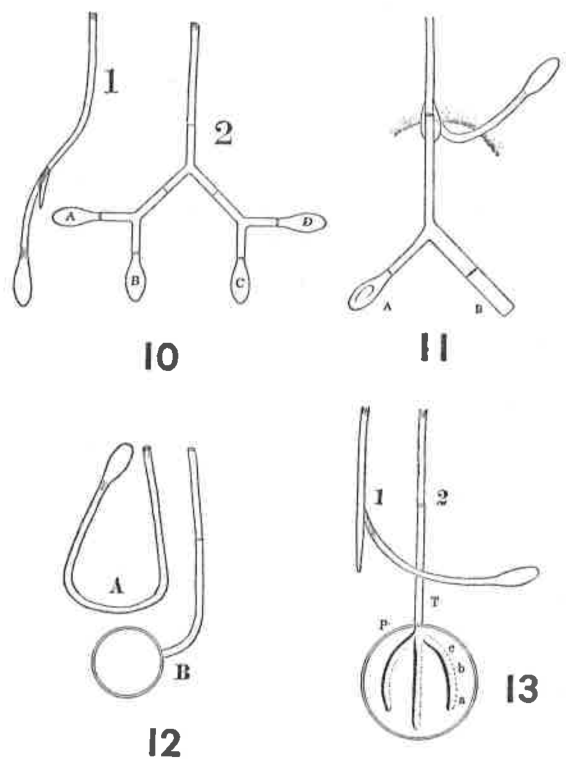
At about 3.00 I saw the wasp enter the nest without carrying a fly, but I did not examine the cell. The next day at 11.15 a.m., I uncovered the cell. The larva had just finished its 3rd moult and was about 14 mm in length. The victims stored in the cell were 4 intact, 2 decapitated and 2 eaten flies, that is to say, the mother wasp carried at least 5 victims to her larva through such a long, smooth und unnaturally waved tunnel.

Judging from the result, the wasp seems not deeply influenced by the striking change occurred on her tunnel.

(5) Wasp No. 93. Aug. 11, 1948. The structure of the nest seen from above was as shown in Figure 10, 1. The experimental arrangement set by using 3 Y-tubes and 4 glass-cells was as shown in the same figure, 2. The larva was soon after hatching out, attaching still to the pedestal fly with its caudal end. No more fly had been brought to the cell. I put

the larva with its pedestal in cell D. At 9.15 a.m., while I was engaging in this preparation, the wasp came back carrying a booty, so I drived her away. Having finished the arrangement, I covered it with thick layer of sand and left her alone. At 1.15, when I examined the nest not a single fly had been taken in the burrow. As the larva, extending and moving its body, was eagerly seeking food to eat, (seeking other than the pedestal !).I placed 2 paralyzed flies about it. At 5 o'clock no change had occurred in any of the cells. The next day, I examined the nest at 11.00 a.m. A pebble which I placed on the entrance was not moved and it was clear that the wasp did not enter the nest. Probably the wasp, having been unable to find her larva owing to the mazy change of the tunnel, abandoned the nest in the end.

(6) Wasp No. 103. Aug. 14, 1948. The tunnel of this nest ran straight for about 25 cm, then turned slightly to the left and ended in a chamber. The larva had just moulted its 3rd instar skin and the victims supplied were 4 in number, namely 2 intact and 2 eaten or partly eaten flies*. I altered the interior of the nest as in the preceding instance and put the larva and a victim in cell B, while in other cells only a victim was placed respectively. At 10.20, the wasp came back empty-handed and, after sweeping the sand in front of the nest a little, flew away. Three minutes later, she returned again, but without capturing the prey, and flew off after raking the surface a little as before. At 11.50, she came back once more bringing no victim, but this time she entered the nest. I opened the instruments at the first branching point and waited for her coming. But, for ten minutes she did not come. Probably she rested in the tunnel. So I covered the nest. At 4.00 p.m., I examined the nest again. Not the least change could be observed in any of the cells. The next day at 1.00 p.m., I went to the nest. In front of the entrance had been thrown out a considerable amount of sand, but the cells remaind without change. The larva had already eaten up the fly and was at the entrance portion of the cell. It lifted its anterior



Figs. 10–13. Nests and experimental arrangements of Wasp Nos. 93 (Fig. 10), 124 (11), 107 (12) and 108 (13).

* It will be worthy to note here that the largest and the hardest fly (*Eristalomyia tenax*) of all the victims had been eaten most. The partly eaten fly (*Eristalis cerealis*) was the pedestal of the egg. Remaining two were the same species as the pedestal and were supposed to be taken in on the morning of the day.

body, drooping its head and was sitting still, as if to wait for the mother wasp to bring food to eat — a posture of the larva always observed when it is hungry and there is no food to eat in the cell. Judging from the developmental degree of the larva it was the time of hard labour of the mother wasp to gather food for her greedy young. However, the wasp did not return until 3.00 p.m., when I took up the larva to use for another experiment. The arrangement was left as it was for two days further. Not a trace of the wasp's activity, however, could be seen upon it. But when I removed the arrangement, I found a short tunnel dug below the first Y-tube. Accordingly it became evident that the wasp abandoned the nest after searching for her own burrow in sand.

(7) Wasp No. 124. This experiment was first planned with the aim of investigating the capacity of discrimination of the wasp with regard to the broadness of the tunnel. But in the result it finished as an experiment concerning the change of the inner aspect of the nest. As the instance contains some interesting observations pertaining not only to the problem concerned here, but also to the general biology of the species, a thorough description will be given below.

I saw the wasp digging her burrow on Aug. 16, 1948. On the 21st of the same month, at 9.33, she brought a victim to her nest. On her emerging I caught and marked her. At 9.40, she returned empty-handed and entered the burrow. I dug the brood-cell at 10.10. I searched it carefully from behind, but by some reason or other, I could not find it. I thought it was dug out at a scoop of my small shovel, so I examined more carefully the dug-out sand. But not a single victim could be found. However, I found the continuation of the entrance gallery at a distance of 15 cm from the orifice. Therefore, I placed at this end a Y-tube of glass, the branches of which were different in diameter from each other, with a bottle at each extremity. I put a larva of the early stage of the 4th instar taken from other nest (because, judging from the activity of the wasp, the larva of this nest was supposed to be in such a developmental stage) together with 3 flies in the end-bottle of the broader branch (B) and arranged it on the right side, while the end-bottle of the narrower branch (A) was left empty and placed on the left side.

At 10.15, the wasp came back holding a large bee-fly between her legs. But at the entrance she showed a manner of surprise (probably caused by the sudden resistance of the imperfectly paralyzed victim), stopped her work of opening the entrance, flew up with the victim and went off. She alighted on the ground 10 meters away from the nest but discarded the fly and flew away. At 10.55, however, she returned with another victim and took it in the nest. At 11.07, she brought a 2nd prey to her nest. At 11.27, a third. I examined the nest at 11.40. In the broader bottle containing the larva, 3 victims had been brought, while in the other nothing. Having learned 3 times to enter the tunnel leading to the brood-chamber, I turned the basal axis of the Y-tube through 180°, so that the broad tunnel together with bottle B came to the left and the narrow tunnel with A to the right. I left the nest alone, but I covered the entrance with a Petri-dish of 10 cm in diameter while I was obsering other nests, lest the wasp should enter without being observed. When I saw the nest 0.10 p.m., the wasp had returned and was alighting on the Petri dish. She was rubbing the surface of the glass with her front pair of legs in the manner ot sweeping the sand, with a fairly loud fricative sound. I removed the vessel to let her in. Uncovering the dichotomous point of the tunnel, I waited for the wasp coming in, to ascertain which way did she select. But the wasp did not appear. I waited with patience for 20 minutes, but she did not come in sight of me. At first when the wasp entered the burrow the sound "dzi ! dzi !" was heard from the interior of the tunnel, the sound that the wasp used to make when she approaches the brood-chamber. However, soon after it also ceased. So I inserted a stalk of grass in the tunnel from in front. The wasp was, without doubt, in the tunnel and answered with a buzzing sound. As I thought I would repeat the experiment from the first, I turned the basal axis of the Y-tube and rearranged the instrument as before. The wasp, keeping herself out of sight, pushed out the sand from the nest from time to time to the entrance orifice. At last I covered the arrangement with sand and left her alone. While I was observing the behaviour of other wasps, however, I gave my attention from time to time upon the nest. The wasp was seen carry in a fly at 1.57 and 2.03 respectively. At 2.06 I went to the nest and examined the arrangement. At that moment the wasp came entering the tube. She came in the narrow tube but before reaching the cell turned round and went back. So I covered the portion of the cells with sand, lest she should fall into confusion. Soon she came again in the same tube as before, but this time arrived at the cell, turned round in the cell and went back in the basal tube. Since then she did not come in sight of me. I examined the contents of both cells and found that a fly had been brought anew in cell B, but cell A was empty as before. However, nowhere were there that 2 victims at least which I saw carried in by the wasp. I removed from cell B all the victims but one. At 2.27 the wasp took in another fly. At 2.47, she brought a large flower fly (*Eristalomyia tenax*), but she was escaped by the victim at the entrace to her nest. She rushed following the run-away, but failed in recapturing it, came back and rested on the near-bye ground.

At 3.40 I uncovered the arrangement. Not the least change had occurred in both cells. So, I removed the instruments and dug along the tunnel forward. A pocket of considerable size was found at the end of the natural tunnel, just beneath the beginning of my glass tube. In the pocket were accumulated 4 victims which had been taken in. I enlarged the excavation and at last succeeded in finding the apical portion of the true tunnel of the wasp. I followed it to find the larval cell at the end. The tunnel which I could not find at first was strongly curved, turning at an angle of about 150° and at last went obliquely forwards (Fig. 11). In the chamber, as I supposed, was a larva of the early stage of the 4th instar which was as large as that which I placed in cell B. The victims stored were 5 in number, including 2 eaten flies. This discovery fully explained the strange events that I had observed. Possibly the wasp was unable to go to the brood-chamber of her own since I set the experimental device. Perhaps she received the stimulus necessary for her provisioning activity by the contact with the larva placed in cell B. Even one of the victims hunted by her was brought in that unnatural cell. Later, however, she dug the pocket by some reason or other and since that time onwards the victims taken in were all stored there, quite mechanically without the immediate connection with the larva. The procedure is apparently similar to the case of Wasp No. 74, but is different in one important point from that. That is, in this instance the wasp did not strive to bring the victim to the larval cell.

I rearranged the instruments as before at the end of the shortened tunnel, placing cell A on the left and cell B on the right. In cell B, as before, I put the substitute larva with 2 intact victims. At 4.10, the wasp carried in a victim. But she did not appear in the tube, making only fricative sounds in her own tunnel; then she emerged from the entrance and swept the surface of the ground. She entered again, but a moment later went out once more. Having supposed that the entrance of the tube was plugged with sand when I connected it with the end of the natural tunnel, I pulled it out a little. At once the wasp came in. She entered cell B and touched the larva and examined it with the antennae, holding it beween them. Then she grasped it between her mandibles and altered its orientation a little; next she touched it again between her antennae as if to measure its size. Meanwhile she felt the light and began to struggle against the glass wall in confusion. So I stopped the observation and covered it with sand. After a while I unearthed the cell. A bee-fly had been brought by the side of the larva and the wasp had gone in the tunnel. Thereafter she stayed in the tunnel, probably to pass the night.

Two days later when I arrived at the colony of the wasps at 8.20 a.m., the wasp was eagerly digging the sand in search of her nest. Because, her nest, together with all others that were under my experiments had unfortunately been dug over the previous day, possibly by an idiotic herdboy who had been observing my behaviour a couple of days before. I examined the nest and knew my arrangement of glass instruments had been entirely disordered. I dug out with care the tube and the cells and could find the larva still alive in the narrow aperture left in cell B which was stuffed with sand. By the side of it were also found the remains of 2 flies. At 9.30, the wasp was still digging in search of her brood-cell. As the entrance of her nest remained undamaged, I examined her tunnel from behind and found that it was not destroyed for about 15 cm. So I tried to place at its end the instruments of glass as before, placing the larva alone in cell B. The wasp soon came in the tube without hesitation, touched the larva which already reached the middle stage of the final instar and hurriedly went out. I covered the nest. At 9.42, she came home carrying a booty. At 9.56, ditto. At 10.15, I examined the cells. Cell A remained empty, while cell B had been provisiohned with 4 flies, of which 2 were placed by the side of the larva and others at the entrance portion. I removed the 2 flies that were placed near the entrance in the cell. At 11.08, 4 flies further had been added in the cell, all being placed at the entrance porion. I then altered my experiment to another relating to the change of the larva. The process of the later experiment will be described in another connection.

Generally speaking, this instance seems to give evidence that even a considerable change of the inner structure of the nest did not affect essentially upon the behaviour of the wasp, unless the larva was removed from the nest. In one point, however, the behaviour of this wasp is very questionable. It is the behaviour regarding the provisionment in the empty pocket made by her just in front of the glass tube. Probably this pocket was made during the time when the entrance of the tube became indistinct owing to the slight change of its location and eventual closure of the place by the 2nd experiment. But later when I replaced the instruments as before, the passage was cleared and in fact the wasp came through the tube in the cell at first. Nevertheless, not only she did not try to retransport the victims to the larval cell, but also she would not come to the cell thereafter. But she continued to gather food in the pocket without the larva, without the stimulus arising from the contact with the larva.

b) *Experiments on the change of the brood-cell*

(1) Wasp No. 107. Aug 15, 1948. The strurcture of the nest seen from above was shown in Figure 12, A. In the chamber were a larva of the early middle stage of the 4th instar and 5 intact and 5 eaten flies. While I was digging the brood-cell, the mother wasp came back with a fly and flew about in the neighbourhood. I took a curved glass tube and a Petri dish, 10 cm in diameter and 1.5 cm in height, and arranged them as shown in the same figure, B. The Petri dish was perforated at the lateral wall so as to be connected with the end of the

tube. It was turned over with the bottom upward, so that the chamber, or rather the hall, came to have a sand floor as in the natural state. The larva was introduced at the opposite end to the entrance, with 1 half-eaten fly. It was at 10.40 a,m. Having finished the preparation, I retreated a step backwards to let the wasp in, leaving the arrangement exposed to the diffused daylight. The wasp at once alighted in front of the nest and hurried in the burrow. After carrying out the sand several times from the burrow, she passed the glass tube without hesitation, sweeping as usual, and proceeded in the Petri-dish. She walked about in the hall slowly and rather hesitatingly with her antennae trembling. Meanwhile she touched the larva, stopped her steps and examined it carefully with the antennae. She then left the larva, walked about, again touched the larva and examind it carefully once more. Then she felt the light and was thrown into confusion. So I covered the vessl with sand. After a while the wasp appeared at the entrance and darted off madly on the wing, without closing there. I doubted if she would come back again. But I closed the entrance myself and placed a pebble upon it.

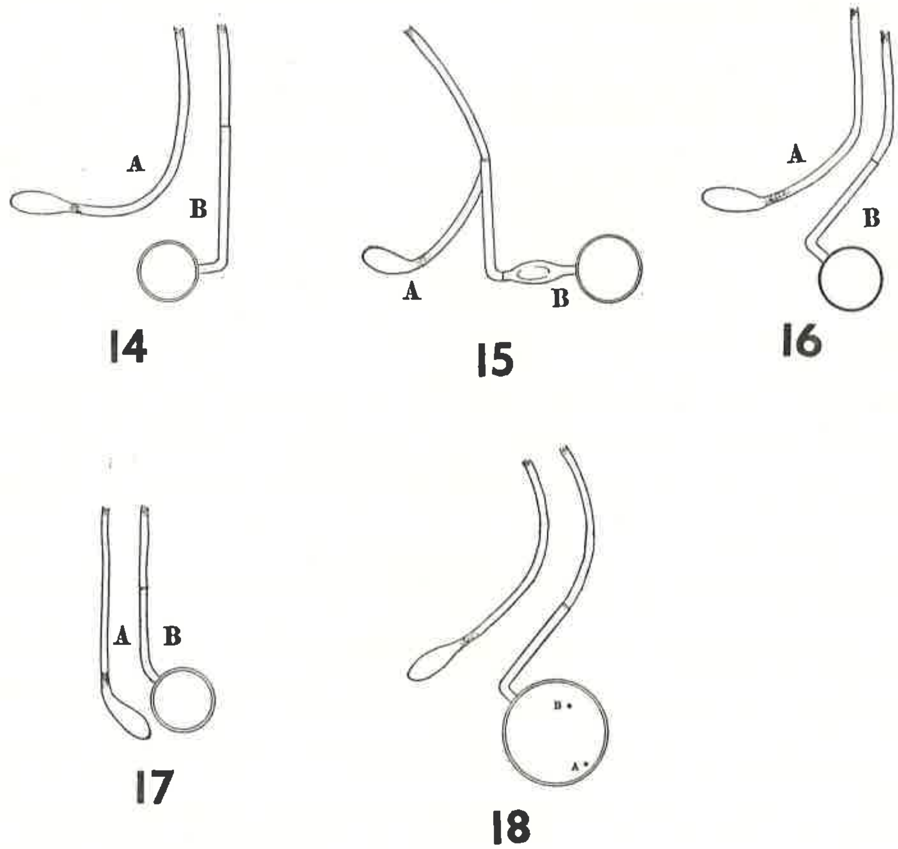
At 0.12, when I saw the nest, however, the pebble was stirred and the entrance was left opened. I awaited the wasp to come out, but she did not appear for 3 minutes, so I uncovered the Petri dish. To my surprise, in the chamber 3 flies were already brought in by the side of the larva and the wasp was resting in the chamber near the entrance, directing her head towards the larva. But she was excited soon by the light and began to fly about in confusion. I covered the vessel with sand. At 2.55, I examined the nest and 9 flies had heen accumulated around the larva, one of which had been already eaten. As I could ascertain that the wasp entered the nest, despite of the marked change of the brood-cell, I then introduced another larva in the cell so that the wasp might rear 2 larvae at a time. The wasp, irrespective of the 2nd change, continued to bring food to the cell.

This instance seems of interest in two points. 1) The wasp, though seemed to be puzzled at first by the striking change of the inner structure of the nest (flew away madly without closing the entrance), nevertheless, continued to bring food to the larva. 2) The victims taken in the nest were all transported by the side of the larva, inspite of the broad space of the brood-chamber.

(2) Wasp No. 108. Aug. 15, 1948. I dug the cell at 3 o'clock in the afternoon. The wasp was observed twice carry in a fly from the morning. The structure of the nest (seen from above) was as shown in Figure 13, 1, and the experiment arrangement set by me was as shown in the same figure, 2. When I opened the nest, the wasp was sitting in the tunnel in front of the accessory branch. The larva was very little, probably in the 2nd instar, attaching still to the pedestal fly. The victim stored were 3 in number, one of which was the pedestal and it had already been half eaten. In the Figure, T is a glass tube, 20 cm in length and is connected with the end of the straight portion of the natural tunnel. P is a large Petri-dish, 20 cm in diameter, 3 cm in height and is perforated at the brim, so as to enable the insertion of the end of the tube. The sand floor of the broad hall was flattened and 3 shallow canals were grooved on it from the entrance. The end of each canal was slightly enlarged into a pocket and in one of which (c) were put the larva and all the victims. These canals were intended to help the wasp to find easily the exit. The next day at 11.15 a.m., I uncovered the nest. In no place within the nest could be found the larva. The flies placed with it had been scattered in the canal leading to the exit of the chamber. Prodably the larva was dragged out of the nest and rejected by the mother wasp. That the result was not produced by the invasion

of some carnivorous insect was clearly indicated by the presence of the flies in the chamber. To account for the result, there seems to be no proper reason other than the confusion occurred in the wasp by the extraordinary change of the inner strucrure of the nest.

(3) Nest No. 110. Aug. 16, 1948. The wasp was burrowing in sand in the afternoon of the 13th. The egg was probably deposited on the same day. I dug the nest 3 days later at noon. The nest and the experimental arrangement were as shown in Figure 14, A and B. The larva had just hatched out at the time of the examination, and stood upright still, without touching its mouth to any of the victims. The victims were 2 in number and one of them was the pedestal of the egg. As for the arrangement, the glass tube was 10 cm in length and the Petri-dish 5 cm in diameter and 1.5 cm in height. The larva and the victims were placed at the innermost portion against the entrance of the vessel. At 1.55 p.m., the wasp came back with a fly. But as the surface of the nest was somewhat disturbed, she failed to



Figs. 14 - 18. Nests and experimental arrangements of Wasp Nos. 110 (Fig. 14), 113 (15), 123 (16), 129 (17) and 113 (18).

penetrate and began at once to search for the entrance. During her work, the fly was dropped from between her legs, but she showed a strong concern for the fly every time she happened to touch it. In such a case, once the fly has dropped from her legs before carrying it in the brood-cell, the wasp, as a rule, becomes quite indifferent to it. At last the wasp succeeded in finding her way and entered the burrow. Soon she came out head first, caught the dropped fly by the neck and dragged it backing in the tunnel. At once she emerged from the entrance, turned round and again went in. Later she did not come out until 2.15, when I left the place without examining the interior. The arrangement was uncovered at 10.15 a.m. of the subsequent day. Within the Petri dish, however, was found a green bottle fly alone which I had seen carried in. The larva and the 2 flies had been transported to somewhere outside the nest. The entrance had been left opened. I opened the glass tube and also the natural tunnel of the wasp. In the former, in its outer half the sand was fairly compactly packed in, while the latter was throughout unpacked. But the missing larva and the flies could not be found there.

This instance seems to show the same result as the preceding case.

(4) Wasp No. 113. Aug. 17, 1948. The wasp brought a prey to her nest at 8.57 a.m. When she came out I caught and marked her. At 9.10 she returned empty-handed and 2 minutes later started off again. At 9.40 she came back capturing a fly. A minute after she flew off. At 10.00 I dug the cell. In the cell there were a larva of the early stage of the 4th instar and 13 flies, of which 7 were already eaten. The structure of the nest and the experimental arrangement were as shown in Figure 15. A swollen tube was placed between the normal glass tube and the Petri-dish, with the aim of observing whether it was utilized by the wasp as a sitting room for herself or as a room for storing food. Moreover, I expected that the wasp used it as the brood-chamber and brought in it her own larva from the abnormal chamber of the Petri dish which was 5 cm in diameter. I made two small impressions on the floor of the chamber and put a larva in each of them, one of which was the larva of this nest and the other was derived from another nest which was in the later middle stage of the 4th instar. Not a single fly was placed in the brood-hall. At 10.15, the wasp carried in a green bottle fly. Thereafter, she brought 7 flies in the burrow in succession, of which the last 5 were stored in the swollen tube. But she did not take out even one of the larvae from the Petri-dish. Finally the tunnel was permanently closed.

This is an instance in which the wasp continued to provision in the nest that was strikingly changed in its inner structure. The fact that the wasp stored 5 flies in the swollen tube will be a good evidence that she carried out the work of the last provisioment quite automatically without examining the larva or the brood-cell.

(5) Nest No. 123. Aug. 21, 1948. The wasp of this nest is the same individual as the preceding instance (No. 113), having a red mark on the mesontum and a yellow marks on the propodeum. After completing the previous nest at 9.00 a.m., on the 18th, the wasp at once began to dig a new burrow at a distance of only 20 cm away from the previous nest. On the 21st, at 11.20 a.m., I dug the nest. It showed the structure analogous to the preceding nest (Fig. 16, A; cf. Fig. 15, A). In the brood-chamber there was a larva of the 4th instar which seemed just finished its moult. It had at its caudal end the shed skin and still attaching to the pedestal. The pedestal fly had already rotten and its abdomen was covered with mould. The larva had eaten the second fly a little that was placed near-bye and at that moment just began to eat the third fly. Besides, 2 intact flies were stored at the entrance portion of the cell. I set the arrangement as shown in the diagram B of the same figure, using a tube that was bent near its end at a right angle and a Petri-dish of 5 cm in diameter. I put the larva together with its pedestal and 3 intact victims in the spacious hall.

At 0.05 p.m., the wasp carried in a bee-fly. But at 0.45 when I saw the nest the fly was discarded in front of the nest. At that moment the wasp came back with a new prey and went in the burrow at once. At 1.00, the bee-fly still remained discarded, half of its body being covered with the thrown-out sand. Moreover, a 2nd fly, a flower fly, was also thrown aside in the same manner. The wasp was working eagerly to carry out the sand from the interior. At 1.28, she was still at work to dig the tunnel. At 2.03 ditto, at 2.13 ditto. So I uncovered the arrangement. In the chamber the victims had not increased in number, but the orientation of them as well as of the larva was slightly changed. Evidently the wasp had entered the Petri-dish and moved the larva and the flies. However, the wasp was still digging. I opened the sand cover of the glass tube throughout and knew that the wasp was digging the extention of the straight portion of her own tunnel. The procedure of the happening is supposed as follows : "The wasp, in her first return, having been unable to find the entrance to her cell (= entrance of the tube) began to search for it by digging in sand, and during the course the bee fly that was laid down in the tunnel was thrown out with the dirts. Meanwhile, the wasp happened to find the entrance to the tube and enter the brood-cell. Then she went on her 2nd hunting excursion. However, when she came back with the newly caught prey, she was again unable to find the entrance to the tube and resumed the same searching work. Probably she closed the tunnel at its turning point." So I connected the glass tube with the end of the straight gallery. Moreover, I set an ellipsoidal bottle with the larva in place of the Petri-dish. The wasp at once came in the tube and the bottle, though both were exposed to the daylight. She touched the larva, returned in the tunnel and emerged out of the entrance. But at once she entered the burrow and after a minute or so came to the larva. She touched the larva again and went back through the bright tube in her own dark tunnel. Then she emerged out of the nest and flew away madly without sealing up the entrance. I exchanged the glass cell again for the Petri-dish and arranged the contents of the chamber as before, excepting that the victims were replaced with 2 fresh flies. I closed the entrance and placed a pebble on it.

At 3.40, the pebble was stirred and a fresh heap of wet sand had been thrown out from the burrow. But I did not examine the brood-chamber. Two days later I went to the colony and examined the chamber at 8.30 a.m. The larva had attained the middle stage of the last instar and was situated at the centre of the room. A dozen victims, namely 2 intact and 10 eaten flies had been found around it. That is to say, 10 victims were taken in the room since 3.40 p.m. of the day before the previous day. I removed from the chamber all the victims but one fresh green bottlw fly. At 8.45, the wasp came back carrying a booty. I left the instruments exposed to the light. She came through the glass tunnel, repeating the sweeping movement as usual and arrived at the Petri-dish. She proceeded in the chamber without hesitation, arrived at the larva straight, touched it with her antennae and gently tapped it twice and thrice as if to examine its condition. Then she walked about in the vessel, hanging her antennae as if she were searching for something. While she was walking about she went to the green bottle fly that was placed between the entrance and the larva. She touched it, caught it at once with her mandibles and brought it to the side of the larva. Again she walked slowly, but finally excited by the stimulus of the light and began to fly about in confusion. So I covered the instrument with sand. A minutes later I made a small window in the sand and peeped in the chamber. The wasp was sitting by the larva. But, as she showed an alarming manner I closed the window perfectly. Two minutes later, I opened the cover. The wasp was still in the chamber and began to fly about in confusion. I was obliged to cover it perfectly. A few minutes later, the wasp emerged from the entrance, took out a little amount of sand from the tunnel, then closed the entrance and flew away. At 9.25, I saw the wasp taking in a large flower fly. At 9.40, I opened the cover. In the chamber 2 large flower flies had been added and the larva was eating the green bottle fly.

At 9.45, I altered the Petri-dish with another that had the diameter of 15 cm and the height of 3 cm. The larva together with 3 flies was placed in the centre of it. At 0.10 p.m., I examined the contents of the vessel and knew that 3 flower flies had been carried in the chamber. Judging from the disordered orientation of their heads, it was evident that they were dragged about in the Petri-dish. Moreover, quite interesting to say, they were all placed some distance away from the larva, though not piled up in a mass. At 0.55, the wasp was throwing some dirts from the entrance. At 1.14, a considerable number of victims were found added in the vessel. At that moment the wasp came back with a prey, so I stopped the examination to let her in. The wasp, though stood on the entrance and began to sweep the entrance stoppage, did not enter there at once. She lifted her head high every time after a sweep was over, and stood still a moment, as if to beware the presence of the observer. At last she penetrated there vigorously, throwing the sand behind her. I uncovered the Petri dish completely, but I took care to keep the inside of the chamber somewhat dark by covering it with my hat and waited for the wasp coming in. After spending 40 seconds to open the inner closure of the tunnel, the wasp appeared through the tube in the Petri dish, sweeping vigorously the floor as usual. But once she entered the brood-cell — that broad hall of the Perri-dish — the speed of her progress was suddenly and markedly diminished. She walked slowly, hanging her antennae and moving them with considerable rapidity, as if to grope for her way to the larva. However, she arrived at it without difficulty and touched it and hold it between her antennae. After a while, she left it and walked about slowly in the chamber in search of the victim. Soon she touched one of the flies. At once she grasped it with her mandibles and carried it by the side of the larva. Again she groped about in the broad room. Meanwhile she became excited by the stimulus of the light and fell into confusion. So I covered the apparatus. At 1.18 p.m., on examining the interior of the nest, I found the fly that was brought in at 1.14 placed near the entrance in the room and the remainder of the victims were arranged around the larva. At this time the larva attained about 8/10 of its full-grown size. Therefore. I changed it with another small one. The subsequent result will be described in another connection (p. 46).

(6) Wasp No. 129. Aug. 23, 1948. At 10.40 a.m., I dug the nest. Through an error, the brood-cell was wholly dug out at a scoop of my small shovel and the larva was missed in the sand. But as the intact victims found in the sand were 4 in number, the larva was supposed to be of the 4th instar. I used a curved glass tube and a Petri dish (10 cm in diameter) and arranged them as shown in Figure 17, B. A larva of the middle stage of the 4th instar taken out of another nest was placed in the centre of the broad room and was supplied with an intact flower fly alone. At 1.10 p.m., the victims in the room came to be 3 in number. At 4.10 things remained as before. Two days later at 8.40 a.m., I examined tho nest. The larva was dead and the victims remained without change, excepting one of them being decapitated. In the chamber a considrable amount of sand had been thrown in. Probably the work was done by the wasp.

In this instance the wasp continued her provisioning activity, despite of the marked change given in the interior structure of the nest. But she abandoned it when the larva was dead.

(7) Wasp No. 133. Aug. 25. 1948. This wasp was observed working on the 21st and on the 23rd. But as her nest was situated in the middle of several marked ones that I was observing, I left it alone. During the time it was repeatedly trampled with my hobnailed shoes. But always she succeeded in finding the entrance after a long patient search. Probably in this case a grass growing near-bye helped her as a good landmark to find her nest. On the 25th, at 8.10 a.m., she entered the nest empty-handed, but soon came out and flew away. At 8.50, I dug the brood-cell. It was situated at the end of the gently curved tunnel of about 25 cm long and was comparatively large, having about 45 cm in length. The larva was at the posterior portion of the cell and was of the early stage of the 4th instar. The victim was, strange to say, but one — an intact *Eristalis cerealis* which was placed at the entrance portion of the cell. No remains could be found in the cell. Possibly they had been all carried out and rejected by the mother wasp. At 9.10, I set a glass tube and a Petri dish in place of the interior portion of the nest (Fig. 18), and put the larva and the victim in the centre of the chamber. At 10.40, when I saw the nest, the entrance showed that the wasp entered the nest, but I did not examine the cell. The next day at 8.30, I uncovered the Petri dish and found the larva at A shown in Figure 18. It grew to about 7/10 grade of the 4th instar. By the side of it were scattered the remains of 5 flies and 2 decapitated ones. The wasp, despite of the astonishing change of her brood-cell, had continued her work of feeding the larva. I shifted the larva to B (Fig. 18) and removed all food but one decapitated flower fly. At 4.00, the larva had been in the centre of the chamber by itself, but not a single prey had been added in the cell. The subsequent day, at 9.30., I examined the chamber. It had been invaded by some carnivorous insect and the larva as well as the fly was missed from there. The tunnel was clear throughout and a considerable amount of sand was thrown in the cell. Possibly the nest was completed on the 26th when I found 7 flies in the chamber.

c) *Consideration of the results*

Table 1. Results of the change experiments on the inner structure of the nest.

No. of descrip.	No. of wasp	Larval instar	Experimental arrangement	Chief results
2	73	1	Circled tube	Refuse to enter, search her tunnel
3	74	3	Bisinuate tube	Continue to work, burrow new tunnel
4	79	3	Trisinuate tube	Continue to work
5	73	1	3 Y-tube	Abandon the nest
6	103	4	〃 〃	Abandon the nest
7	124	4	Y-tube	Continue to work
1	107	4	Petri dish	Continue to work
2	108	2	〃 〃	Abandon the nest
3	110	1	〃 〃	Abandon the nest
4	113	4	〃 〃	Continue to work
5	123	4	〃 〃	Continue to work
6	129	4	〃 〃	Continue to work
7	133	4	〃 〃	Continue to work

Now, if we put in order the data obtained from the experiments described above, the results can be tabulated as in Table 1.

From the table we can perceive that the percentage of the nest abandonment is markedly high in the instances in which the larva of the earlier instar was dealt with in comparison with those wherein the larva of the later inster was employed. In order to ascertain whether the nest abandonment depends merely upon the larval instar or not, I examined the results of all of my experiments made with the young larvae and obtained Table 2.

Table 2. Results of the experiments obtained from the nests containing a young larva or an egg.

No. of wasp	Larval instar	Experimental arrangement	Chief results
52	2	Glass bottle	Continued to work
69	1	T-tube and 2 cells	Continued to work
73	1	Fig. 19	Refused to enter, dug in original direction.
73	2	Fig. 20	Continued to work
84	Egg	Y-tube, 2 cells	Abandoned the nest
93	1	Triple-Y-tube, 4 cells	Abandoned the nest
95	1	The same as Fig. 62	Abandoned the nest
108	1	Petri-dish	Abandoned the nest
110	1	Petri-dish	Abandoned the nest
121	Egg	Glass bottle	Abandoned the nest
128	2	Y-tube, 2 cells	Continued to work

This table indicates that the nest abandonmet is not always the case in the instances wherein the larva of the earlier instar is dealt with in the experiments. However, at the same time, it indicates clearly that the instances of the nest abandonment in such cases surpass half of all. On the other hand, according to Table 1, the nest abandonment seldom occurs in the nests containing the larva of the later instar under the similar condition. Judging from the results, the chief factor of the nest abandonment seems to lie in the fact that the change is given during the time when the larva is still in the earlier instar.

d) Summary of the results

1) The wasp, when she finds that the nest has been changed in its internal structure, always shows some unusual behaviour. She usually repeats the ingress and egress to and from the nest. Probably this is an expression of the disturbance of her psychical condition.

2) Sometimes when the change given is very striking, especially in the case when the larva is still in the earlier instar, the wasp, after examining the interior of the nest, abandons it in the end. At that time the larva is usually dragged out

of the nest and discarded by the wasp.

3) Sometimes, the wasp refuses to enter the glass tube, or after examining the interior of the experimental arrangement ceases to enter it again and begins to search for her missing nest by digging a tunnel in sand.

4) In such cases, the direction of the tunnel dug by her anew from in front of the arrangement usually agrees well with that of the original one.

5) In most cases, however, the wasp, so long as the larva was left in the nest, even in the cases when the change is extraordinarily striking, continues her hunting and feeding activities, especially when the larva is of the later instar.

6) Sometimes, after digging a new burrow in the direction of the original tunnel, the wasp still enters the glass tube to meet the larva. Then she continues to provision the nest under the stimulus obtained from the contact with the larva. In such a case, however, the victims brought in the nest is usually dragged in the tunnel dug by her, resulting in the spatial separation of the larva and its food.

The sole source of stimulus necessary for the hunting and privisioning activities of the mother wasp seems always to lie in the contact with the larva in her nest. So far as this stimulus is retained, although sometimes more or less disturbance is observed at first, she continues, as a rule, her normal feeding activities, despite of the marked change occurred in the interior structure of the nest. In some instances, however, the striking change of the inner aspects of the nest results in the nest abandonment. But, even in such a case, the cause seems to lie not so much in the very change of the inner aspect of the nest as the disturbance introduced upon the larva which is still in its earlier instar.

In conclusion, we can say that the structure of the nest has some significance in relation to the cognition of the wasp of her larva — the larva as a releasor of the hunting activity, — and sometimes when the larva is still very young, the marked disturbance inside the nest gives rise to the complete loss of the releasing significance of the larval wasp itself. According to the fact, therefore, the releasing value of the larval wasp is considered to increase as its development proceeds.

3. Kinds and characters of the larva

By the above described experiments, it has been made clear that the hunting and provisioning activities of our *Bembix*, excepting for its final phase, is not carried out without connecticn with the external conditions, as is usually observed in most of other solitary wasps that have the habits of mass-provisionment, but is promoted by the contact with the larva in the cell. In other words, this fact indicates that a certain degree of recognizing capacity with respect to the larva must be present on the part of the mother wasp. In order to investigate how far reaches the range of kinds and characters of the larva that can release the hunting activity on the mother wasp, the following experiments were conducted:

a) Experiments of putting a paralyzed cabbage-caterpillar in place of the true larva

(1) Wasp No. 83. Aug. 8, 1948. A simple nest, with the tunnel of 23 cm in length. The larva in the cell was of the 3rd instar and was supplied with 5 flies, of which 2 were decapitated and partly eaten. I replaced the natural brood-cell with a glass cell and put in it a cabbage caterpillar of moderate size with 2 intact flies. The caterpillar had artificially been paralysed by means of injection. In the course of my preparation at 10.00 a.m., the mother wasp came back with a prey. She entered the tunnel and came in the burrow empty-handed, but happened to come out of the nest through the posterior opening made by digging. She flew up, went at once to the entrance and entered again. I hurriedly connected the glass bottle with the posterior opening. But this time she did not come in at once. On the contrary she appeared at the entrance backing with the dirts to throw away. There she touched a dried up fly that had been rejected since the beginning of my observation, caught it between her mandibles and proceeded backward for about 130 cm and threw it off. She then carried out of the nest a fresh green botte fly, probably the victim she had just before taken in, and swept it away. Then she entered the burrow, but did not come in sight in the glass bottle for about 3 minutes. Having supposed that she might be afraid of the light, I covered the cell with sand. At 10.26, I found her come back with another victim. I cleared the sand cover on the bottle and waited for her coming. She came in the chamber without hesitation, touched the caterpillar and hurriedly returned in the tunnel. She came in again empty-handed, but soon fell into confusion by the stimulus of the light. I covered the glass cell. At 2.40, I examined the nest. The victim that she brought in for the second time had been carried in the cell. But the entrance to the nest was left opened. I closed the nest and placed a pebble on the surface. Two days later, I arrived at the place at 6.15 a.m. to observe the results of the wasp's work of the previous day. The nest remained as before. In the cell, 3 maggots of a parasitic fly were feeding upon the caterpillar and the 3 flies. It was evident that the wasp abandoned the nest.

(2) Wasp No. 85. Aug. 9, 1948. I failed in digging upon the larval cell and the contents of the brood-cell became unknown. But as the wasp carried in her nest 2 victims until 10.25 a.m. under my observation, the larva was supposed to be either of the 3rd or of the 4th instar. I put at the end of the tunnel a Y-tube of glass, with a cell of glass at each apex. In one of the cells a paralyzed caterpillar of an *Ammophila* was placed together with a green bottle fly, while in the other, a larva of the 3rd instar taken out of another nest together with 2 flies (a house fly and a horse fly). At 2.40 p.m., I uncovered the nest. The caterpillar had been missed from bottle A, but the flies remained untouched, while in bottle B a house fly, a flower fly and a flesh fiy had been added. Thenceforth the wasp continued to bring food to the larva.

It seems clear that the wasp in this instance made a discrimination between the larva of her species and the caterpillar, and took the latter out of the nest and discarded.

(3) Wasp No. 86. Aug. 9, 1948. At 11.40, I dug the nest. It was simple in structure and in the brood-cell were a larva of the 3rd instar and 4 flies. The larva was attached still to the pedestal (*Tabanus mandarinus* !) and was eating a flesh fly supplied by the side of it. I put a paralyzed caterpillar and 3 intact flies in a tube bottle and connected it with the end of the tunnel. At 2.50 p.m., a horse fly had been added in the cell, but the wasp was digging

a tunnel newly just beneath the cell of glass. On the 11th, at 6.45 a.m., I examined the nest. It was abandoned by the wasp with the entrance left opened.

b) *Experiments of putting a larva of the honeybee in place of the true larva*

(1) Wasp No. 109. Aug. 16. 1948. This wasp was observed making the nest on the 14th. When I dug the nest, therefore, it was supposed that her larva was still very young, probably of the 1st instar. The nest was simple in structure and had a typical accessory branch. However, by failure of digging the contents of the brood cell became unknown. I placed a T-tube of glass at the end of the tunnel just in front of the accessory branch and attached at both ends a glass cell respectively. A larva of the moderate size of the honey bee together with one flesh fly was put in one of the bottles, while the other bottle was left empty. The larva of the honey bee is different in form and in body odour from that of *Bembix*, but rather similar to it in the surface condition of the integument and in this case also in the body dimension.

Soon after the arrangement, at 1.54 p.m., the wasp came back without a fly and entered the nest. She came in the bottle containing the larva without hesitation, touched it and then touched the fly, both with her antennae and then, quite unusually, retreated backwards in the tunnel. She then proceeded again in the bottle, touched the larva and fly alternately once more, strided over them and came to the innermost wall of the cell. There she turned round and began to return in the tunnel, when she was excited by the stimulus of the light and fell into confusion. So I covered the bottle with sand. After a while the wasp appeared at the entrance, rubbed her antennae with her front leg and appeared very inactive. She then entered again, but soon came sweeping from the entrance. Once more she entered. But after a little while, she came out of the nest, rubbed her wings with her hind pair of legs, then rested still for a short time and at last flew away. The next day when I examined the nest the larva had already died and not a single fly had been brought in either of the cells. On the 18th ditto, the fly began to rotten.

This instance indicates that the larva of the honey bee can not release the hunting behaviour upon the mother *Bembix*.

(2) Wasp No. 112. Aug. 16, 1948. Simple nest. In the brood-cell there were a larva of the early stage of the 4th instar and 9 victims, of which 2 were eaten, 2 were decapitated and the remainder were intact. I connected a glass bottle with the end of the tunnel and placed in it a larva of the honey bee and an intact fly. It was at 1.50 p.m. At 1.55, the wasp came back without a prey apd entered the nest. Soon after the entering, she carried out the sand repeatedly from the burrow. As I was occupied by the observations of other nests I could not directly see the wasp's behaviour in the nest. At 2.05, she had been flew off. At 2.37, I opened the nest. To my surprise, one fresh fly had been brought in the chamber. Probably it was taken in while I did not know. The next day at 9.00 a.m., things remained as before. The subsequent day at 2.00 p.m., no change could be observed. But on examining the tunnel I found it fairly compactly packed with sand, especially so in front of the cell. Though the victims brought in the cell were comparatively small in number, the nest should be considered to have been completed. That is to say, when I made the experiment upon the nest the work of the mother wasp was probably in the course of the final automatic activity. Therefore, she might pay no special attention to the larva in the nest. The behaviour

of the wasp shown in carrying out the sand from the burrow when she entered the nest for the first time after the glass bottle was placed seems not represent the disturbance caused by the change of the larva in the nest, but merely the disordered arrangement of the glass tunnel.

c) Experiments of placing a larva of the Crabronid wasp as a substitute for the true larva

In order to bring the characters of the substitute much closer to those of the larva of *Bembix*, I attempted to use a larva of other species of wasps. For this purpose I adopted a larva of a large Cradronid, *Ectemnius konowii* kohl. This species is a very close kindred of the European *E. fossorius* L. Its nest is made in decayed wood and it is a hunter of the Dipterous insects*. Quite favourably in point of analogy of food, probably also of analogy of body odour, the victims supplied to the larva in this Crabronid consist of various species of the flower flies. But the form of the larva of this species is more or less different from that of *Bembix*. In the former the body is subcylindrical and narrowed gradually towards both ends; its body is of rather a compact constitution and slightly curved, so that if placed on a flat floor it lies always on one side. While in the latter the body is rather flattened dorso-ventrally and swollen posteriorly; its constitution is rather soft and it can easily lie in a normal attitude on its ventral side.

(1) Wasp No. 81. Sept. 11, 1947. At 0.07 p.m., I dug the nest. The tunnel was nearly straight, about 30 cm in length. In the brood-chamber was a larva of the early stage of the 4th instar with 4 intact and 2 eaten flies. I placed in a glass cell a larva of *E. konowii* which was only slightly smaller than the rightful inhabitant of the nest together with 2 untouched flies, joining the cell to the end of the natural tunnel. Soon after the operation, the wasp came back carrying a victim and entered the nest. She came straight in the cell without the prey as usual. She walked to the larva and touched it with her antennae. Then she turned round and went back in the tunnel, apparently without taking notice the change of the larva. Soon she came backing with the prey, but after laying it aside she felt the light and began to struggle against the glass-wall. I covered the cell with sand. After a while she appeared at the entrance, but at once turned round and entered the nest again. She came out soon but at once went in again. Once more she repeated the same manoeuvre. I unearthed the bottle. The wasp walked in the chamber, touched the larva, trampled over it to the interior of the chamber, turned round and went back in the tunnel. But instantly she returned and repeated the same movement as before. The larva was still alive and remained motionless while the wasp touched it or trampled on it. One of the flies which I placed by the side of it had been transported to the entrance portion of the chamber and only a decapitated fly was left within its reach. The wasp actively sweeping the sand out of the burrow. The same behaviour was continued for about 5 minutes. Then I covered the cell. At 3.30 p.m., I

* Tsuneki, K. 1948. Ecological observations on hunting wasps IV. Seibutsu (Sapporo), Vol. III, No. 1, pp. 22 — 26. (In Japanese with English sammary).

Tsuneki, K. 1948. On the wasps of the genus Crabro s. l. from Hokkaido with descriptions of new species and subspecies. J. Fac. Sci. Hokkaido Univ., Ser. VI, Vol. IX, No. 4, ref. p. 298.

uncovered the cell. The larva had been transported to the innermost portion of the chamber, and the flies that I gave, together with the victim that was taken in by the wasp at 0.07, were placed in a mass at the entrance portion. The larva was moving its anterior body in vain, seeking food to eat. So I replaced the flies by the side of it.

From the next day to the 18th, excepting the 14th, the weather was bad and I did not go to the colony. On the 19th, I examined the cell. In the chamber at the innermost portion remained the 3 flies as they had been placed by me, but the larva had disappeared. I examined the tunnel thoroughly, but it was not found even there. But I found a drop of glutinous substance attached to the floor of the chamber at the anterior portion. Judging from the state of the flies that remained almost untouched, the larva may have been carried out soon after my observation on the 11th and possibly it was killed by the wasp before it was dragged out of the nest. I suppose that the glutinous substance found on the floor of the cell may be the trace of the blood of the larva. This supposition, though so strange it may appear, is based on the similar occurrence observed at times during the course of experiments on our *Bembix*.

(2) Wasp No. 79. As regards the states of the nest of this wasp and the experiment first made on this nest I have already described elsewhere in this paper (p. 24). I arranged a deeply trisinuate glass tube, having a length of 80 cm, at the end of the natural tunnel of the wasp. I connected a bottle with the end of the tube and put the larva of the nest in it. The wasp, despite the great change occurred on the structure of the tunnel and the larval cell, brought food to the nest and transported it through such a long and unnaturally waved glass tube to the larva. As it was confirmed that the wasp did not undergo any essential influence from the change of the inner aspects of the nest, I removed the larva of the *Bembix* (about 16 mm in length and was in the early middle stage of the 4th instar) from the bottle and put instead a larva of the Crabronid. The substitute was much less in length than the rightful larva, measuring only 12 mm and much slender in form. Therefore, it seemed a very easy matter to distinguish the difference between the 2 larvae through the contact of the antennae. Besides the larva, I placed 2 intact flower flies.

I could not examine the nest until the 19th owing to the bad weather. When I examined it, the larva was found beneath the tampon of sand made just in front of the brood-cell (the tampon was made of the sand that dropped from the aperture between the tunnel and the cell). No victim had been added in the chamber. The fly that I placed remained entirely untouched. The long curved tube was clear throughout excepting the posterior tampon of sand mentioned above which was not observed when I changed the larva. The tunnel of her own was normally closed at the entrance for about 3 cm. Just in front of the beginning of the glass tube was dug an accessory branch directing obliquely below. Judging from the above data, it seems to follow that : 1) The wasp probably examined the larva after it was introduced in place of her own, since the inner closure of the tunnel was founded anew. 2) Probably the wasp had no doubt about the changed larva, because, the nest is normally closed by means of the usual temporal closure. 3) The larva was not killed nor pulled out of the cell; it proceeded and penetrated for itself beneath the tampon of sand in search of the favourable place to spin the cocoon and eventually died. Because, it has the habits of pushing aside the tampon of saw dusts in the normal circumstance when it is about to spin the cocoon. 4) Probably the wasp did not return after she had departed the nest. She seemed to be killed soon after by the severe cold of the night. The fact that more than half of the wasps of the colony died during the period seems to support such a presumation.

3) No. 73. This instance is also one of the secondary experiments. As to the first

experiment I have already related in the preceding section (p. 20). In the second experiment I changed the arrangement into a more simple form (Fig. 7). Under such an arrangement I observed first how the wasp dealt with the 2 larvae of her own species given her, one of which was already dead. Then, on Sept. 11th, I removed all the content out of cell A and placed instead 2 paralyzed flies and a larva of the Crabronid measuring about 13 mm in length. In cell B, after cleaning the interior were put 3 intact flies and the larva of the *Bembix*. It was about 10 mm in length and probably of the 3rd instar*. At 4.10 p.m., I examined the arrangement and found that interesting transfer of the larva which is so often observed in the nests in which 2 bottles and 2 larvae were given also occurred here. That is to say, the larva of the Crabronid had been shifted in cell B. Besides, all the victims in cell A had also been transferred in cell B. Hence, cell B became very crowded. The Crabronid larva was at the entrance portion of the cell, while the Bembicine larva occupied the interior space. Between and the around them were scattered 8 victims belonging to 5 species. On examining, it was made clear that among them 2 flesh flies and I bee fly were newly carried in by the wasp. The wasp was resting in the glass tube, with her head directing toward the entrance. She seemed to pass the night there. I closed the arrangement with thick layer of sand. It was on the 19th that I examine the result of the experiment. Cell A remained empty. In cell B the larva of the *Bembix* was dead and already became rotten. The larva of the Crabronid was also dead at its previous position, but it was as fresh as alive, showing that it was soon after the death. The victims all putrefied and there could be admitted no increase in number.

This result indicates at least that while the wasp was working for the provisionment of the nest, she did not make any different treatment upon a larva of the wasp of another Family. That is to say, she could not make any discrimination between the larvae of the 2 species. As for the fact that the work of the wasp was stopped it will not depend upon the abandonment of the nest, but merely upon the death of the wasp, as was probably the case in the previous instance.

d) *Summary of the results.*

1) When the larva of her own was changed with a paralyzed caterpillar of the cabbage butterfly, the wasp always abandoned the nest. When the caterpillar is given in addition to her larva in another place of the same nest, the wasp carried it out and discarded. But she continued to feed her own larva thereafter.
2) When the larva was replaced with a larva of the honeybee, the wasp eventually abandoned the nest. But in the case when she was in the course of the final mechanical provisioning activities she did not show any remarkable response upon the change.
3) When it was replaced with a larva of *Ectemnius konowii* Kohl, a fly-catching hunting wasp, one of the wasps showed a marked disturbance in her behaviour and eventually abandoned the nest, after dragging the given larva out of the nest. While others treated the given larva quite indifferently.
4) As for the sensory elements working in the discrimination, probably the sense

* This larva had already hatched out when I opened the cell on the 7th. Such a slow development depends upon the low temperature of the time.

of odour will play the leading rôle. At the same time, however, judging from the behaviour of the wasp in the brood-cell, we can not deny the cooperation of the tactile sense.

4. Dimension of the larva

In the preceding experiments it was clarified that our *Bembix* could easily distinguish a larva of the butterfly and that of the honey bee from her own. As to the discrimination between the fly-eating larva of a Crabronid and that of her own it was rather difficult to do so and the results were inconstant with the iudividual employed. The difference of the results among the 3 kinds of the material mentioned above seems to me to depend in the main upon the difference of the olfactory stimuli given forth from the bodies of the material dealt with; because the difference of the body odour among the material is even sensible to the human olfactory sensation which is very feeble. However, as mentioned above, the contact stimuli seem also to take some part in the discrimination in this case.

The following experiments were carried out to make out whether or not the dimension of the larval wasp has some releasing value upon the hunting behaviour of mother *Bembix*.

The larvae of *Bembix* are regarded as having essentially the same body odour, though the nature of the food they eat varies somewhat from one individual to another. Therefore, if a larva having a certain body dimension is replaced with another that has another body dimension, the discrimination between them must be made through the tactile stimuli.

a) *Indicator response*

The problem as to whether the larval dimension has some releasing value on the hunting activity of the mother wasp or not is the problem as to whether the mother wasp, when the larva of her own is replaced with another having different body dimension, can respond to the changed body dimension of the larva or not, that is to say, can show the hunting activity well fitted to the developmental state of the newly given larva or not. If only this problem is treated, the observation of the results only of the hunting behaviour will do. But if we deal with the discrimination capacity of the wasp, we must make out the detailed procedure of the wasp's activities. Because, it is by no means a rare phenomenon that the wasp cannot correctly adjust her behaviour to the changed states of things which is considered to have been noticed by herself. Therefore, we must take special care with regard to the following behaviour of the wasp :

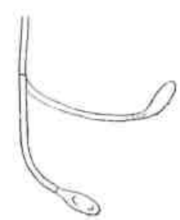
1) Differential behaviour of the wasp when she touched the larva.
2) Whether or not some marked difference occurs thereafter in the activity of the wasp.

In order to make easy the judgement upon the results of the 2nd point, the victims stored in the cell must be all or nearly all removed. Because by doing so the activities of the wasp to store food for the larva are, as a rule, markedly accelerated. As for the results of the first point, they must be moderately appreciated when the change of the environment is given at the same time. However, when the change of the larva is made while the wasp continues normally her provisioning activity after the brood-chamber was replaced with glass instruments, the confusion in the behaviour of the wasp, if shown, must be appreciated high. As for the results of the second point, when the provisioning activities of the wasp are renewed thereafter and are carried out in accordance with the developmental grade of the newly given larva, or the wasp abandons her nest without any other presumable reason, the results are considered positive for the question. On the other hand, when the wasp continues her activities, regardless of the developmental degree of the given larva, the result is considered negative. However, even in such a casse, if the disturbance in her behaviour when she touches the altered larva in the cell is so remarkable, we may be better to reserve the negative conclusion, although her behaviour may be negative in the end. Moreover, when the victims brought by the wasp to the brood-cell are successively removed, if the wasp works in succession to compensate the removed flies, the amount of her work may be released by the dimension of the larva and may be regulated by the amount of the prey in front of the larva. Such a behaviour is apparently very similar to that based upon the true judgement in human beings.

b) *Experiments of replacing the larva with a smaller one*

(1) Wasp No. 75. On this wasp, an account has been given elsewhere in connection with the care of the young (Part I, p. 162). I stopped my description at the point where the wasp carried in a victim for the first time to her opened brood-cell. It was on Sept. 10, 1947. At 10.45 a.m., I set my arrangement by using a glass tube of 10 cm in length and a tube bottle of 6 cm in length and 1.5 cm in diameter as shown in Figure 19. The natural tunnel of the wasp was left untouched for only 13 cm in length. I removed the rightful larva of the nest together with the victims from the cell. It was in the later middle stage of the 4th instar, about 20 mm in length and considerably flattened dorso-ventrally. The victims were 11 in number, of which 7 were already eaten. I placed as a substitute a larva of the 2nd instar with 3 flies in the glass cell This larva was very small and slender, measuring only 8 mm in length and was still attaching to the pedestal fly. The change was very striking. Probably the wasp, under the unaltered conditions, soon completed her provisionment by gathering 4 or 5 more flies on the day. On the other hand, under the changed condition, she must work for several days to store at least 10 flies to feed adequately the given larva. Moreover, if the activity of the wasp can be altered according

19



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Figs. 19 and 20. Nests and experiments of Wasp Nos. 75 (Fig. 19) and 130.

to the size of the newly given larva, she must restrain herself in accumulating food. I covered only the anterior portion of the tube and left the rest of the arrangement exposed to the diffused daylight.

At 0.30 p.m., the wasp entered the nest without a prey. She came through the glass tube, sweeping the floor as usual, into the brood-cell. She went to the larva, but without touching it, returned in the tunnel and emerged from the entrance. At once, however, she entered the burrow again, came in the glass tube, turned round and, after performing the closing movement in vain, went in the natural tunnel, sealed up the entrance and flew away. At 2.00 p.m., I examined the nest. A bee fly was brought in the cell. The larva was put to it and was feeding upon it. A small quantity of sand had been carried in the cell and the wasp was resting in the dark portion of the tube, directing her head forwards. At 3.00, conditions were as before, so I covered the nest. The next day (the 10th) at 11.50 a.m., the wasp was observed sweeping the dirts from the burrow. In the cell the larva was eating a victim at the innermost portion of the chamber and 5 victims were piled up at the entrance portion. The larva had attained the 3rd instar. At 3.00 p.m., the larva was eating at the same place as before. The victims appeared to have increased somewhat in number, but I did not count them. The wasp was resting in the glass tube as in the previous day and behind her a small amount of sand was gathered up. On the 11th at 0.45 p.m., I saw the wasp closing the entrance. The larva already developed into the 4th instar, having a fatty body of about 16 mm in length. The prey found in the cell were 3 eaten, 5 partly eaten and 4 untouched flies. Among them 3 were those which I had introduced. I removed all the victims but 2, cleaning the interior of the bottle and replaced it as before. At 3.50, 2 further flies had been collected in the brood-cell, so that once more I put away the added flies from the bottle.

Having been prevented by the bad weather and the distance of 5 miles, I could not examine the result of the activities of the wasp until the 19th. When I examined, the larva had been dead and already rotten beneath the 2nd tampon of sand made just in front of the brood-cell. Probably it proceeded forwards, after fully grown, in search of the favourable place to spin the cocoon and died in failure of spinning. The tunnel had been closed compactly also in the middle of the glass tube for about 3 cm, but remained opened at the entrance. These states told that the nest was accomplished and was closed permanently by the wasp. In the chamber were remains of 11 flies. Beside them 4 more flies were found in the glass tube, some of them in the sand of the tampon. Summing up, the number of the victims stored by the wasp since 4 o'clock of the 11th comes up to 13. Possibly they were collected mostly on the 14th, the only day that allowed the activity of the wasp during the period.

This wasp accumulated 24 flies for the larva given her anew. Judging from every presumable condition, this number is too great to be accepted as provisioned for the larva of her own which had been removed previously by me. Because, it had been given 11 flies already and reached about 8/10 of its final growth. Moreover, such a lengthened period of her activity is by no means proper for such a developed larva. Under the original condition, the wasp was supposed to finish her work on the 9th or, at the latest, on the 10th. Whereas, she worked probably uutil the 14th (even if the weather condition was good, she might work at least until the 12th). On the other hand, when we consider that the work done by the wasp is for the newly given larva, the amount of food provisioned anew, the manner of her feeding activity (especially relatively small number of victims supplied to the larva when it was still young) and the period of her work, all these results become quite suitable for the confronted conditions (Table 3). In short, the activity of the wasp renewed after receiving the small larva can be explained only on the basis of her proper reaction to the given external condition, independent of the influence of her preceding acts or of the innately predetermined schedule.

Table 3. Compensatory activity of Wasp No. 75.
(Indicated by the number of prey collected)

Nu. of experiment	1	2	3	4	5	6	Total	
Developmental degree of the larva	4.7/10	2. inst.	3. inst.	4.3/10	4.3/10	Dead		
Number of prey left in the cell		3	4	8	2	2		
Time examined / Species of prey	IX. 9 $10^{h}.50$	IX. 9 $3^{h}.30$	IX. 10 $11^{h}.50$	IX. 11 $0^{h}.45$	IX. 11 $3^{h}.50$	IX. 19		
Eristalis cerealis	3		2	3	1	4	13	
Eristalomyia tenax				1			1	
Eristalinus sepulchralis						4	4	
Pipizella bigulonis						1	1	
Helophitus virgatus	1						1	35
Ochrops fulvus	1						1	
Tabanus mandarinus	4		1				5	
Sarcophaga carnaria	2		1				3	
Lucilia caesar					1	3	4	
Villa limbatus		1				1	2	
Total prey in the cell	11	4	8	12	4	15		
Remarks intact	4	1	5	4	3	–		
Remarks eaten	7	3	3	8	1	15		

(2) Wasp No. 76. Sept. 9, 1947. Having failed in digging, I could not know the detail on the brood-cell of this nest. I only found 8 prey including some remains buried in sand. The wasp was observed taking in a victim twice until the time of digging (1.25 p.m.). Moreover I knew that the wasp was working there for several days. Judging from these data, the larva of this nest was supposed to be in the 4th instar. I put in a glass cell a larva of the 3rd instar derived from another nest and connected it with the end of the tunnel. No victim was placed in the bottle. An hour later I examined the cell. The larva was shifted to the innermost portion of the cell and a newly brought fly was placed at the centre of it. At 2.57 p.m., the wasp carried in a fly once more. She touched the larva with her antennae, but did not show any differential behaviour. The next day, at noon, I observed the larva eating the first victim which had been carried by the side of it and the 2nd fly was placed at the centre of the cell slightly apart from the larva. But no more fly had been added in the cell. The tunnel was sealed up by means of the permanent closure.

In this instance things were quite different from the previous case. Probably this wasp was already in the final course of the provisioning activities when she was given a smaller larva. Accordingly it seemed that the amount of her work was determined innately and mechanically, the only necessary external stimulus being obtained from the contact with the given larva, regardless of the dimension it possessed.

(3) Wasp No. 123. As to this instance I have already given descriptions elsewhere in the foregoing section. I succeeded in inducing the wasp to bring victims in the brood-chamber formed by a Petri-dish, 15 cm in diameter and 3 cm high. The growth of the larva normally proceeded and on the 23rd at 1.18 p.m., when I examined the nest it had attained about 8/10 of the final size. At 1.25 I removed the plump larva with its victims (8 in number) from the cell and placed instead a larva of the 3rd instar derived from another nest with 2 flies. The new larva was less than 1/2 as large as the previous larva in thickness and about 3/5 in length. At 2.15, a pebble placed on the entrance was moved, so I examined the nest. The wasp was absent from the chamber and no victim had been added in it. But the larva was shifted to the posterior portion of the room and the flies were half buried with sand. It was supposed that the mother wasp fell into confusion. I replaced the larva and the victims to the centre of the room. At 3.07, the wasp was closing the entrance by means of the permanent closure. Two minutes after its accomplishment, the wasp began to search for the place to dig a new burrow. I opened the brood-cell. The larva and the prey were at the previous place in the cell, but the latter were almost buried with sand. I found among them a black flower fly which had been newly brought in by the wasp. The larva was feeding upon it.

Judging from the result it may be presumed that the wasp took notice the change of the larva, nevertheless her behaviour could not adjust properly to the altered condition. Because, it is certain that the confusion shown by the wasp was not given rise to by the change of the brood-chamber itself, since, before the change of the larva the wasp used to come in and go out of the same room without confusion. Probably she was already under the postitive egg pressure which compelled her to close permanently the entrance tunnel.

This instance seems to me especially of interest in that the primitive state of intelligence is intertwined with the automatic instinct, where the former is so feeble that it cannot control the pressure from the latter.

(4) Wasp No. 124. As to this instance, too, description was given elsewhere (p. 26). The experimental arrangement was as given in Figure 11. The experimental conditions were as follows : In the figure, A is empty, B contains a larva of the middle stage of the 4th instar together with 6 flies. The wasp carried in 8 victims to the nest from 9.35 to 11.08 a.m. of the day. I removed all the victims but one from the chamber and replaced the larva with another of the 3rd instar. The change was very striking. It was at 11.10.

Three minutes later the wasp carried in a fly. At 0.30 p.m., she was flying about low above the ground probably in search of the place for the next burrow. So I opened the nest. In bottle B the larva had been shifted from the innermost portion to the centre of the chamber and 2 flies were placed in front of it and one fly behind it. In bottle A, too, one fly had been stored, probably by the mechanical mistake made on the occasion of her backing progress. The tunnel was distinctly permanently sealed up.

In this instance, the wasp must have touched the larva that was newly placed in the cell. Nevertheless, she ceased her work after accomplishing the remaining parts of the work predestined for the previous larva. Probably she was compelled to do so by the positive egg pressure in her ovary.

(5) Wasp No. 130. Aug. 23, 1948. The form of the nest and the experimental arrangement set by me were shown in Figure 20. The larva was of the 4th instar, just moulted. The victims supplied to it were 7 in number. Among them one was the pedestal and the larva was still attaching to it and eating the next fly. At 11.15, I exchanged the larva for another of the 2nd instar and placed with it a flesh fly. At 0.15 p.m., the wasp came back empty-handed. She carried out the dirts repeatedly from the tunnel. At 1.05, no change was observed in the cell. Two days later at 8.20 a.m., I examined the nest. It was being invaded by a troop of small red ants, *Solenopsis fugax*. But the contents of the nest had not as yet been carried out, though the larva had been killed already. It had grown into the 4th instar and the victims brought to it were 8 in number. The tunnel of the glass tube had been compactly stuffed with sand. It was clear that the nest was permanently closed.

In this instance, too, the wasp could not correctly respond to the altered condition, only mechanically completing the rest of her work for the preceding larva.

(6) Wasp No. 134. Aug. 25, 1948. This wasp carried in her nest a victim at 9.45 a.m., when I opened the nest. The tunnel was straight and 27 cm in length. In the brood-chamber was a larva of the middle stage of the 4th instar. The victims were 13 in number, of which 9 were eaten or partly eaten. I placed the larva alone in a bottle and put it at the end of the tunnel. At 10.30, the wasp came back without a prey. She stayed inside the nest for about 4 minutes. Then she flew away and did not return until 11 o'clock. The next day at 8.45, while I was examining the chamber, the wasp came back empty-handed. In the chamber was placed one flower-fly which had been well devoured. The larva attained about 7/10 of its full grown size. I removed the remains of the victim and left the larva alone in the cell. As soon as I finished the arrangement of the bottle, the wasp entered the nest. She carried out the sand from the burrow for a short while. During the work she dragged out an intact fly from the tunnel and carried it backward for about 80 cm and threw away. Probably it had been laid down in the tunnel since the previous day. At just 9 she came in the brood-chamber, proceeded slowly to the interior, hanging her antennae and moving them actively as if to grope for something. On arriving at the larva that was placed at the innermost portion of the chamber she touched it with the antennae and was suddenly activated, strided upon it and touched again with the antennae from both sides. Two minutes later she emerged from the entrance, gathered up the sand in the entrance and flew off. At 10.07 I saw the wasp alighted near the nest capturing a flewer-fly and sucking a syrup from the throat of the prey. Then she carried it in the nest and flew away. At 0.32 p.m. I examined the nest. The larva became nearly full-grown and the victims gathered up were 8 in number, of which only one was eaten. I then exchanged the larva for another of the 3rd instar, attaching a shed skin to its caudal end, and placed with it 2 flower-flies. At 1.35 I saw the wasp bring in a new victim. But I could not observe the detailed behaviour of the wasp in her nest. At 3.10, again she took in a fly. At 4.10 I examined the nest. Four flies had been added in the cell. I removed all the fly but one from the cell. At 4.20, the wasp came back without carrying a prey and entered the nest, probably to pass the night. The next day at 8.50 I uncovered the nest. The larva attained the early stage of the 4th instar and beside it 2 flies were found, indicating that one of them was hunted late in the afternoon of the previons day, because no wasp was seen working when I arrived at the place on that morning. At 11.50 a.m., I saw the wasp carrying out the sand from the nest. On a 3rd day (Aug. 28) at 9.10 when I reached the place it began to rain and continued all day long. I opened the nest at 10.10. In the cell had been added 10

flies, greater part of them were placed in the adjacent tunnel. The larva reached the middle stage of the last instar. While I was examining the nest the wasp returned empty-handed and entered the nest. Thus this wasp was still in the course of the provisioning activities, but I was obliged to stop the observation.

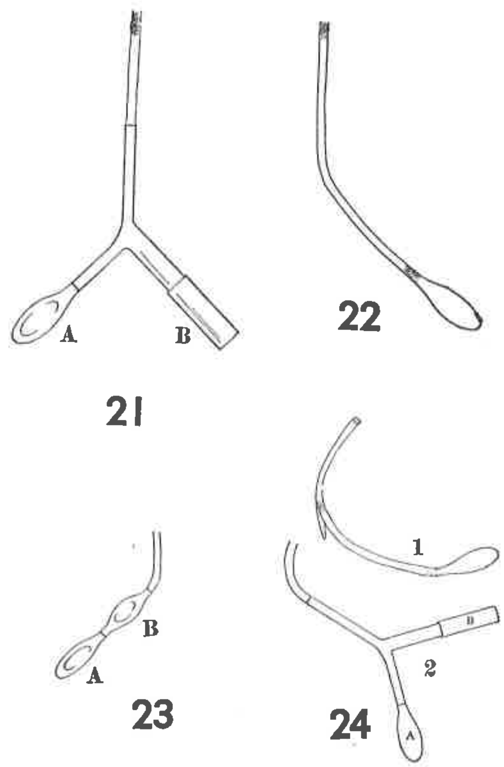
This wasp, despite of the fact that her work for the larva of her own was nearly accomplished, when it was exchanged for another young one, continued to work to provision for the second larva. The victims accumulated for the first larva were 23 in number. It was rather over the normal amount of the larval diet. Whereas, when the exchange was made she stored for the 2nd larva as many as 15 flies, and moreover the provisionment was still going on. Judging from the result it must be said that the wasp worked, adjusting her behaviour not only to the developmental degree of the given larva, but also to the amount of food accumulated at that moment in the larval cell. According to this result, the positive egg pressure can be controlled to some extent by the reversed unit of behaviour released through the altered external conditions. The process of her privisioning activities was shown in Table 4.

Table 4. Compensatory activity of Wasp No. 134.
(Shown by the number of prey collected.)

No. of examination	1	2	3	4	5	6	
Larval development	4.5/10	4.9/10	full-grown	3. inst.	4.2/10	4.5/10	Total
Number of prey left in the cell		0	0	2	1	2	
Time examined / Species of prey	VIII. 25 $9^{h}.45$	VIII. 26 $8^{h}.45$	VIII. 26 $12^{h}.32$	VIII. 26 $4^{h}.10$	VIII. 27 $8^{h}.50$	VIII. 28 $9^{h}.10$	
Eristalis cerealis	6		3		1	5	15
Eristalomyia tenax		1					1
Eristalinus sepulchralis		1					1
Syrphidae sp.				1			1
Chrysotoxum japonicum						1	1
Calliphora erythrocephala			3				3
Lucilia caesar	2		1	1		1	5
Muscidae sp.	1						1
Sarcophaga carnaria	2		1	1		2	6
Tachynidae large sp.	1					1	2
Ochrops fulvus				1			1
Villa limbatus	1						1
Total prey in the cell	13	2	8	6	2	12	38

(7) Wasp No. 150. Sept. 5, 1949. At 10.30 a.m., I saw the wasp take in a second fly

of the day to her nest and at once opened the brood-chamber. The tunnel ran straight, about 23 cm in length. In the brood-cell was a larva of the later stage of the 4th instar (about 23 mm), supplied with 19 victims, of which 6 were already eaten. The breeding activity of the wasp was supposed to be about to complete. I replaced the larva with another of the early middle stage of the same instar (about 16 mm) and put it in a glass cell with 3 flies. This experiment was originally undertaken to analyze the discriminating ability of the wasp regarding the broadness of the tunnel. Therefore, I used a specially prepared Y-tube of glass having the branches of different diameter, attached with a glass cell at each end (Fig. 21). The transported larva and 3 flies were put in bottle A, while in the other bottle, B, was placed a single fly only. The detailed records on the procedure of the wasp's behaviour will be treated in another connection. Here will be given only the description relating to the subject in question.



Figs. 21 – 24. Nests or experimental equipments of Wasp Nos. 150 (Fig. 21), 92 (22), 101 (23) and 128 (24).

At 10.55, the wasp brought a victim to her nest. As I observed the behaviour of the wasp only at the branching point of the tube, I could not see what happened when the wasp touched the substitute larva in the cell. But judging from the length of the time spent by her in the brood-cell and from the subsequent behaviour of her, no noticeable disturbance seemed to have occurred there. Thereafter I continued to observe her activities until 2.10 p.m. During the time I removed from the brood-cell from time to time the victims she collected, so as to set spur to her privisioning activity. To my surprise, she brought no less than 17 flies in the cell during 3 hours and a quarter. In addition to the above, the examination made on the next moring clarified that 3 more flies had been added in the cell. It seems worthy of special notice that during the period of her maddy activities to compensate the missing victims, no other wasp was working in the settlement of the wasps. The next day, from 8.20 to 11.15 a.m., the wasp in accordance with my removal of the victims she stored, brought, in reality, 13 flies to the larva. At that time the larva approached full development, so I replaced it again with another of the 3rd instar. It was attached still to the pedestal with its caudal end, having the body length of about 13 mm. The change was very distinct. I placed with it 2 flies. The wasp came back with a prey at just noon. At that time in the cell, no remarkable disturbance nor noticeable peculiarity of behaviour could be observed. She touched the larva rather mechanically and at once flew away. From that time onwards until 1.55 p.m., she brought as many as 16 flies further in her nest. Moreover, according to the examination on the next morning it was made clear that she added 2 more flies on the day. On a third day, the larva arrived at the 4th instar. But, to my regret, the experiment was forced to be stopped by accicent. At that time the wasp was still in the course of her provisioning activities and in fact at 9.00, she brought a fly to her nest.

With regard to the behaviour of this wasp, we can say as follows :

The wasp showed a compensatory activity of high grade (vide Table 15). However, she could not properly adjust her behaviour to the small larva given her as a substitute of her own large one; since she piled up a large amount of food in front of the 3rd instar larva. According to the result it appears that the energetic activity of this wasp depends solely upon the recognition of the scanty food supplied in front of the larva, not upon that of the developmental degree of the larva.

By the series of the experiments described above, it was ellucidated that there exists a very interesting individual difference regarding the response of the mother wasps to the altered condition of the larval dimension among them. In such instances as Wasp Nos. 76, 123, 124 and 130, the wasp did not show the proper response at least in regard to the altered condition of the larva, although some of them were supposed to have taken notice the change in the larval dimension. While in other 3 instances (Nos. 75, 134 and 150), the wasp showed distinctly a response to the change in the larval dimension, even sometimes repeating a certain range of a behaviour unit from the first. In such a case, it seems especially of importance that even such an internal factor as the positive egg pressure which has been considered one of the strongest of all the releasing factors was controlled to a considerable extent by the mother wasp when she has been stimulated by such an external factor as the dimension of the larva.

c) *Experiments of changing the larva with a more developed one*

(1) Wasp No. 74. Sept. 7, 1947. As to the condition of the nest and the chief experiment conducted upon this wasp (change of the inner structure of the nest), a detailed description has been given elsewhere in this paper (p. 21). During the experiment, I replaced the larva of the 3rd instar of the nest with another of the middle stage of the 4th instar. The former was about 12 mm, while the latter was nearly 20 mm in length. In this case, the wasp, though she showed an interesting confusion on the change of the inner struncture of the nest, did not give any noteworthy response to the change of the dimension between the two larvae. She continued to bring the victims in the nest as before.

(2) Wasp No. 92. Aug. 11, 1948. The structure of the nest was as shown in Figure 22. A larva of the 3rd instar and 3 flies includlng the pedestal were found in the brood-chamber. I used a tube and a bottle of glass and arranged them at 8.40 a.m., as in the natural condition. But in the glass chamber I placed a nearly fullgrown larva and 4 flies. This larva was taken out of another nest which was already accomplished. It had already devoured 29 flies coarsely and in front of it 5 intact flies still remained. At 9.50 a.m., I saw the wasp carrying in a fly. But I could not observe the behaviour of the wasp in the cell. At 11.05, she was sweeping out the sand from the burrow. In the course of her work she carried a fresh victim out of the tunnel, and when she came out next time she caught and dragged it for about 30 cm and threw off. At 11.15, a green bottle fly had been added in the cell. At 11.40, the wasp took in one further fly. At 1.00 p.m., 2 more flies had been added in the brood-cell. The next day at 11.45, I saw the wasp working for the first time on that morning. She was sweeping

out the dirts from her nest. At 0.30 p.m., I uncovered the nest and found the larva beginning to spin the cocoon. On a third day I did not see the wasp working. On a fourth day, however, I saw the wasp enter the nest empty-handed in the forenoon. At 3.10 a green bottle fly had been discarded at the entrance. I examined the nest. In the tunnel a fly was found laid down. In the chamber the cocoon had already completely been spun up and was about to become dry. On a fifth day I saw the wasp digging a new burrow at other corner of the colony.

From the result we can say that the activity of the wasp was entirely conducted on the standard of her own larva which had been removed from the brood-cell. She was compelled to stop her provisioning work merely by the encasement of the given larva.

(3) Wasp No. 96. Aug. 11, 1948. By failure of digging I could not find the brood-chamber of this nest. But judging from the manner of her work, the larva was supposed to be of the 2nd or of the 3rd instar, because the wasp carried in her nest only two flies from the morning till 2.30 p.m., when the nest was opened. I placed at the end of the tunnel a Y-tube attached with 2 bottles. A larva of the early stage of the 4th instar and 7 victims were put in one (A) of the bottles, while in the other (B) another nearly full-grown larva and 4 flies were placed. It was at 2.40 p.m. The next day, all through the afternoon, I could not see the wasp working at her nest. At noon, I opened the arrangement. The larger larva placed in bottle B was absent, but the victims were left as before. In cell A no change occurred. I uncovered the tunnel forwards in search of the missing larva. It could not be found anywhere. But the wasp was found there, resting still.

There is no doubt that the large larva was rejected by the wasp herself. It is uncertain, however, whether the rejection depends upon the change of the dimension between the given larva and her own, or merely upon the presence of two larvae inside her nest. At any rate, it seems very suggestive that the larger larva was rejected from the cell.

(4) Wasp No. 99. Aug. 12, 1948. I could not examine the brood-cell of this nest also by failure of digging. But as the wasp was working only since the preceding day, it was supposed that the larva was of the 2nd or the 3rd instar. I placed at the end of the tunnel a glass tube which was swollen in the middle and connected with it an usual ellipsoidal bottle. A larva of the later stage of the 4th instar, together with 2 flies was introduced in the bottle. It was at 9.50 a.m. Soon after it was arranged, the wasp carried in a fly. She did not come, however, in the brood cell for a long while, so I covered the bottle with sand. But I peeped through a small window left in the sand the occurrence in the cell. The wasp soon came in, walked about in the cell, turned round and went back in the tunnel as usual. Then she came backing with the prey and placed it in the chamber. But thenceforth her behaviour could not be well confirmed. However, about a minute later she flew out of the entrance madly, circling once or twice around the neighbourhood and at last flew away. I thought that she would not return. But, at 10.37, she came back with a fly and carried it in the cell. This time she came out of the nest without confusion. I captured and marked her. At 11.55, she carried in another fly. At 1.00 p.m., she returned carrying nothing and entered the burrow. After a minute she emerged and went away. The next day when I arrived at the place at 11.30 a.m., the wasp was at the entrance. At 0.20, I examined the nest. The larva seemed to have finished its development. Strange to say, however, the remainder of the victims were only two. I examined the tunnel. It was permanently closed and nowhere the remains or untouched victims

of the 3 flies out of the 5 that I knew could be discovered.

This instance seems to give evidence that the wasp took notice the change of the developmental state of the newly given larva, though she did not show the proper response in point of the provisioning behaviour for it. This wasp is the same individual as that which made Nest No. 110 (p. 30).

(5) Wasp No. 101. Aug. 13, 1948. The activity of the wasp was observed since two days before. I dug the nest at 0.30 p.m. The form of the nest and the experimental arrangement set by me are as shown in Figure 23. In the brood-cell a larva of the 2nd instar, attached still to the pedestal was found, which was supplied with 2 flies. I put in bottle A a full grown larva and 3 intact flies, while in the adjacent chamder (B) nothing. Ten minutes later I saw the wasp enter the nest with a fly, but I did not observe the behaviour of the wasp. The next day (the 14th) at 3.38 p.m., I examined the nest. All the victims that I placed with the larva had been well devoured. While the flies newly brought in by the wasp ware only 3 in number and were being devoured by the larva. The number of the victims collected by the wasp might be suitable for her own earlier instar larva, unless the change was introduced. On a third day (the 15th) at at 11.00 a.m., the wasp was seen carry-ing in a fly. At 11.10 I examined the nest. The prey stored were 12 in number, of which only 3 were untouched*. The result of the identification of the prey revealed that a half of which were brought in on that morning. The larva was about to spin the cocoon. So I replaced it with another of the early stage of the 4th instar and removed all the victims including remains from the chamber. At 3.43 when I examined the nest, in the chamber were 2 eaten

Table 5. Provisioning activity of Wasp No. 101.
(Shown by the number of prey collected.)

Date	13th	14th	15th	16th	17th	
Growth degree of her own larva	2. inst.	3. inst.	4. inst.	4. 4/10	4. 7/10	
Growth degree of the given larva	4. 8/10	full-grown	f-grown 4. 3/10	4. 6/10	4. 6/10	
Number of prey left in the cell. / Species of prey	3	3	0	1	0	Total
Eristalis cerealis	2	2	2	2		8
Theloria sp.	1					1
Lucilia caesar		1	3	2		6
Sarcophaga carnaria			3			3
Villa limbatus			1			1
Total	3	3	9	4		19

* This is an instance that the larva eats excess of food when supplied with very abunbant food. The victims were very roughly eaten. In most of them integumental parts were all left untouehed.

and 1 intact flies. Again these flies were all taken away. On a fourth day (the 16th) at 10.30 a.m., the cells were examined. In the adjacent swollen cavity was an intact fly, while in the larval cell 1 intact and 2 eaten flies. The larva was of about 6/10 in dimension of the full-grown size. At 3.05 p.m., not a single fly had been added in the cell and the larva was waiting for the wasp to bring a victim to eat. On a fifth day, at 8.00 in the morning when I examined the nest things remained as before. The larva seemed to be hungry. At 8.40 I saw the wasp sealing up the tunnel permanently. The state of the brood-cell was unchanged.

The procedure of the activity of the wasp, viewed in relation to the developmental degree of the given larva and her own, became as shown in Table 5.

The activity of the wasp ahown on the last two days was very strange and may be inexplicable on the basis of the developmental degree of either the given or her own larva. But as to the remainder of the activities of the wasp, they will be best explained on the consideration that the wasp continued to work mechanically for her missing larva. In other words, the manner of activity of this wasp is quite of a sort of predetermined type, save that she worked under the stimulus obained from the actual contact with a larva.

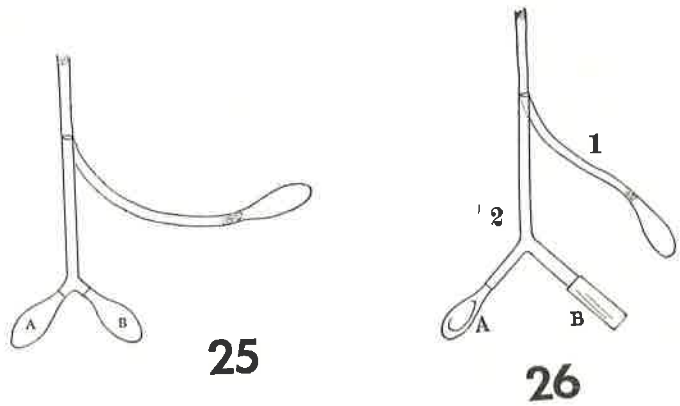
(6) Wasp No. 128. Aug 23, 1948. The nest and the experimental arrangement were as shown in Figure 24. In the nest were a larva of the 2nd instar* and 2 intact flies. In bottle B I put a larva of the middle stage of the 4th instar and one intact fly, while cell A was left empty. At 10.00 a.m. the wasp was calmly sitting in the tunnel; at 10.30 she was still there. No change occurred in both cells. Probably the wasp, having finished the provisionment of the day for her 2nd instar larva, was spending the time in the burrow. At 1.30 p.m. things remained as before. I then introduced another larva of the later stage of the final instar (about 8/10) in cell A together with 2 intact flies. At 3.00 p.m., the wasp was still resting in the tunnel and not a single fly had been brought in either of the cells. Two days later, I went to the colony early in the morning, in order to observe the results of the wasp's activity of the previous day. The tunnel, especially the basal portion of the Y-tube of glass had been compactly packed with sand, indicating that the nest was accomplished and permanently closed. In cell A not a single fly had been added, while in the other cell, as well as in the adjacent tunnel a great many victims had been accumtlated, namely in the cell 10 flies and in the adjacent tunnel 5 more.

As the larva of her own was probably in the 3rd instar on the day of permanent closure of the nest, the work of the wasp can not be regarded as done for her own missing larva. Rather it should be considered to have been done as a proper response to the developmental degree of the newly given larva — the larva placed in cell B. This result was quite different in the response of the wasp from those of the previous instances.

(7) Wasp No. 135. Aug. 25, 1948. I opened the nest at 10.20 a.m. The structure of the nest and the axperimental arrangement set by me were as shown in Figure 25. In the brood-chamber of the nest was a larva of the 4th instar just after the moult, supplied with 5 flies, of which 1 was the pedestal and it alone had been eaten. I put in cell B a full-grown larva

* Strange to say, it was laid down without the pedestal. Probably the pedestal was taken out of the nest by the wasp. and indeed I could find a partly eaten fly at the entrance, half buried in sand.

without a prey, while in cell A nothing. The next day, at 9.05 a.m., I examined the nest. The entrance was left opened and a considerable quantity of sand had been thrown out of the nest. In cell B the larva was beginning to spin the cocoon and no fly had been carried in, while in the other chamber a victim had been placed. In the tunnel at the connecting point with each of the glass chambers, a partition wall had been made. At 9.18, the wasp came back empty-hnaded. At 9.26 she returned again without a prey. She entered the nest, but soon came out again and thenceforth repeated the same manoeuvre for a while. But when I saw her at 9.45, she was flying about low above the ground with a buzzing sound in search of the site of her new burrow. Two hours later she finished the selection of the nesting site and was eagerly digging in sand. The previous nest was permanently closed.



Figs. 25 and 26. Nests and experimental arrangements of Wasp Nos. 135 (Fig. 25) and 139.

In this instance, the mother wasp ceased her work in accordance with the full-development of the given larva and gave the nest the permanent closure. Though it appears that the cessation of her work is compelled by the encasement of the larva, it must be highly appreciated that she gaved the nest the permanent closure wherein she has stored only 6 victims in all.

According to the result of this instance, it is evident that the positive egg pressure in *Bembix* is not a so definite releasor as to determine the detailed schedule of her activity. The time of oviposition is, rather to a broad extent, regulated by the wasp itself according to the external conditions.

(8) Wasp No. 139. Aug. 26, 1948. I saw the wasp take in a prey to her nest at 10.30 and 11.20 a.m. respectively and dug it at 0.10 p.m. It was burrowed in from a trampled impression of a cattle and quite interesting to say, the tunnel was closed with a piece of dried dung of a cow at a distance of 5 cm from the entrance. Of course, the tunnel was closed, beside this closure, both at the entrance and in front of the brood-chamber. In the cell was a larva of the early stage of the 4th instar with 7 victims, of which 1 was already devoured. I arranged a Y-tube of glass and two bottles as shown in Figure 26. In one of the bottles (A) a nearly full-grown larva with 2 flies was placed, while in the other bottle (B) nothing. At 3.30 p.m., the wasp came back without carrying a fly. The tunnel of her own which remained untouched was only 4 cm in length. But the wasp entered the nest without showing any disturbance in her succeeding returns. The next day at 8.30 a.m., when I examined the nest, not a single fly had been added in either of the bottles and the wasp was resting in bottle B. She stayed there until 10.07, when she emerged from the entrance, closed there as usual and flew away. But she did not go far away, flying about around the nest as if she were

searching for the burrowing place for her new nest. On a third day at 9.00 a.m. the larva was spinning the cocoon already and no change was observed with regard to the prey of the larval cell. But in the other cell (B) a Syrphid fly had been taken in. Therefore, the mother wasp brought a victim after 10.00 a.m. of the previous day. The tunnel was permanently closed.

The behaviour of the wasp in this instance can generally be said to show the proper response to the change introduced on the larval development, in her irregular activity as well as in her earlier permanent closure given to the nest in comparison with the small amount of food brought by her in the nest.

d) Experiments of replacing the larva with the egg

(1) Wasp No. 77. Sept. 10, 1947. The nest was simple in structure, containing a larva of the early stage of the 4th instar and 8 victims, of which 2 were already devoured. I placed a bottle at the end of the tunnel and put in it an egg of another wasp with the pedestal fly. At about 2 o'clock in the afternoon, I saw the wasp repeatedly carrying out the sand from the burrow. The next day at noon I examined the nest. The egg together with the pedestal had been missing from the cell and a new tunnel was dug just beneath the bottle for some distance. Probably the wasp, carried out of her burrow the pedestal fly attached with the egg and threw it away as if it were a pebble or some other obstacle and then dug the tunnel in search of her own larva.

e) Summary of the results

In all the experiments conducted here a considerable variation on the response of the wasps to the given condition could be observed as described below.

1) *In the case when the larva was replaced with another of the earlier instar or of the smaller size* :

a. Some of the wasps did not or could not show the appropriate response to the altered condition, although a few of them were supposed to have taken notice the condition altered. They stopped their provisioning activity quite mechanically once they had accomplished a certain amount of her work responsible for her own larva, regardless of the state of the newly given larva and closed the nest permanently.

b. Others renewed their activity and continued to work in full harmony with the altered condition. A few of them could response to the repeatedly altered condition; hence the time of their next oviposition was markedly postponed.

c. Some others similarly showed the renewed activity and continued to work. But the manner of their activity was not well fitted to the state of the newly given larva.

d. In no case, however, the nest was abandoned.

2) *In the case when the larva was replaced with another of the later instar or of the larger size* :

a. Some of them did not or could not show the appropriate response to the altered condition, though a few of them seemed to notice the condition changed. The process of their activities can be explained in general on the assumption that they work merely on the standard of their missing larva. Therefore, they stopped their work only by being compelled to do so by the larva that began to spin the cocoon.

b. However, even in the above cases, some of them sealed up the nest by means of the permanent closure. But others did so only by means of the temporary closure.

c. Still others showed a proper response to the newly given circumstance and soon after the introduction of the full-grown larva closed the tunnel permanently, though they accumulated only a few victims in the cell since the beginning of their work.

d. But none of them did abandon the nest, save few in which the structure of the nest was also very markedly changed and at the same time the larva of their own was still very young.

3) *In the case when the larva was exchanged for an egg attaching still to the pedestal* :

a. The wasp invariably abandoned the nest after searching for her missing larva by digging a tunnel in sand.

5. Response of the wasp to the dead larva

(1) Wasp No. 62. Aug. 29, 1947. The larva of this nsst was in the 3rd instar, attaching still to the pedestal fly and bearing the shed skin at its posterior end. The prey accumulated were 6 in number, of which 1 (pedestal) was half eaten, 2 were decapitated and others were intact. I removed all the victims and put the larva in the bottle with a paralyzed spider of which I deprived a Pompilid wasp (*Episyron rufipes*). After a while the wasp retunred without a prey and entered the nest. She came in the bottle, walked in the chamber and touched the larva and the spider casually with her legs. But she did not show any special manner of examination of the contents of the cell with the antennae. Soon she came out and flew away. At 2.30 p.m., the cell was examined, but no victim had been brought in. The next day it was rainy, only temporarily fine in the morning. The subsequent day at 9.30, I opened the bottle. The larva had been dead and already rotten. The spider also had been rotten but it showed no trace of being eaten. On the other hand, quite interesting to say, 5 intact flower-flies and 1 intact bee-fly had been scattered on the dead larva. In addition to these untouched flies, remains of the thorax of a middle-sized flesh fly was found on the floor of the cell. Possibly the flesh fly was taken in late in the afternoon of the 29th and was eaten by the larva on the night. The larva might die by some reason (probably by failure of the moult owing to the excess of humidity of the cell) toward early in the morning of the 30th and the mother wasp gathered food for her young in the forenoon of the day. But whether or not she took notice the death of her larva I can not say. However, the state of the victims scattered irregularly in the cell seemed to indicate that the wasp might carry them about in the cell, that is to say, some disturbance might occur in the behaviour of the wasp. The reason of her confusion, however, was uncertain. It may occur by the presence of the spider,

or by her recognition of the death of the larva.

I removed all the victim but one flower-fly from the cell. At that time the dead larva was completely rotten and was about to decompose. The wasp did not return until the noon when the weather became clouded and began to rain. The next day (Sept. 1) it was rainy, but fine later, the succeeding day fine. It was supposed that the wasp worked on both days. But I could not go. On Sept. 3, at 11.00 a.m., I examined the nest. To my surprise, a fresh flower fly had been added in the chamber. It moved actively its mouthpart, indicating that it had been newly taken in. I continued the observation until the afternoon of the subsequent day. But no further fly was brought to the nest. The manner of the closure of the tunnel was of the temporary nature. It seems probable that the wasp did not respond to the death of the larva at least on the 30th when she gathered 6 flies for her dead larva. Judging from the presumable conditions it is supposed that the larva was not rotten as yet at that time. Probably the wasp became aware of the death of the larva for the first time when she brought the last fly to the brood-cell.

(2) Wasp No. 69. Sept. 3, 1947. In this instance I used a T-tube of glass and 2 bottles (Fig. 28) and placed in each bottle a just hatched larva and 2 flies including the pedestal. One of the larvae was the rightful offspring of the wasp. When I unearthed the apparatus on the 7th, the two larvae were brought together in one of the cells and several victims were also accumulated in the cell. The wasp was utilizing the other bottle as her sitting room, as if it were an accessory branch. On the 29th, whenever the behaviour of the wasp was observed, she touched with her antennae only one of the larvae which located interiorly; while she did not examine the other which located anteriorly excepting once when she entered the nest for the first time on that day. The wasp, on one occasion, was observed carry two of the flies from the entrance portion of the cell by the side of the interior larva. An hour later I found the anterior larva was dead. But at that time it appeared as lively as the other. It seems highly probable that this wasp could be aware of the death of the anterior larva at the first touch of her antennae, before it became rotten.

(3) Wasp No. 73. The condition of this nest were already described in p. 20 and the experimental arrangement in Figure 6. I put a just hatched larva of this nest and 3 flies in bottle B, while in the other (bottle A) a larva of the 2nd instar and 3 flies. The arrangement was set on Sept. 7, 1947. Two days later I knew that the conditions of the nest remained as thay had been excepting that the larva in cell B was dead and turned brownish. On a fourth day at 11.30 I changed the arrangement as shown in Figure 7, with the contents of both cells untouched. At 3 o'clock of the same day I knew that the interesting transfer of the larva which is so often observed in the nests wherein two larvae were placed in each separate cells had also taken place here. In this instance the living larva in cell A was transferred into cell B, in which the dead larva remained rotten at the interior portion. But no transportation occurred as to the victims. This wasp continued to bring food to the nest, but, so long as my observation continued, she remained the dead and rotten larva untouched.

(4) Wasp No. 98. Aug. 12, 1948. This nest was of the simple structure, involving a larva of the middle stage of the 4th instar and 9 flies, of which 4 were intact. I replaced the larva with another of the 3rd instar and put it in a glass bottle with 3 flies. It was at 9.10 in the morning. At 9.37, the wasp carried in a fly, but she did not come to the larva and went out again, only leaving the fly at the entrance portion of the cell. Later she took in 3 flies further until 10.09 a.m. But after that she did not work on the day, on account of the fact that her thoracic stigma happened to be painted by me through the failure of marking.

The next day, however, she recovered completely and was resting near the nest when I saw her at 11. 45 a.m. On examining the nest, however, I knew that no victim had been collected since that time and that the larva had been dead. On a third day at 0.23 p.m. the wasp returned empty-handed and went in the burrow, but soon she appeared at the entrance, roughly closed the entrance and at once began to search for the nesting place. The interior of the cell remained as before.

(5) Wasp No. 119. Aug. 17, 1948. The nest was of the simple structure and the larva in the brood-cell was in the early stage of the 4th instar. The larva was seriously injured at its caudal end by touch of the digging scopf. The prey were 9, of which 4 were already devoured. I placed the larva and a fly in a glass bottle and connected it with the end of the natural tunnel. The next day at 9.30 a.m., when I uncovered the bottle the larva was dead and began to rotten. No victim had been added in the cell. The subsequent day things remained as before. The entrance of the nest was closed roughly by means of the temporal closure.

(6) Wasp No. 138. I have already described regarding the condition of this nest (p. 18. Fig. 5). In this instance the larva was injured in the course of the preparation for the experiment. But the wasp accumulated for the larva 2 flies, one of whch was transferred from the other cell. When the rotten larva was found in the nest with the two flies, the nest had been permanently closed. Judging from the fact that the wounded larva dies very quickly and at once becomes rotten, it is presumable that the store of the flies in the larval cell was carried out after the death of the larva.

(7) Wasp No. 143. Aug. 13, 1949. The 4th instar larva of this nest was wounded in the course of digging by touch of the scopf. The victims found in the cell were only 3 in number. I placed the larva alone in a bottle at 9.00 a.m. and connected it with the end of the tunnel. Soon the mother wasp came back carrying a fly. She entered the bottle, touched the larva and returned in the tunnel. She came back at once in the chamber but without dragging the prey, touched the larva and returned again in the tunnel. Once more she repeated the same manoeuvre,' but did not bring in the prey. I cover the bottle and left her alone. At 3.00 p.m., the larva was dead and already changed blackish. The prey carried in under my observation in the forenoon was placed by the side of it. But no further fly had been added in the nest. Things remained unchanged for the subsequent several days and it was evident that the nest was abandoned by the wasp.

Summary of the results

(1) The response of the wasps was varied and the following cases were observed :

a. The wasp showed an unusual behaviour as soon as she touched the dead lerva with the antennae. In this case the nest was sooner or later abandoned, without being provisioned thereafter (Wasp Nos. 4, 5 and 7)

b. When one of the two larvae which were experimentally given died, the wasp became indifferent to the dead larva, prior to the putrefaction commenced (No. 2).

c. The wasp continued the provisioning activity until the larva became rotten, but then she stopped the work and abandoned the nest (No. 1).

d. The behaviour of the wasp appeared unchanged after the death of the larva. But in this case the following 2 types of response could be observed :

i) The wasp is supposed to treat the dead and rotten larva as if it were alive (No. 3, cf. the following section). But the subsequent activity was unknown.

ii) The wasp appeared to have accomplished the nest by the stimulus of the internal releasing factor alone, regardless of the death of the larva. But it was uncertain whether or not the wasp stopped the work by noticing the death of the larva, only closing the nest by following mechanically the course of the final part of the behaviour system.

(2) When they abandoned the nests, none of them remained the entrance opened. Some closed it by means of the temporary closure and others by means of the permanent closure.

(3) Judging from the results, it seems that the wasp can be aware of the death of the larva, as a rule, prior to its putrefaction. As an indicative response to such a recognition, the nest is sooner or later abandoned. However, as to the behaviour that follows the recognition, it is influenced in a differcnt degree by the innate automatism.

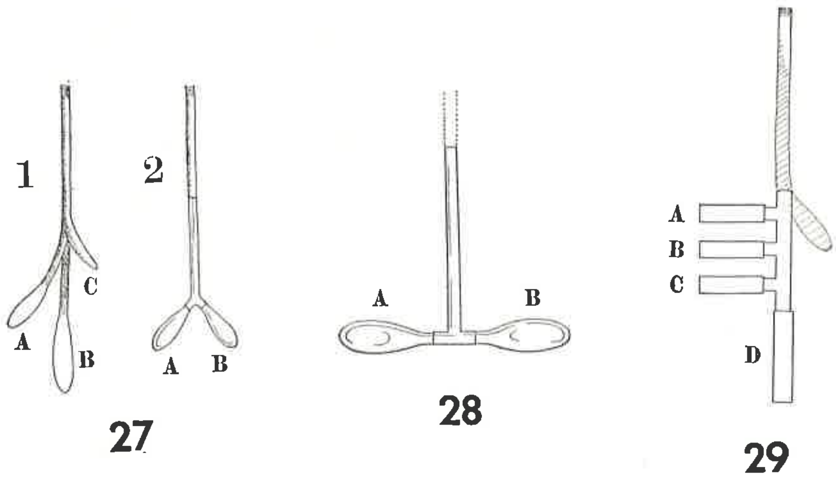
III. RESPONSE TO THE PRESENCE OF MORE THAN ONE LARVA IN A NEST

1. Experiments of placing two larvae in a nest

Our *Bembix* as stated in Part I of this paper, shows at times the interesting habits of rearing two larvae at a time in the same nest. Though in such a case the actual care of the two larvae taken by the mother wasp is quite restricted in time, the phenomenon seems to indicate that some possibility towards the sociall ife may be concealed in the life of *Bembix*. That is to say, if the wasp, when she is given experimentally more than one brood-cell, each containing a larva, in her nest, is able to feed them in harmony with the developmental conditions of each of them, we can be able to expect her a promising future towards the socia llife. With the aim of confirming whether or not such an ability is endowed to this wasp, I have made the experiments as described below.

(1) Wasp No. 68. Sept. 3, 1947. The nest was of the compound type as shown in Figure 27, 1. In brood-cell B, the larva had alredy encased, in brood-cell A a third instar larva with 7 victims was present. C in this figure was an accessory branch, probably the beginning of the 3rd brood-cell in this case. I cut open the burrow from behind until in front of its accessory branch and arranged a Y-tube of glass with 2 bottles attached to the end of each branch as shown in the same figure, 2. In bottle A was put the larva of this nest with 2 flies, in B a larva of the 2nd instar derived from another nest with also 2 flies. On a 2nd day at 10.30 a.m., the apparatus was uncovered. In A were added 2 flies and the larva grew into the 4th instar, while in bottle B no victim was brought in, but the larva attained the 3rd instar. In order to ascertain whether the wasp brought victim to bottle A only, as a response to her own larva, or as a result of the learning with regard to the direction of her own tunnel (vide Fig. 27, 1), I replaced bottles A and B with each other, together with each contents. At 3.15 p.m., I opened the nest. In bottle B were added 2 flies, while in bottle A nothing. The wasp seemed to carry in the victim to the left-hand cell according to her memory of the direction

of the previous tunnel. On a third and a 4th days the weather was bad. On a 5th day (the 7th) at 10.40 a.m., I examined the nest. In cell A there were remains of 4 flies, indicating that no victim had been brought in since the time of the bottle exchange; while in cell B the remains of 6 flies, showing that a fly had been taken in, probably late on the 4th. Both larvae attained the 4th instar and both were situated at the entrance of each cell in that characteristic pose which was usually seen when no eatable food remained in the brood-cell. The tunnel of the nest was already permanently closed.



Figs. 27 – 29. Nests and experimental equipments of Wasp Nos. 68 (Fig. 27), 69 (28) and 78 (29).

This wasp, though she must have contact with either of the larvae and brought food to either of them apparently did not respond to each of them as a separate individual. Accordingly she could not respond to them as two individuals. Other results obtained with regard to this wasp :

a) This wasp could not respond correctly to the larval dimension.

b) This wasp could not respond correctly to the scanty provisionment in front of the larva.

(2) Wasp No. 68 (B). Sept. 7, 1947. The nest was of the simple structure, having a straight tunnel of 25 cm in length and in the brood-cell there was a larva of the 2nd instar with 3 victims, of which 2 were already partly eaten. I cut off the brood-chamber and placed instead the arrangement used in the previous instance (No. 68) together with its contents. But bottles A and B were exchanged in situation for each other, namely A came on the left side and B on the right side. In order not the larvae to starve to death, I gave each of them one intact fly. The change given to wasp No. 68 (B) was not only that of the structure of the nest, but also that of the number and developmental degree of the larva. It was 11.00 a.m. At 3.30 p.m., I examined the nest. The entrance condition showed that the wasp had not entered the nest. As her own larva was in the 2nd instar it might be natural that she did not return so frequently to her nest after taking in one victim in the morning. It was a bad weather the next day. The subsequent day at 11.50 I uncovered the brood-cell and found that the larva placed in B had been transferred into A. Both larvae became so similar in size

that I could not distinguish one from the other. One of them was placed at the interior of the chamber and the other near the entrance. In the course of my examination the wasp returned empty-handed. She entered the nest and came in chamber A without hesitation. She touched the larvae one after the other in an inexpressive manner as usual. But nothing happened. She turned around, emerged from the entrance but at once entered again. The wasp came in A, touched the exterior larva and went back in the tunnel. There she stayed for a short while. During the time I hurriedly examined the contents of both chambers and knew not a single victim had been added in either of the chambers. I then exchanged the glass chambers for each other together with each contents. Thus chamber A including the 2 larvae came on the right side. The wasp soon came in the glass tube and, after repeating several times of the strange proceeding and retreating in front of the brood-cell, entered the right-hand cell (A) in this case, and carried out the exterior larva to the main tunnel. She appeared soon at the forking point of the tunnel and resumed the same queer manoeuvre of short proceeding and returning. At last, for the 9th time, she brought the larva from the tunnel into bottle B, the left-hand empty cell. Then she turned round aud went back in the main tunnel. Soon she emerged from the entrance but at once came in again. However, she did not come up to the brood-chamber and reappeared at the entrance. She entered again, came to the forking point, thrust her head in the right and then in the left, but without entering either of them went back. She emerged, entered again, went out without coming in the glass tube, penetrated once more, came in the right-hand chamber, touched the larva and went back. Then she went out of the entrance, flew about a little, alighted in front the nest, entered, came in the right bottle, touched the larva and returned in the tunnel. The next moment she began to closed the entrance, but instantly stopped the work, turned round and appeared at the branching point. There she thrust her head first in the right- and then in the left-branch, but without entering went back again. She resumed to close the entrance, this time fairly actively, but soon ceased the work once more and returned in the tunnel. Without coming up to the glass she appeared at the entrance at once, and finally the strange ingress and egress of the wasp came to the end. She closed the entrance by means of the temporary closure and, after making a simple orientation flight around the nest, flew away.

This strange behaviour of the wasp seems to me not to depend upon the mere change of the structure or of the illumination of the nest. Also the exchange of the brood-chamber in position does not seem to be the sufficient reason for the disturbance of the wasp. Probably the presence of 2 larvae in her nest was the principal reason of her confusion.

At 2.00 p.m., I uncovered the arrangement. One victim had been carried in the left-hand cell (B), but none in the other. At 2.47, in the left-hand cell had been brought 2 further flies, while in the other nothing. The next day (10th) at 9.40, the wasp was carrying out the sand eagerly from her nest. At 10.00 she was already out of sight. 1.00 p.m., on uncovering the cells I found that the small red ante, *Solenopsis fugax*, had ravaged the nest.

This instance may be regarded as showing the recognition of the wasp on the presence of more than one larva in her nest.

(3) Wasp No. 69. Sept. 3, 1947. The nest was of the simple structure, having a straight tunnel of 30 cm in length. In the end pocket was a larva of the 1st instar with 2 flies, one of which was the pedestal. I cut off the interior portion of the burrow and placed at the end of the tunnel a T-tube of glass attached with 2 bottles as shown in Figure 28. In A were put the larva and the 2 flies found in the nest, while in B the other 1st instar larva obtained from another nest together with 2 flies. The condition of both cells closely resembles with each

other. It was at 3.30 in the afternoon. The next day at 10.30 the nest was uncovered. All remained as they had been. Both of the larvae were eating respectively the 2nd victim across the thorax of each pedestal. At 3.35 I found 3 victims had been added in A and 1 in B. The 2 subsequent days the weather was bad. On a 5th day (the 7th) at 10.50 I dug open the arrangement and knew that the same interesting transfer of the larva as we saw in the preceding instance had occurred also here. Cell B became empty, while cell A contained the 2 larvae inside, one at the entrance- and the other at the interior portion of the chamber, keeping some distance between them. Probably the interior one might be the regitimate larva of the wasp. By the side of this larva was placed a horse fly, transported by the mother wasp. The wasp was resting in the empty bottle (B) and when I opened the nest she crept slowly and went in the main tube. As the surface of the entrance remained evened by the rain of the previous day, it was supposed that the wasp passed a long time in her nest. While she was absent I examined the contents of bottle A without touching it and knew that the prey were 10 in number, including remains, that is to say, 2 were increased since 3.30 p.m. of the 4th. Soon the wasp opend the entrance from the inside and flew away. At 1.47 p.m. she came back with a prey. But as I disturbed her repeatedly by my photographing, she discarded the fly at last and flew off. However, only a minute lafer she returned carrying another fly. At 2.40 again she took in a victim. But later until 3.30 she did not return. On examining the the burrow I knew that the flies were placed in A. The larvae, keeping a distance of 1 cm between them, were peacefully feeding upon the victims. A 6th day, it was rainy. On a 7th day (the 9th) at 1.20 p.m., I saw the wasp enter the nest and at once uncovered the arrangement. The larvae were in bottle A as before and in the chamber were scattered many flies, not regularly piled up at the entrance portion. The mother wasp spent the time in the tunnel and did not appear in the glass tube. But soon after, she carried the victim in A as usual and then rested in B. Meanwhile she proceeded slowly, with the sweeping movement into A, then walked to the interior larva and touched it with her antennae. She then turned round and went back to the entrance of the cell. There she stopped a moment and touched the 2nd larva also with her antennae. Then she took up a fly and carried it backward to the interior larva. Once more she transported a fly from the entrance by the side of the larva. Next she returned to B. From that time for a while the wasp repeated going and coming between A and B. Whenever she passed the tube between the cells, always she showed the sweeping movement. The manner of her walk was always of the forward proceeding. In both cells she went to the interiormost wall and returned from there. Probably she could not find her wasy out. But whenever she entered cell A she touched the interior larva. At last she turned to the main tunnel, but at once returned in A, touched the interior larva once more and went in B (probably by error). Then she turned to the basal tunnel and flew away. At 1.40 p.m. she returned carrying a booty. Uncovering the branching portion of the tube I waited for her coming. The wasp opened the closure that had been made there and went in A. I uncovered the bottle also. The wasp suddenly stopped her step, stretched out her antennae forward (probably a pose of self alarming), then grasped one of the victims that were under her jaws and carried it backward in B. She did not appear from there. So I covered the arrangement. After a while she came out of the burrow, closed the entrance and started off. At 2.30 I examined cell A and found that the larva at the entrance portion was already dead, though it was as fresh as alive. It was in the 3rd instar. The interior larva had just moulted the 3rd instar skin. The prey were numerous, but I did not count them.

I removed the dead larva from cell A and introduced another larva which was of the later stage of the 4th instar (about 8/10) in cell B and gave it 3 flies. The next day (a 8th day — the 10th), at 0.03 p.m. I saw the wasp enter her burrow with a victim. She stayed inside till 0.10 and went off. At 1.15 she brought in another victim. At 0.30 ditto, at 0.41 ditto. At 1.20 I examined the nest and was greatly surprised. In cell B the larva had been killed. About two thirds of its neck (the first thoracic segment) had been cut off and the larva was dead. As the 2 flies that I placed with it were entirely devoured excepting the thoracic skeletons, it was supposed that the larva was alive for a considerable period in the chamber. Moreover, the freshness of the dead body of the larva told that the murder was taken place not long before. Rest of the victims were pulled out of the cell and discarded in the adjacent tube. I convinced that the murderer must be the wasp of this nest and the time of murder may be from 0.03 to 0.10 p.m. when the wasp carried in the victim for the first time on that day*. Later I made the food-eliminating experiment with this wasp. She worked hard and brought a number of flies to the nest during the work of her compensatory activities (p. 83).

Judging from the behaviour of the wasp —— gathering 2 larvae in one of the cells and examining them distinguishably when one of them became dead in the first experiment, and killing one of them which was markedly larger than her own in the second experiment ——, it seems considerable that the wasp recognized the existence of more than one larva in her nest. But it is quite unknown why she killed the newly introduced large larva in the second experiment.

(4) Wasp No. 78. Sept. 10, 1947. A part of the present experiment has already been given in Part I of this paper (p. 164). The nest was of the simple structure (Fig. 29) containing in the brood cell a larva of the early stage of the 4th instar and 9 victims, of which 7 were untouched. I set the arrangement at 10.00 a.m., as shown in Figure 29. The contents in each cell were as follows : A — the larva (a) of this nest which was at the early stage of the 4th instar and 2 flies. B — A just moulted 4th instar larva (b) and 2 flies. C — Two intact flies alone. D — Seven intact flies without a larva. I covered the arrangement with sand. At 11.07, the wasp entered the nest dragging a fly. But I let her alone. At 3.00 p.m., I examined the nest. The change occurred inside the nest since 10.00 a.m. was as follows : A — The larva (a) and 9 flies. B — The larva (b) and 4 flies. C and D — empty. In addition, one fly was laid down in the glass tube close to the entrance to A. The results evidently indicate that the response of the wasp to the cell including a larva was quite different from that which was directed to the cell without a larva. It is uncertain, however, whether she recognized the larvae as separate individuals or as one and the same larva.

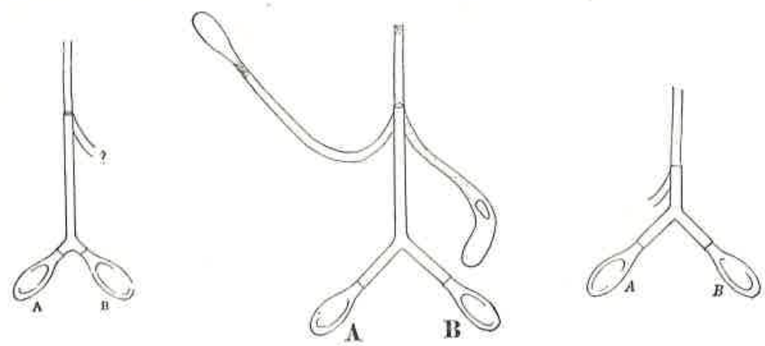
I changed the relaitve position of each cell together with the contents of some of the bottles as follows : C (in the place of A) — No larva but 2 flies. B (in its original position) — The lasva (b) and 4 flies. A (in the place of C) — The larva (a) and 7 flies. D (in its original position) — empty. The next day in the forenoon, several times I saw the wasp carrying in a victim to her burrow. At 1.45 p.m., she was closing the tunnel permanently using the tip of her abdomen. I examined the nest at once. The results were as follows : C — Five flies, namely 3 were added. B — The larva (b) and remains of 5 flies, namely 1

* When I arrived at the place at 9.40 a.m. the entrance of this nest was closed and it remained closed, until the first return of the wasp at 0.03 p.m. This is an evidence that the murder is not the result of invasion of some other carnivorous insects, since these intruders usually leaves the nest with the entrance opened. Moreover, if the larva was killed by some intruder, it must not remain without being devoured.

fly was brought in. A — The larva (a) and remains of 9 flies, namely 2 flies were taken in. D — empty. In addition, in the tube between the entrances to C and B 1 fly was laid down and between those to B and A 1 more fly.

In this instance it is very obvious that the wasp recognized the larva and brought food to it. But it is still uncertain whether she reponded to the 2 larvae as separate individuals or not.

(5) Wasp No. 80. Sept. 10, 1947. The wasp of this nest was in the course of provisionment, but I could not find the brood-chamber. I set the arrangement composed of a Y-tube of glass and 2 bottles as shown in Figure 30. In cell A were put a larva of the middle sfage of the 4th instar and one fly, while in cell B an egg attached to the pedestal. Thirty minutes later (at 2.30 p.m.) I examined the nest. The mother wasp was in the tunnel and when I uncovered the arrangement she came in cell A, touched the larva and returned in the tunnel. Again she



30 31 32

Figs. 30 - 32. Nests and experimental equipments of Wasp Nos. 80 (Fig. 30), 89 (31) and 96 (32).

entered bottle A, touched the larva with her antennae and went back in the dark tunnel. The same behaviour was repeated twice further. But she never entered bottle B. The entrance to it was half closed with sand, probably by the mother wasp with the material fallen from the aperture between the tube and the bottle. Soon, she appeared at the entrance, closed there roughly and flew awav. I cleaned off the sand stoppage at the entrance of cell B. The next day at 2.00 p.m., I examined the nest. No change had occurred excepting that the larva in A was dead. The entrance was closed by means of the temporary closure. As I did not see the wasp working at her nest since that morning, it was clear that the nest was abandoned. Probably the death of the larva and the introduction of an egg were the causes of her nest abandonment.

In this instance it seems that the wasp recognized the larva and the egg as separate beings, since she closed only the entrance to the egg cell.

(6) Wasp No. 89. Aug. 9, 1948. The nest was opened at 0.20 p.m. This was a branched nest, having 2 brood-cells inside. In one of them was a larva of the 3rd instar attaching still to the pedestal with 3 victims. Only the pedestal fly had been partly eaten. In the other cell was a cocoon. The remains of victims in this cell were correspondent to 22 flies. I placed a Y-tube of glass at the end of the straight portion of the tunnel and attached at the tip of

eash branch a bottle of the same size and form (Fig. 31). In bottle A were placed 3 flies without a larva, in the other (B) the larva of this nest with its pedestal-fly. Under these conditions I attempted, in the first experiment, to confirm whether or not she can make a compensatory activity for the missing provisions, by removing from time to time the victims stored in the brood-cell. The wasp, from that time onward until 9.25 a.m. of the 12th, carried in the brood-cell 31 flies. During the period the prey were removed 5 times successively from the cell and the larva was replaced once with another of the 3rd instar. At 9.25 a.m. of the 12th, I changed the contents of the nest as follows : In the left-hand bottle (B) was put a larva of the 2nd instar with its pedestal fly, in the right-hand bottle (A) the larva used in the preceding experiment (a larva of the middle stage of the 4th instar) with 2 flies. At 9.54 the wasp entered the nest carrying a fly. She came in the exposed portion of the tube but retired in hesitation. So I covered the tube up to the branch. The wasp came in at once. First she entered the branch leading to B and in the bottle touched the larva. Then she turned round and went back in the tunnel. The next moment she returned backing with the prey and dragged it in A. She then proceeded in B, touched the larva and again went in A. There she went up to the interiormost wall of the chamber, touched the larva and returned in the main tunnel. Soon she emerged out of the entrance and flew away. This time, in spite of the change occurred both in size and in number of the larva in her burrow, she dtd not show any noteworthy confusion. At 1.10 p.m., in bottle A had been accumulated 6 flies further and in bottle B 3 more. The larva in bottle B grew into the 3rd instar. I buried the arrangement without giving any change. On the 13th, at 11.30, in A not a single fly had been stored and the larva was devouring the remains of food by crambling them minutely, while in B 7 flies had b eenadded. The larva had grown into the early stage (about 2/10) of the 4th instar. The basal portion of the glass tube had been closed temporarily with sand. I cleaned both bottles and put in B the younger larva with 2 intact flies and in A the elder larva (at 7/10 grade of the 4th instar) with 1 uneaten fly. On the 14th, when I arrived at the place the surface of the sand remained evened by the rain of the previous night and no trace of the work of the wasp could be observed. At 8.43, the wasp returned from the field without carrying a prey and entered the nest. Soon she came out and flew away. At 9.07 when I saw the nest a flower-fly was rejected in front of the nest. The wasp was in the nest aud pushed out the sand from within. When I went to the nest at 9.35, the flower-fly was half buried in the thrown-out sand and a yellow horse fly was also discarded in addition. The wasp was in the burrow and digging the tunnel. At 10.36 the entrance was closed and the 2 victims thrown aside in front of it was missing. At 10.42, she carried in another fly, this time without showing any disturbance. Two minutes later I examined the nest. In A : The larva (nearly full-grown) and the remains of 2 flies. The branch-tunnel of glass leading to the bottle was compactly stuffed with sand. In B : The larva (nearly 4/10 grade of the 4th instar) and 6 flies, including remains. The results indicate that one fly was added in A and 4 in B. Examination of the species of the victims made clear that the discarded flies were taken in bottle B (such a phenomenon is rather exceptional).

I exchanged the bottles together with the larvae for each other, namely, put A on the left and B on the right. As for the victim I placed only 1 in B and none in A. The closure of the tunnel leading to the newly placed B was cleaned off. At 11.14, just after fhe wasp took in a victim, I examined the nest. In the right-hand bottle (B) were added 2 flies, one of which was placed by the side of the larva and the other left near the entrance of the cell. In the left-hand bottle (A) was brought one fly and the larva was feeding upon it. At noon one fly had been carried in bottle A, while in B nothing. I removed the large larva from bottle A and placed instead another larva of the 4th instar which was just moulting, together with one victim. At 0.05 p.m., the wasp took in one more fly and dragged it in the left-hand bottle (A). At 0.21 she carried in another fly and flew away a minute later. From 1.04 to 1.13, the wasp was packing the tunnel of her burrow with sand by means of the permanent closure. At 3.35 I examined the nest. In the left-hand bottle (A) were added 5 flies and in the right-hand bottle (B) 3.

Now, if we put in order the prey supplied to each larva by the wasp, we obtain Table 6.

Table 6. Provisioning activity of Wasp No. 89 for the 4 larvae (2nd–5th) which were given successively. (Shown by the Number of prey collected.)

Larva	The 1st	The 2nd	The 3rd	The 4th	The 5th	
Species / Period	Egg – encasem.	Egg – 4.7/10	3 inst. – 4.8/10	2. inst. – 4.5/10	4. inst. – 4.2/10	Total
Tabanus mandarinus				1		1
Ochrops fulvus	2			1		3
Heterochrysops sp.			2			2
Eristalis cerealis	1		9	9	2	21
Eristalinus sp.			1		1	2
Rhagionidae sp.				1		1
Villa limbatus		4	2			6
Lucilia spp.	3	7	6	5	2	23
Sarcophaga spp.	16	6	3	1	1	27
Gymnochaeta elegans		1	1			2
Anthomyiidae spp.		2				2
Neoitamus angusticornis				1		1
Total	22	20	24	19	6	91

According to the above table, the victims supplied to each larva are nearly equal in number and seem to be proper to the standard quantity of food of our *Bembix*, excepting for the 5th larva. As for the exceptional case, it is considered that, when I introduced the larva in the nest, the wasp has already entered the final course of provisionment that is usually carried out automatically. If we account for the results of the wasp's activities as above, it appears that the manner of her work was correct as responses to the developmental degree of each larva excepting for the 5th larva. On the other hand, if we put in order the same data aaccording to the direction of the tunnel laeding to the brood-cell, the conclusion becomes quite another thing. Table 7 was made according to such a consideraion. In this table the same type of letter represents the same larva. However, before setting on the consideration upon the results, we must take into account the following facts : 1) In the Y-tube, the direction in which the victim is transported does not always agree with the direction intended by the wasp, since the transportation is carried out by the backing progress and the victim is sometimes carried in another direction than that in which the wasp has gone in her first visit. 2) But when the victim has been transported to the erroneous place, the wasp frequently retransports it to the correct larval cell. Taking into consideration the above described facts, we may be able to give the following interpretation to the Table :

Table 7. The analytical table of the adaptive provisionment of Wasp No. 89.

	Column	a	b	c	d	e	f	g	h	i	j	k	l	m
	Date examined	VII. 9	〃	.11	〃	〃	〃	.12	〃	.13	.14	〃	〃	〃
	Time examined	12.15	2.55	7.00	9.00	12.25	1.05	9.25	1.10	11.30	9.42	11.14	12.05	1.15
Left	Larval growth	3.–	3.–	$4.\frac{6}{10}$	$4.\frac{6}{10}$	*3.–*	*3.–*	$4.\frac{5}{10}$	2–3	$4.\frac{2}{10}$	$4.\frac{4}{10}$	$4.\frac{8}{10}$	$4.\frac{9}{10}$	$4.\frac{1}{10}$
	Prey remained	–	1	4	13	*3*	*3*	*5*	1	4	2	*0*	*1*	*1*
	Prey taken in	4	3	9	4	*11*	*2*	*2*	3	7	4	*1*	*2*	*5*
Right	Prey taken in	–	2	0	0	0	2	0	*6*	*0*	*1*	2	0	3
	Prey remained	–	3	1	1	1	3	1	*2*	*8*	*1*	1	3	3
	Larval growth	–	–	–	–	–	–	–	$4.\frac{6}{10}$	$4.\frac{7}{10}$	$4.\frac{8}{10}$	$4.\frac{4}{10}$	$4.\frac{4}{10}$	$4.\frac{5}{10}$

a) Columns b – g indicate that the wasp worked as a response to the larva placed in one of the cells, probably under the recognition of the presence of one larva, since she brought the flies to the larval cell not only from the field, but also from the other uninhabited cell.

b) Columns e and f, however, represent improper activities as responses to the third instar larva. These will be merely an extension of the previous work carried out for the 4th instar larva (the 2nd larva). Probably here is no proper response to the developmental degree of the given larva.

c) After 2 larvae were placed in the nest, one in each cell, the number of the prey transported in the left-hand cell — the cell located in the learned direction — is 22, while to the right-hand cell only 12, in spite of the fact that the developmental conditions of the larvae in both cells are approximately equal on an average.

d) Columns h – k appear to indicate the proper reaction of the wasp to each larva.

e) Especially column h, when we take into consideration the prepossessed memory regarding the left hand direction, must be appreciated high.

f) Whereas, columns l and m are improper activity for either of the larva.

The above accounts show that the behaviour of the wasp is full of self-contradiction. The principal reasons for such a self-contradiction, however, seem to me to lie not only in that the number of prey transported in one cell does not always correctly represent the intention of the wasp, but also in that the work of the wasp is not carried out under the general view of the inner conditions of the nest. It is easily considerable that the wasp responds only to the transient impulse of the moment received from this or that larva. In reality, the wasp does not always examine both larvae before she transports the prey from the tunnel. It may come, therefore, that the larva to which the wasp attends first is likely to become the direct impulse of the subsequent behaviour of the wasp. At any rate, judging from all the results of the experiment given above we may be able to draw the following conclusion :

i) The wasp continued her provisioning activities under the impulse obtained from the larva and also from the amount of its food.

ii) It is not conclusive but highly probable that the wasp can respond to the developmental degree of each larva and supplied food in consonance with it, except for the 5th larva.

iii) Nevertheless, it is uncertain whether she responded to the 2 larvae in her nest as separate individuals or not.

(7) Wasp No. 96. Aug. 11, 1948. The nest was dug at 11.00 a.m. The brood-chamber became unknown by failure of digging. However, the wasp was seen carrying in a prey only twice since early that morning, it was supposed that the larva was in the early instar. I set the arrangement as shown in Figure 32. In bottle A were put a larva of the early stage of the 4th instar and 7 flies, while in bottle B a full-grown larva and 4 flies. At noon, I examined the nest. The larva in B was absent from the cell and no fly had been taken in either of the cells. I examined the natural tunnel throughout from behind so as to find the missing larva. The mother wasp was sitting in the tunnel, but the larva was not located even there. Probably it was carried out by the mother wasp and thrown away.

In this instance the wasp responded differently to the two larvae placed in her nest. Possibly she became aware of the presence of more than one larva in her nest. Especially it seems interesting that the larger larva was discarded from the nest.

(8) Wasp No. 107. Aug. 15. 1948. As to the conditions of the nest and the first experiment made with this wasp an account has been given elsewhere in this papar (p. 28). In short, I succeeded in inducing the wasp to enter the abnormal brood-cell formed by a Petri dish of 10 cm in diameter, with the legitimate larva of the wasp in it. The larva was in the middle stage of the 4th instar. The wasp carried in 8 flies for the larva from 10.40 a.m. to 2.52 p.m. of the day.

I then introduced another larva of the same size in the brood-chamber, supplying it with 2 victims (Fig. 33, B). The next day at 10.20 a.m., I opened the brood-room. The larvae and the victims accumulated were located as shown in the same Figure, C. The victims left on the previous day were all devoured, and those newly brought in were 6 in number. I removed all the victims and the remains from the chamber and put 2 flies by the side of each larva respectively. At 10.40, the wasp carried in a green bottle fly and 2 minutes later flew off. On examining the chamber I found a flesh fly lying near the entrance of the room, but the green bottle fly was not in the chamber, At 1,00 p.m., I saw the wasp carrying in a large bee-fly. I uncovered the chamber. The wasp was in it carrying the prey and was thrown into confusion by the sudden illumination. She flew buzzing inside the chamber, so I covered the glass. As she responded very sensitively to the light I could not observe her behaviour. At 2.40 I uncovered the Petri-dish. The prey were 11 in number, including the remains (Fig. 33, D). Among them was placed the green bottle fly. According to the fact it is inferred that sometimes the wasp leaves the victim temporarily in the tunnel in the course of her busy hunting activities. The location of the prey was as follows : By the side of one larva 2 intact and 3 eaten flies, by the other 1 untouched and 5 eaten flies. I then shifted the larvae so as to give a considerable space between them, lest they should open hostility with each other, and placed one victim respectively by the side of them, removing all the rest from the chamber.

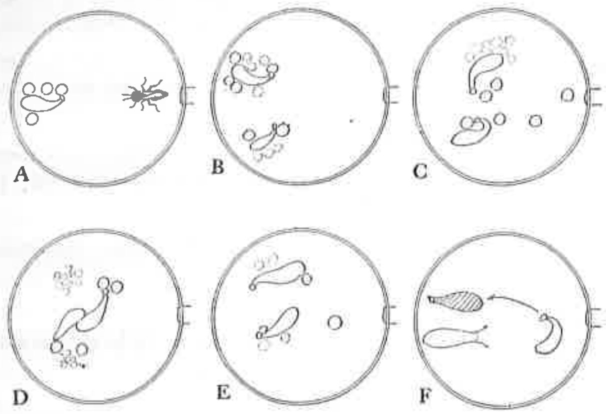


Fig. 33. Successive states of two larvae in a Petri dish. Circlets in solid line rspresent the intact flies, those in dotted line remains of flies. Experiments on Wasp No 107.

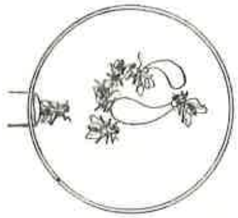
On a third day at 9. o'clock in the morning, one of the larvae became full-grown and the remains of 3 flies were scattered by the side of it, while the other larva was of 7/10 grade of the 4th instar and was supplied with 3 flies, of which 2 had been remains (Fig. 33, E). The first larva was searching for the foot-hold to spin the cocoon. But the second larva was lying still in a characteristic pose of waiting for food. Both larvae directed their heads towards the interior. The tunnel, however, had been permanently compactly closed. Probably the victims might have been taken in the previous day. The larvae were left alone for 2 days more. The larger one spun the normal cocoon, while the smaller one died possibly in starvation.

In this instance, judging from the situation of the larvae in the chamber, the wasp is supposed to have become aware of the presence of more than one larva in her nest. Moreover she seems to have worked to a certain degree for the provisionment of the two larvae, although she could not perfectly adjust her activity to the given conditions.

(9) Wasp No. 113. Aug. 17, 1948. As to this instance, the form of the nest, the experimental arrangement, the first observation on the behaviour of the wasp in the altered brood-cell and so on, were already described (p. 31, Fig. 15). I placed in the chamber formed by a Petri-dish of 5 cm in diameter two larvae, one of which was the rightful offspring of the wasp and of the 3/10 rank of the final instar, while the other was brought from another nest and was of the 6/10 rank of the same instar. Not a single fly was supplied to either of the larvae. At 10.15, the wasp took in a green bottle fly to her nest. She came in the exposed Petri-dish, walked about in it and touched the larvae one after the other. But she soon felt the light and was thrown into confusion. So I covered the chamber. But by peeping through an aperture left in the sand-cover I could observe the wasp touching the 2 larvae alternately with her antennae and then searching about for the exit. Soon she went

in the tunnel. While she was absent I opened the chamber and placed 5 victims in the centre of it, putting the larvae to the pile of the food, one from the south and the other from the north (the exit was situated in the west). The wasp emerged from the entrance at 10.30. During her stay in the burrow I did not observe her behaviour. She swept in a little quantity of sand to close the tunnel, but stopped the work at once and entered the burrow again. This is a simbol of disturbance of the wasp. Soon she appeared again and this time completely closed the entrance and flew away. At 11.10 I examined the chamber. The larvae had moved, probably for themselves, as shown in Figure 34. The green bottle fly had been placed near the entrance in the cell. At 11.27, the wasp took in a fly and 2 minutes later flew off. In the chamber the larvae shifted their position (or they might be shifted by the mother wasp) and were eating side by side, with their heads directing to the opposite sides. The green bottle fly taken in the previous return of the wasp was brought by the side of the larvae and a flower fly that was carried in just before was placed near the entrance in the chamber. At 0.20 p.m., again the wasp brought a victim to her nest. Four minutes later she flew away. In the chamber were found 7 flies as before. But in the adjacent enlarged tube 3 more flies were found. The state of the provisionment told that the wasp already entered the final automatic course of her work. At 3.40 in the enlarged tube were added 3 more flies. The wasp was in the glass tube and was at work for the permanent closure. The subsequent day at 9.00 a.m., the wasp was digging a new burrow at a distance of only 20 cm from the previous nest. In the chamber the 2 larvae were growing peacefully. They were spinning the cocoon when I observe them the next day.

In this instance, the wasp is supposed to have known the existence of more than one larva in the brood-chamber. It is interesting that she fed the 2 larvae peacefully, without taking out either of them. But it is uncertain whether the provionment made by her since that time was intended as food for the 2 larvae or not.



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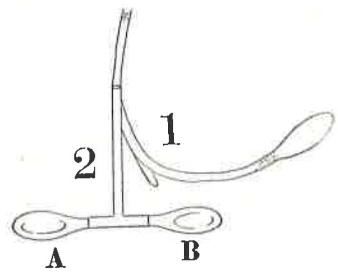

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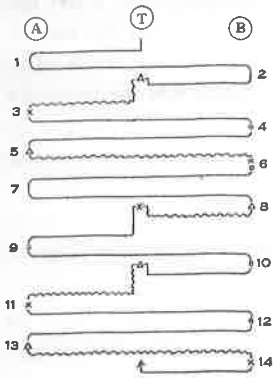
Figs. 34 and 35. An experiment on Wasp No. 113 (Fig. 34) and the nest and experimental equipment of Wasp No, 114.

(10) Wasp No. 114. Aug. 17, 1948. I saw a wasp carry in a green bottle fly to her nest at 10.50 a.m. and dug it at 11.00. The tunnel was gently curved, about 28 cm in length and had an accessory branch behind the middle. It was of the simple type. In the chamber was a just hatched larva on the pedestal fly (*Sarcophaga carnaria*) which was already covered with mould and by the side of it was placed the green bottle fly that I had observed to be

carried in. I used a Y-tube and 2 glass bottles and arranged them as shown in Fig. 35. In bottle A were put the larva and the 2 flies, while in bottle B nothing. At 1.00 p.m. the wasp was resting in bottle B, and the entrance to A was closed with sand. Probably the closure was made by using the material dropped from the joint between the tube and the bottle. After the wasp went out I put in bottle B another first instar larva attaching to the pedestal (*Theloria leucozona*) with one flower fly (*Eristalinus sepulchralis*). At 3.30, in A had been transported the flower fly from bottle B and was placed at the innermost portion of the cell, while in B the larva with its pedestal remained as before. The next day at 10.04 a.m., while I was examining the nest the wasp came back carrying a green bottle fly and at once entered the nest. The contents of each cell remained as on the previous day. I uncovered the arrangement excepting for the basal portion of the T-tube and observed the wasp's behaviour. It was as shown in Figure 36.



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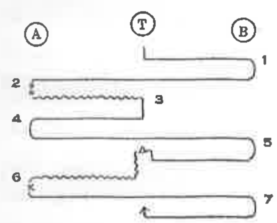

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Figs. 36 and 37. Behaviour diagram of Wasp No. 114 in the T-maze. Detailed explanation in the text.

In the figure, *the solid line stands for the normal forward progress of the wasp without carrying the fly, the wave line for the backing progress dragging the fly,* △ *for the behaviour of taking up the fly,* × *for laying down the fly,* ○ *for touching the larva, T for the main tunnel, A for bottle A placed on the left, B for bottle B placed on the right.*

After showing the movement and behaviour represented in the above figure, the wasp emerged out of the nest, but at once entered again. She came in the basal tube, but did not proceed in the branch-tunnel, retreating only from the turning point repeatedly, so I covered the arrangement with sand and left the place. After 5 minutes the wasp was observed closing the entrance and flying away. I examined both chambers and found a very interesting result of the wasp's behaviour. In chamber A were a larva attaching to the Tachinid fly (which had been in bottle B) and 2 victims (a green bottle fly and the flower fly), while in chamber B the green bottle fly alone which had been just carried in. The larva attached to the rotten flesh fly (which had been in bottle A) was missing from either of the cells. I examined the surface of the ground in front of the nest if it was thrown out of the nest. Certainly it was there, discarded at a distance of 15 cm from the entrance. The larva was still alive and was attaching to the pedestal. I replaced it again in the chamber, but this time in B. Both larvae had attained the 3rd instar. Probably the wasp, while I was away, carried out the rotten fly together with the attaching larva. But it is, of course, uncertain whether she discarded the larva as an excessive and needless one or without taking notice on its existence upon the fly. Moreover, if the latter consideration holds true it is still uncertain whether the wasp carried the flesh fly out of the nest because of its getting musty or merely as an obstacle in her burrow. But it will be certain that the cause of the event does not lie in that the structure of the nest was altered, since the wasp had become famillar with the structural change beforehand. Probably it will be one of the expression of the wasp's confusion given rise to by the presence of more than one larva inside her nest.

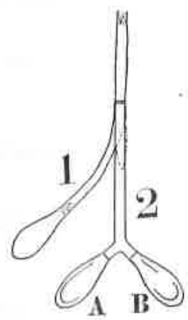
At 0.20 p.m. I examined the nest and found that the larva replaced in B had been transported in A and the 2 larvae were pecaefully feeding upon a near-bye victim respectively. The green bottle fly that was carried in B in the preceding observation, too, had been in A, and instead a newly brought horse-fly had been placed in B. The victims found in A were 7 in number including the 2 pedetsal, of which 2 were the newly brought ones. I left the contents of both cells *in situ*. The next day (the 19th) at 9.00 a.m., I dug open the brood-chamber and found both larvae in bottle A remained as before. Both were already in the early stage of the 4th instar. In the bottle had been added 5 victims, one of which was the horse-fly which had been in the other bottle the previous day, while the latter bottle was empty. At 9.12, the wasp came back capturing a fly. Her behaviour in the exposed arrangement was as shown graphically in Figure 37.

After the manoeuvre she entered the tunnel once more, but returned from the dichotomous point without visiting the brood-chamber, closed the entrance and flew away. I then changed the experiment into another sort regarding the maze learning (p. 92).

In this instance it seems that the wasp did not respond at all to the larva in cell B at first. But later she became to respond to it. However, her behaviour shown since then until she brought together the 2 larvae in one cell indicates clearly that she did not respond to the 2 larvae as separate larval wasps. Especially from Figure 36 we can easily perceive that her responses to the two larvae are perfectly the same as she responded to one and the same larva. There is no discrimination made between them, since the meeting with a certain larva appears always to give rise to the impulse in her to bring food to it. Therefore, when she met with larva b in cell B, she carried a fly from cell A to B. But, the next moment, when she met with larva a in cell A, she at once carried a fly from cell B to A. Howerver, after gathering the 2 larvae in one of the cells, apparently she responded to the 2 larvae (or, rather to more than one larva) as separate individuals. Moreover, the behaviour itself of gathering 2 lavae in one cell may be regarded as showing the beginning of such a response, since it may be a casual result of the wasp's behaviour evoked in order to remove something like uncertainty or uneasiness, which is given rise to by the vague recognition of the presence of more than one larva in her nest.

(11) Wasp No. 131. Aug. 23, 1948. The structure of the nest and the experimental arrangement were as shown in Figure 38. In the brood-cell was a just moulted 4th instar larva having the shed skin at its caudal end and still attaching to the pedestal fly. The victims were only 4 in number, of which 1 was eaten, 1 was just being eaten and the remaining 2 were intact. In bottle A I put the larva and 3 flies, in bottle B a larva of the 3rd instar from another nest with also 3 flies. Two days later, when I examined the nest it was in the course of invasion of a troop of small red ants. The larvae were both killed and together with the flies were swarmed by the ants. But as it was not long after the invasion, the results of the wasp's work of the previous day remained without undergoing any essential change. In bottle A, 3 flies had been added and the larva was in the early middle stage, while in bottle B only 1 fly was newly carried in and the larva was soon after the final moult.

From the result it seems that : (a) The victims carried in by the wasp are comparatively small in number to be regarded as the mere succession of her previous work. The wasp may receive some restraining impulse from the 3rd instar larva placed in cell B. (b) Notwithstanding, the ratio in the number of the taken-in prey to each larva is proper as compared with each developmental degree. However, at



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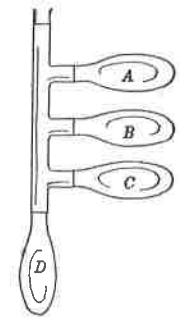

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Figs. 38 and 39. Experimental equipments of Wasp Nos. 131 (Fig. 38, 2) and 94.

the same time we must take into accout that cell A is situated in the vantage direction as compared with cell B. Therefore. it may be better not to emphasize account (b) of the above statement. What we can safely say regarding the result of this experiment is that the wasp did not thrown away either of the larvae nor bring together both larvae in one cell but brought food to each of them which lived in separate cells.

Summary of the results

(1) Out of 11 instances stated above, 9 were concerned with the experiment using a Y-tube and two bottles.

a. In 3 instances out of the 9, one of the larvae was transported to the other cell and placed with the other larva, keeping some distance between them.

b. In 2 instances, one of the larvae were carried out of the nest and was discarded by the wasp.

c. In 1 instance, one of the larvae was killed probably by the wasp.

d. In the remaining instances the wasp did not bring together the larvae in one cell and she fed either both of them or one of them, though in most instances the victims carried in the nest could not be regarded as sufficient for the nurriture of the given larvae.

(2) In the remaining 2 instances a Peti-dish was used as a brood-chamber and 2 larvae were placed in it. In these instances the larvae were fed peacefully in the chamber, not one of them being killed nor carried out of the nest.

2. Experiments of placing more than two larvae in a nest

(1) Wasp No. 94. Aug. 11, 1948. At 10.20 a.m., I dug the nest. It was of the simple

structure and contained in the brood-chamber a larva of the early stage (1/10 grade) of the final instar which attached still to the pedestal-fly. The prey stored were 6, 2 of which were already eaten. I arranged instruments of glass at the end of the natural tunnel of the wasp as shown in Figure 39. In bottle A I put a grown larva (in about 7/10 rank) of the 4th instar and 2 flies, in B a full-grown larva with 3 flies, in C the larva of this nest and 3 flies and in D 5 flies alone without a larva.

At 10.37, the wasp returned with a victim. She came in the exposed portion of the tunnel — the gallery of glass — empty-handed and without confusion and first entered A. There she touched the larva without showing any appearance of surprise, turned round and went out of the cell. She then came inwards through the gallery, but at that moment the larva placed in bottle B had moved out of the chamber, thrusting its anterior body in the gallery, probably in search of the place to spin the cocoon. The wasp was impeded by it and returned once more in A. Soon, however, she came through the gallery again, touched larva B and went back in the entrance tunnel. The next moment she came backing with the fly, passed the narrowed gallery by force, elbowing aside larva B that thrust itself more and more in the gallery. The wasp carried the victim atraight in bottle D and, after placing it down in the cell, went in bottle C, touched the larva and then walked about trampling on it. Next she came out of the chamber and went toward her own tunnel. But larva B had completely emerged from its own chamber into the gallery, so that she could not pass through there. The wasp grasped it with her mandibles, pulled it vigorously. The larva wriggled and struggled, so the wasp laid it down at last and returned to enter cell D. She then went in C, then came out to the gallery again, captured larva B once more and pulled it about, either straight toward cell D or obliquely towards cell C, with the tip of her abdomen bending towards the respective cell. The larva writhed more violently and the wasp could not move it. At last she let it free, went in C again, caught a flower-fly and dragged it in D. Then she took up the fly just carried in once more and went backing with it in C. There she laid it down and returned to D empty-handed, captured one of the victims stored in it and once more transported it in C. Then she went to larva B, pushed it aside vigorously and passed there with great difficulty. She went back in her own tunnel and soon appeared out of the entrance to the open air. But at once she turned round and entered the burrow. She soon came in sight in the glass tube, passed the gallery, elbowing aside larva B, and arrived at cell D. There she took up a fly once more, dragged it backing straight, through the side of larva B till out of the nest and discarded it off. She then rose on the wing and flew about a little while around the nest, but soon alighted in front of the entrance and penetrated the tunnel. While she was thus flying about I replaced the larva B in its own chamber. The wasp entered cell A, touched the larva, came out of the chamber and proceeded in cell C. There she grasped a fly that was located near the entrance and dragged it in cell D. Next she went to cell B empty-handed, but without entering the cell, retreated backward in the gallery and returned to C. She entered the cell and touched the larva, came out of it, but once more entered the chamber. Then she proceeded to D → C → D → C → B → T (tunnel), always without carrying a fly. Next she emerged from the entrance, but at once returned in the tunnel. She turned to B, touched the larva and went back in the dark tunnel. Then, at last, she closed the entrance and flew away. It was at 10.50 a.m., that is to say, she spent 13 minutes during the course of her confused movement in the apparatus.

At 11.30, the wasp carried in a new victim. Her behaviour at this time was as follows : She came in the glass tube empty-handed and went → A (t.l. — touched the larva) → T.

Then → D → C (t.l.) → A (t.l.) → T. T → D → A → T. T → A → B (only in the entrance) → T → out of the entrance. T → A (t.l.) → T. T → B → C (t.l.) → D. She then took up a fly and dragged it backing → T. Soon she came in empty-handed → C (t.l.) → D, took up a fly and carried it backward → A (p.f. — placed the fly) → C (t.l.) → T. She then came dragging a fly → D (p.f.). Next she went empty-handed in A → C (t.l.) → D. There she caught a fly and carried it backing to → T. (At 11.40).

The wasp then came in the apparatus empty-handed, turned her head toward A, but passed by and → C — (backing) → B, and came in contact with the larva at her abdominal tip and proceeded forward and → T. She returned backing with a prey → B. By her backing progress the larva that had come near the entrance of the cell was pushed back in the chamber. The wasp trampled over the larva and placed the fly at the innermost portion of the cell. Then she proceeded → C → A (only thrusting her anterior body) → T. Again she came in without having a fly → A → D → T. T → D → C (t.l.) → A. She took a fly and carried it backing → D (p.f.) → C → D → A (only the head and the thorax) → T. Larva B turned around and began to eat the fly. The wasp came from her tunnel → D (c.f. — caught a fly) → T (p.f.). T → A (anterior body only) → T. T → A (anterior body) → C (t.l.) → T. T (c.f.) → D (p.f.), took up another fly and carried it → T. T → B (only the head) → T. T → A → C (t.l.) → T. T (c.f.) → C (p.f.) → T. T (c.f.) → C (p.f.) → D → T (at 11.49). The wasp, after spending thus 19 minutes in the nest, closed the entrance and flew away.

At 11.53, she returned with a fly and came in → A (t.l.) → T. T → A → T. T → A → C (t.l.) → D (c.f.) → C (p.f.) → A — (backing out and turned to) → T. T (c.f.) → D (p.f.) → C (c.f.) → T (p.f.). T → D → A → T. T (c.f.) → D (p.f.), but at once took it up and → C (p.f.) → D (c.f.) → T (p.f.). T → D, caught a fly that located near the entrance, carried it to the interior and dropped it, then → T. T → B (only the anterior body) — (backing out) → T. T — A (t.l.) — (backing out) → T. T → out of the nest and flew about a while. Then came in the tunnel → C (t.l.) → T. T (c.f.) → D (p.f.) → T. T → C → T → out → came in → B → D (c.f.) → T (p.f.). T → D → T → B → T. Then she stayed in the tunnel for 2 minutes, and → A (t.l.) → T → went out. Entered again → A → C → D (c.f.) → C (p.f.) → T. T → A → T. T (c.f.) → D (p.f.) → T. T → A (only the head) → B (ditto) → D (c.f.) → T (p.f.). Thus bottle D became empty. She then → C (t.l.) → D → C (t.l.) → D → C (t.l.) → D → C (t.l.) → D → T. T (c.f.) → D (p.f.) → T. At 0.06 the wasp emerged from the burrow, but at once entered again. She then went out of the nest carrying a fly and discarded it off and flew about near the nest. Then she returned to her burrow. I placed the discarded fly in front of the entance. The wasp came back with the dirts but, without taking notice the fly, crept in the tunnel again. Soon she came out and this time touched the fly. She captured the fly at once with her jaws and dragged it backing for about 50 cm away from the entrance. There she flew up with the fly and threw it away from in the air. Then she entered the nest once more, but emerged at once, closed the entrance and departed on the next hunting excursion. The victims remained in each chamber as follows : A — 2, B — 4, C — 7 and D — 1. A diagramatic presentation of the process of the transportation of the flies between the cells was given in Figure 40.

At 0.30 p.m., the wasp returned to her nest carrying a fly. She came without the fly in the glass tube and → A (t.l.) → B (t. l.) → C (t.l.) → D → C (t.l.) → D → T. Then, T (c.f.) → D (d.f.) → A (t.l.) → T → out of the nest and flew up. Soon she entered the nest and → A (head only)→B (ditto) → D → A. There she captured the larva between her mandibles and pushed it inwards, but the next moment she proceeded backwards into the tunnel holding the larva with her jaws. Soon she appeared at the entrance without carrying the larva, closed there as usual and flew away.

She came back at 1.15 carrying a prey and dragged it in the burrow. Soon she went away without spending time in the nest. At 1.25 do., at 2.05 do., at 2.14 do. At 2.20 I examined the nest. The larva A was absent from the arrangement, while the states of the cells remained unaltered. At 2.23, the wasp was closing the tunnel permanently.

At 3.10, I opened the nest. The tunnel was closed with a partition wall of sand just in front of the experimental arrangement and the natural tunnel was enlarged into a pocket at its end. There, larva A was placed and 6 flies were accumulated in front of it.

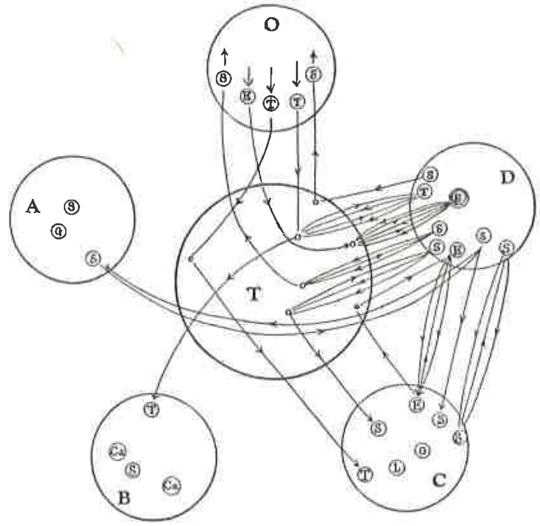


Fig. 40. Diagram showing the transportation of flies between brood-cells by wasp No. 94. A, B, C and D stand for cells A, B, C and D respectively, T for tunnel and O for outside the nest. Letters within circlets represent flies : S — *Sarcophaga*, E — *Eristalis*, T — *Tabanus*, L — *Lucilia*, O — *Ophyra*, Ca — *Calliphora*, G — *Gymnochaeta* and E within double circlet — *Eristalomyia*.

The deailted behaviour of the wasp was diagramatically represented in Figure 41. From the data given above, we may be able to give the following summary.

a) Apparently the wasp specially concerned with larvae A and C, while she was rather indifferent to larva B.

b) As for larva C, a special effort was made by the wasp to accumulate food for it.

c) After the examination of a certain larva, followed very frequently the transportation of a victim. The victim thus transported was sometimes brought to the larva correctly, but more often it was carried to another chamber.

d) When, however, the transportation of a prey coms to a wrong end, the wasp, in her next visit, appears to make an effort to correct the error. Therefore, in spite of the repeated errors, all the prey but one were shifted in the end to some brood-chamber including a larva. Moreover, the exceptional case was that to which sufficient time was not given to correct the error of the first transportation.

e) While the wasp proceeded forwards, she frequently stopped to enter a certain brood-chamber, only thrusting her head and thorax in the branch-tunnel leading to it.

f) The transportation of the victim was most frequently carried out between the tunnel and the end chamber (D).

g) At last, the wasp transported larva A in the tunnel, made a partition wall

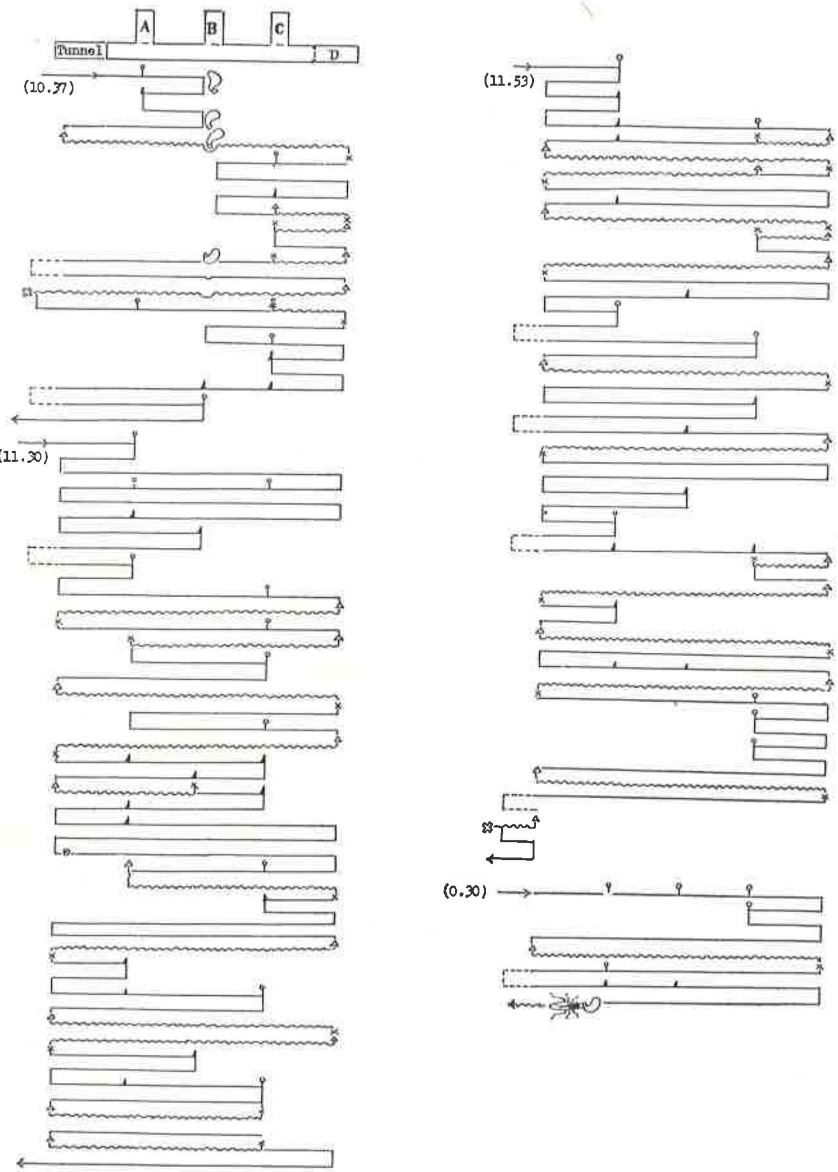


Fig. 41. Behaviour diagram of Wasp No. 94 between brood-cells and the tunnel. The circlet at the top of the short branch of the lines indicates "touched the larva". Other nature of the lines and symbols are as in Fig. 36, excepting that the dotted line represents here "flying about a short while above the entrance".

behind it so as to form a brood-chamber there and later accumulated food for this larva only.

Each item given in the above summary will be explained as follows :

a) The result seems to me dependent upon the fact that the wasp discriminated larva B as a different individual from the others. Probably she has an ability to distinguish the full-grown larva from others that need much food to be transported.

b) It seems that the special care shown by the wasp upon larva C does not depend upon the result of her response to the larva of her own, but merely upon the result of her proper response to the developmental degree of the larva. Speaking of the relationships between larvae C and A, probably the wasp did not distinguish one from the other. The special care shown upon larva C seems to be due merely to the positional advantage of its cell against cell D in which there was no larva and to which the prey were most easily transported.

c) When the wasp examined a larva and then transported a fly, I had an impression that it was intended by the wasp to take it to the larva*. That the result of her activity came very frequently to a different end from her seeming intention is probably effected only by her backing progress.

d) Such a purposive behaviour as mentioned seems to be accounted for by admitting a nervous mechanism which can be stabilized only by bringing together both the larva and the prey within the same cavity. Therefore, the ultimate result of the transportation of the prey between or among the chambers represents a selective activity. This may be considered wrong at first sight, because of errors of the transportation due to the backing progress.

e) This behaviour may be either the correction of an error when the wasp becomes aware of the mistake of the way, or simple examination of the chamber to know the contents of it. In both cases it seems possible that the sense of smell plays some rôle to obtain an information about the cell.

f) This is possibly due to the fact that the course between T and D is straight and easiest to pass. Therefore, when the wasp intended to carry a fly from the tunnel to a cerain brood-chamber, she was apt to comit an error in her backing progress to go to the empty cell (D). On the other hand, frequent transportation of the prey from D to T seems to involve two significances in itself. One may be the result of the same error as occurred in the above case, namely when she intends to carry a fly from D to C or B or A, she goes through an error in the tunnel. The other may be a case of such a repetition of behaviour unit from the first as usually observed when the wasp is plunged into confusion by some accident in the course of her work.

g) This behaviour may indicate simply her inability of feeding more than one larva at a time. The fact that larva A (not larva C) was adopted by the wasp may hsve no important significance. It may show at most that the wasp made no discrimination between them.

* *Vide* following behaviour of the wasp when D was empty : C (t.l.) → D → C (t.l.) → D → T. T (c.f.) → D (p.f.) → T. The behaviour, C (t.l.) →, seems to represent the intention of the wasp to bring a fly and T → D may show the error of T → C.

Besides the above statements, it must be added here that a considerable confusion can be perceived during the course of transportation of the prey between the cells.

(2) Wasp No. 82. Sept. 11, 1947. By failure of digging, I could not know the details of this nest. But as 4 victims were found in sand, the larva of this nest was supposed to be in the 3rd or, more probably in the early stage of the 4th instar. I connected the same set of the experimental arrangement as used in the preceding instance with the end of the natural tunnel of the wasp. In each chamber was put a larva with 2 victims as given below (from the side of the entrance in turn).

A — A larva of the 3rd instar and 2 flies. B — A larva of the 2nd instar and 2 files. C — A larva of *Ectemnius konowii* Kohl of about 13 mm long and 2 flies. D — A larva of the middle stage of the 4th instar and 2 flies. About ten minutes later, the wasp came back without having a fly. She came in the glass tube and first entered A. There she touched the larva, without showing any unusual behaviour, turned round and went out to the gallery. Next she entered B, touched the larva and then went out of the cell. She then turned to the tunnel and emerged from the entrance. But soon she entered the burrow again and came in sight in the apparatus. She entered A, B, C and D in turn. In chambers A, B and D the wasp trampled on the larva as well as victims indifferently and in chamber C returned as soon as she touched one of the victims with one of her front pair of legs. At last she was thrown into confusion in bottle D by the stimulus of the light. So I covered the apparatus with sand. After a short while, she came out of the nest but at once returned in the burrow. I uncovered the chambers and the gallery of glass. She came straight in the gallery, but, without entering any of the cells returned in the tunnel and appeared from the entrance. She then entered the tunnel once more. This time, however, she did not come in sight in the apparatus, but carried out the sand very actively from the entrance. Thencefrth, she continued the digging work for a long time. On removing the apparatus, I found that she was digging her tunnel anew through the sand just beneath the apparatus. So I connected the entrance of the apparatus again with the end of her new tunnel. The wasp that flew away while I was examining her work, did not return to the place again.

Probably the extraordinary change of the inner structure of her nest make her search for her own tunnel at first and abandon the nest at last.

3. Consideration and conclusion

Judging from the results and especially from the procedure of the foregoing experiments, it seems possible to give the following conclusion with regard to the manner of response of the wasp when two larvae are placed in her nest:

1) As regards the manner of response, there is a considerable difference amog the individuals.

2) Even when a wasp touched the 2 larvae placed in her nest separatately and supplied food to each of them, it is difficult in some cases to believe that the wasp responded to each of them as separate larvae. Sometimes it seems to me rather that the image, if any, of the first larva melt into that of the second at the moment of her meeting with the latter. In a common expression, she cannot fundamentally distinguish one from the other even when she found them in separate locations. In such a case, therefore, all the larvae in the nest are one and the same to the

wasp. Some of the instances in which 2 larvae were fed peacefully in separate cells without undergoing any transportation will be involved within the scope of this category.

3) However, when the wasp shows her confusion in her behaviour by making frequent going and coming between the 2 cells, always touching the larva in each cell, as if some doubt arose in her, she may be said to begin to respond to them as two, or as more than one.

4) This state of instability seems to induce the wasp to assemble the 2 larvae in one of the chambers or to discard off one of them out of the nest.

5) Even after bringing together the 2 larvae in one cell, it is not necessarily doubtless that the wasp always responds to them as separate individual, or she recognizes them as 2 or more than one. Because the behaviour of bringing together itself seems to show that wasp deals with the larvae as one, although the motivation of the behaviour of bringing together may be the psychie instability evoked by the vague recognition of the presence of more than one larva in the nest.

6) Bringing together of the 2 larvae, rejection of one of them and isolation of one of many — these acts seem to indicate respectively that the wasp is incapable of feeding moe than one larva at a time.

7) However, either in the case when more than one larva is placed in one cell, or in the case when they are placed respectively in a separate cell, if the wasp touches them successively one after the other with a very short interval of time, she is supposed to respond to them as separate ones, or she recognizes them as two or more than one, although it is quite unknown how long such an image is retained in her.

8) Different responses shown by the wasp to the larvae of different development indicate that the wasp can respond to the difference of the larval dimesion. But, the fact does not necessarily allow to admit the recognition of the wasp on the presence of more than one larva in her nest. Because these responses may be evoked independently, without any combination with each other.

Moreover, it will not be needless to note here that the weill fitted provisioning activity shown by some wasps when the larva was replaced with another of different instar or of different growth is not the result of the reasonal response, but of the innate response wherein the act of the wasp, released by confronting conditions, is sometimes drawn back, sometimes passed over rather reflexively some steps in its prescribed order within a behavioer unit. This represents certainly a plasticity of the innate behaviour, not the spatial plasticity, but the temporal plasticity wherein the external releasor acts more strongly than that internal leading power which drives the innately predetermined schedule of the behaviour system.

IV. RESPONSE TO THE AMOUNT OF FOOD IN FRONT OF THE LARVA

It has become obvious in the foregoing experiments that most of the individuals of our *Bembix*, when the victims already stored in their brood-cells are removed from time to time from the place during the course of their provisioning activities, usually work compensatorily and restore about as many flies as are supposed to be necessary for feeding the larva. Having made use of this habit I have succeeded in performing various kinds of experiments repeatedly upon the same individual. However, some individuals did not show such a compensatory activity. They finished their work, apparently without any connection with the environmental change occurred, after completing a certain amount of provisioment that might be sufficient for feeding her own larva. In order to know the scope and the degree of their compensatory provisionment I have put in order the data obtained from the experiments conducted heretofore in Tables 8 – 11.

Table 8. Provisioning activity of the wasp when the larval food is removed from the brood-cell. I. In the case when the larva was remained untouched.

Wasp No.	Larval instar	Victims found in the larval cell		Victims brought anew (remained) in the cell							Remarks
				No. of the remove experiment							
		Eaten	Intact	1	2	3	4	5	6	Total	
52	2.–	1	2	6 (2)	0 (1)					9	P
59	4.5/10	3	7	2 (1)						12	P
60	4.2/10	3	7	5 (0)	5 (1)	0 (1)				20	P
62	4.1/10	2	4	7 (1)	1 (1)					14	P
63	4.3/10	2	17	3 (2)	? (5)					22	A
102	4.5/10	11	1	1 (3)	1 (1)	2 (0)	4 (2)			20	P
104	4.3/10	5	12	10 (1)	2 (1)					29	P
105	4.4/10	7	8	4 (1)	5 (1)	6 (2)	2 (4)	4 (2)	0 (1)	36	P
120	3.–	3	2	18 (3)	1 (1)					24	P
123	4.1/10	2	4	2 (4)	10 (2)	7 (1)	1 (2)*			26	P
124	4.3/10	2	3	4 (3)	7 (1)	1 (2)	4 (0)	4 (2)*	3(1)*	28	P
133	4.2/10	?	1	5 (1)	? (1)					?	B
136	4.4/10	9	6	5 (0)	3 (0)	3 (1)	2 (1)			28	P
137	4.6/10	8	11	5 (1)						24	P
138	4.3/10	2	5	2 (1)						9	P
148	4.3/10	2	10	7 (1)	5 (1)	0 (3)				23	S
154	4.8/10	6	8	8 (0)	0 (1)					22	P
157	4.2/10	4	2	2 (1)	3 (1)	3 (1)	1 (1)			15	S

Remarks. P — permanent closure, A — invaded by ants, B — invaded by some beetle, S — stopped the observation, * — exchanged for other small larva.

Table 9. Ditto. II. In the case when the larva was changed with another of the small size. (Showing only the compensated number.)

Wasp No.	Larval instar	Victims E.	Victims I.	Victims brought anew (remained) in the cell 1*	2(9)	3(10)	4(11)	5(12)	6(13)	7(14)	8(15)	T.	R.
75	4.7/10	7	4	$1(3)^4$	$4(4)^3$	$4(8)^4$	$2(2)^4$	$9(2)^4$				31	P
76	4.-	?	?	$2(0)^3$								?	P
89	3.-	1	3	$3(1)^3$	$13(4)^4$	$11(3)^3$	$4(3)^4$	$16(3)^{34}$	$5(3)^{44}$	$5(1)^{44}$	$8(4)^{44}$	69	P
130	4.1/10	1	6	$8(1)^2$								15	P
134	4.5/10	9	4	$2(4)^4$	$8(0)^4$	$4(2)^3$	$11(1)^4$					38	S
150	4.3/10	6	13	$2(0)^4$	$3(2)^4$	$4(3)^4$	$6(1)^4$	$1(3)^4$	$3(2)^4$	$7(3)^4$	$5(0)^4$		
					$1(1)^4$	$7(2)^3$	$3(5)^3$	$6(2)^3$	$2(2)^4$	$1(4)^4$	—	70	S

* Numerals in this line show the order of the remove experiment, those within parenthesis are upplied only to Wasp No. 150.

Reference numerals show the instars of the given larva.

Table 10. Ditto, III. In the case when the larva was changed with another of the larger size.

Wasp No.	Larval instar	Victims E	Victims I	Given larva	Victims brought anew (remained) in the cell 1st*	2nd	3rd	4th	5th	Total	Remarks
74	3.-	1	2	4.7/10	4 (2)					-	S
92	3.-	1	2	4. full	3 (4)					6	P
101	2.-	2	1	4.5/10	3 (4)	6 (3)	3 (0)	4 (0)		19	P
128	2.-	2	1	4.5/10	15 (1)					18	P
				4.8/10	0 (2)						
135	4.1/10	1	4	4. full	1 (0)					6	P
139	4.3/10	1	6	4.8/10	1 (2)					8	P

* See Table 9.

In the instances here tabulated the removal of the prey was not carried out at the same interval and under a constant ratio. This is true not only between the different individuals, but also within the same individual. Therefore, they can not strictly be compared with one another. But generally speaking, we may be able to admit the following summary:

1) Our species captures commonly from 13 to 20 flies as food for her single larva, only rarely the number attains over 20. It is an extremely rare ocasion that it surpasses 30. Whereas, as shown in the tables, the wasp which was deprived of the flies that were stored in her cell used to continue her work very actively and to bring in the nest by far the larger number of victims than usual. Accordingly the prey brought by such a wasp attained, as a rule, more than as many as 20 in number, usually the number centered around 30, rarely it reached no less than 70.

Table 11. Ditto, IV. In the case when two larvae were given.

Wasp No.	Larval instar	Victims		Given larva	Victims brought anew (remained) in the cell							
		E	I		1st*	2nd	3rd	4th	5th	6th	T.	R.
68	4.2/10	2	5	4.2/10 4.1/10	2 (4) – ·	3 (6)	0 (4)				12	
68′	3.-	2	1	4.6/10 4.5/10	1(10)	2 (1)	? (2)				6+?	A
69	1.-	0	2	1.- 1.-	4 (4)	4 (8)	7(12)	4 (2)	11(2)	? (2)	32+?	B
107	4.4/10	5	5	4.5/10 4.5/10	7 (1)	6(10)	7 (4)	4 (2)			34	P
113	4.3/10	7	6	4.3/10 4.6/10	13 (0)	0 (8)					26	P
131	4.1/10	2	2	4.1/10 3.-	4 (6)						8+?	A

* See Table 9.

2) However, the larval wasp continued to eat in the course of the experiment, so that it approached sooner or later the full-development, although it fed upon much less victums than those accumulated in nature by the wasp. Then the wasp, quite indifferently to the small number of victims found in front of the larva, closed the nest by means of the permanent closure.

3) In the above case, however, if the larva was replaced with another smaller one, the period of the wasp's activity for one nest used to be evidently lengthened and much more victims were brought to the nest. This is an evidence for the fact that the external releasor dominates the internal stimulus in this species, in so far as the latter can physiologically be suppressed. Wasp No. 89, under repeated renewal of the smaller larva and under repeated removal of the gathered prey, brought to one of her nest as many number of flies as 91 (*vide* table 6)

4) Some individuals, however, closed their nests permanently after completing the accumulation of a comparatively small number of flies, without showing any connection with the developmental degee of the newly given larva. These individuals are supposed to have already entered the final course of provisionment which used to be carried out quite automatically.

5) On the other hand, even those wasps which performed the compensatory activity for the missing victims or for the small larva newly given, came to close the nest permanently in the end of several experiments, in spite of the fact that very inadequate amount of food remained in the cell. That is to say, there is a certain limit in their compensatory activity, although it is not uniform among the individuals. This shows that the positive egg pressure which has come to the limit of suppression, dominates the external releasor and set free that behaviour which is innately related with it.

6) On the contrary, in the case when a small larva was replaced with a large one that had already become full-grown or nearly, the wasp, as soon as she responded to the given larva, changed its manner of activity to accommodate to the new conditons. Thus, the wasp used to close the nest permanently after provisionment of only a few flies. Some wasps among many, however, were apparently forced to do so by the fact that the larva already entered the course of its encasement. In both cases, after closing the nest, the wasp used to search for the nesting site to deposite her next egg. According to this fact the time of the oviposition can be advanced, to a considerable extent, by the change of the external conditions. This is also a proof that the power of the positive egg pressure, as a releasor, is not always a leading factor in this species.

7) When two larvae were given in a nest at a time, the wasp was not always induced to gather much food than usual. Because, the wasp did not always respond to them as separate larvae. Moreover. if she responded to them so, it was very doubtful whether or not she brought food to them respectively. In general, it appeared that the doubled chance of meeting with the larva that had only a scanty food supply stimulated the mother wasp to gather food more actively than usual. Therefore, in these cases only the frequent removal of food from the brood-cell (not the presence of two larvae in one cell) gives rise to a state of insufficency of food supply and this alone becomes a direct releasor of provisioning activity.

Table 12. Compensatory provisionment of Wasp No. 105.

No. of examination	1	2	3	4	5	6	7	P.
Larva used	4.4/10	4.5/10	4.5/10	4.6/10	4.8/10	4.8/10	4.9/10	
Prey remaining in the cell		1	5	1	2	4	2	
Time examined / Species of prey	VIII.14 1.55	VIII.15 10.25	VIII.15 0.40	VIII.15 3.15	VIII.16 10.00	VIII.16 10.53	VIII.16 1.00	Total
Eristalomyia tenax	1	1						2
Eristalis cerealis	9	2	2	3	1	1	1	19
Syrphidae spp.			1			1		2
Stratiomyia japonica	1		1				2	4
Villa limbatus	1	1		1				3
Tabanus mandarinus	1							1
Lucilia caesar	1							1
Sarcophaga carnaria	1					1		2
Tachynidae sp.								1
Anthomyidae sp.				1			1	1
Total	15	4	4	5	1	3	4	36

8) The most remarkable 4 instances of the compensatory activty (not only in the number of victims collected, but also in the lengthened period of activity) will

Table 13. Compensatory provisionment of Wasp No. 123.

No. of examination	1	2	3	4	5	6	7	P
Larva used	4.1/10	4.2/10	4.5/10	4.5/10	4.6/10	4.8/10	3.8-	
Prey remaining in the cell		4	2	1	3	6	2	
Time examined / Species of prey	VIII.21 11.20	VIII.21 2.13	VIII.23 8.30	VIII.23 9.40	VIII.23 0.10	VIII.23 2.18	VIII.23 3.45	Total
Eristalomyia japonica	1		1	2				4
Eristalis cerealis	3	1	5		3	1		13
Eristalinus sepulchralis			1				1	2
Villa limbatus		1	2					3
Lucilia caesar	1		1					2
Sarcophaga carnaria	1							1
Tachynidae sp.						1		1
Total	6	2	10	2	3	2	1	26

Table 14. Compensatory provisionment of Wasp No. 107.

No. of examination	1	2	3	4	5	6	
Larva used	4.4/10	4.5/10	4.5/10	4.5/10 4.5/10	4.7/10 4.8/10	4.9/10 4.8/10	encased died
Prey remaining in the cell		1	3	8 2	2 2	1 1	
Time examined / Species of prey	VII.15 10.40	VII.15 2.15	VII.15 2.52	VII.16 10.20	VII.16 2.40	VII.17 9.00	Total
Stratiomyia japonica	1						1
Villa limbatus	2	2	3		4	3	14
Eristalomyia tenax				1			1
Eristalis cerealis	4				1		5
Eristalinus sepulchralis	1						1
Anthomyidae sp.	1						1
Lucilia caesar	1	1			1	1	4
Muscidae sp.				4			4
Sarcophaga carnaria			1	1	1		3
Total	10	3	4	6	7	4	34

Table 15. Compensatory provisionment of

No. of examination	1	2	3	4	5	6	7
Larva used	4. 8/10	4. 5/10	4. 5/10	4. 5/10	4. 6/10	4. 6/10	4. 7/10
Number of prey remaining in the cell		4	2	3	1	3	2
Time examined / Species of prey	IX. 51 0. 30	IX. 5 11. 05	IX. 5 11. 25	IX. 5 0. 40	IX. 5 2. 00	IX. 5 2. 10	IX. 6 8. 20
Eristalomyia tenax							
Eristalis cerealis	8	1	1	3	3		1
Eristalinus sepulchralis	10	1	1	1		1	1
Syrphus ribesii							1
Stratiomyia japonica							
Villa limbatus			1				
Tabanus mandarinus					1		
Lucilia caesar	1				2		
Sarcophaga carnaria							
Total	19	2	3	4	6	1	3

be tabulated here.

V. LEARNING EXPERIMENTS

1. Learning of the direction

Some of the instances shown in the foregoing experiments give evidence that the wasp has a sort of memory with reference to the direction of her tunnel. In the case when the glass tube is not well connected with the end of the tunnel, and especially when it is arranged in a direction other than the orignal state, the wasp sometimes digs a new tunnel in sand in the same direction as in the orignal case (Wasp Nos. 60, 73, 74, 86, etc.).

With regard to this problem the behaviour of the wasp in the Y-tube of glass leading to two cells, in one alone of which a larva is placed has given more definite informations. At first I had an intention to slove the problem by supposing the wasp's behaviour from the results of her provisioning work. I thought that the number of the stored flies in each cell should show respectively the number of times of the entering of the wasp to the cell, and that her entering must be the result of her learning regarding the previous condition of the nest. However, it has been clarified by the later investigations that this method can not always be applied to every case, since, according to the direct observation of the behaviour of the wasp the following processes were confirmed: 1) When the wasp brings a

Wasp No. 150.

8	9	10	11	12	13	14	15	
4.7/10	4.7/10	4.8/10	3.–	3.–	3.–	4.2/10	4.2/10	
3	0	1	2	5	2	2	4	
IX.6 10.02	IX.6 11.00	IX.6 11.15	IX.6 12.25	IX.6 12.58	IX.6 1.55	IX.7 9.00	IX.7 10.00	Total
	1		1		1			3
6	3		6	1	4	1		39
	1			1				17
								1
								1
		1						1
								1
1					1	1	1	6
				1				1
7	5	1	7	3	6	2	1	70

victim in her nest, first she always visits the brood-chamber empty-handed, always proceeding head first. 2) But when she carries the victim to the chamber in her second visit, she always drags it backwards. Therefore, at the bifurcation she is likely to proceed in the direction that happened to be entered by one of her hind pair of legs, rather independently from the direction of her first visit, although in reality, the entering to the correct direction occurs more frequently than to the wrong direction. 3) Sometimes the wasp, when she is in the nest, retransports the victims that happened to be carried in the wrong chamber to the correct larval cell.

In order to solve the problem, therefore, it is absolutely necessary to make the direct observations on the behaviour of the wasp in her first visit. When the indirect method of counting the stored flies is adopted, the facts mentioned above must prudently be taken into consideration.

a. Experiments using a Y-maze

The apparatus used in the following experiments consists of a Y-tube and two bottles, both made of glass and specially prepared for the present purpose. The Y-tube is uniformly 1 cm in diameter and has the branches, 2 – 10 cm. long, diverging at an angle of 60°. The basal axis is 13 – 15 cm in length and can be connected at its basal extremity with the end of the natural tunnel. The bottle consists of the body and the stalk. The body is ellipsoidal in shape, 5 cm long and 1.5 cm wide at the medial widest portion. The stalk is 1 cm in both length and diameter and can be connected well with the end of the branches of the Y-tube. First the nest is dug open from behind and the brood-cell is exposed, without damaging the entrance of the nest. The portion of the brood-cell is cut off and the basal axis of the Y-tube is jointed to the end of the wasp's sand tunnel. As motivation in learning breeding drive of the mother wasp was employed. In one alone of the cells, a larva is placed with scanty food. The arrangement is covered with sand excepting for the time when the observation is carried out.

In the indirect method, the number of the prey stored in each cell is counted in connection with the direction of the original tunnel. Then, after a certain number of times of the wasp's visits, both the bottles with each contents are replaced in position with each other, sometimes with the instruments also completely exchanged for new one. The results of the provisioning activity of the wasp is examined after a proper period. In the direct method, the detailed behaviour of the wasp when she entered the nest is directly observed and stenographically noted. Test method is similar to the above, consisting of the exchange of bottles and the observation of the results on the behaviour of the wasp. In this method the number of times of learning is more strictly controlled as compared with the indirect one.

(1) Wasp No. 68. Sept. 3, 1947. The nest was of the compound type (Fig. 27) and the larva was in the early stage of the 4th instar. Glass cell A that was attached to the end of the left branch of the Y-tube was considered having an advantage of being provisioned much as compared with the other cell, B, if the wasp has a menory of any sort regarding the direction of the tunnel and if it has a power of controlling the direction of her backing progress, since A was situated in the same direction as the original cell. In A was put the larva of this nest with 2 victims, and in B a larva of the 3rd instar with also 2 flies. It was at 3. o'clock p.m. The next day at 10.30 a.m., I examined the nest. In A had been added 2 flies, while in B nothing. Both cells were interchanged. At 3.15 p.m., in B had been brought 3 flies, while in A nothing. I left the conditions in situ. The subsequent day the weather was bad. On a 4th day at 10.40 a.m., all the victims had become remains. But careful examination revealed that one fly only had been added in B, but no fly in A. The tunnel had already been permanently closed.

In this instance the wasp had a solid inclination of taking the left-hand branch even in her backing progress. The results seem to favour the view that the wasp possesses some sort of memory regarding the direction of her way.

(2) Wasp No. 68 (B). Sept. 7, 1947. The nest was of the simple structure and the tunnel ran straight for about 25 cm. The larva was in the 3rd instar. I used the same instruments that used in the preceding instance together with the contents. But I put cell A on the left side as in the first experiment. It was at 11.00 a.m. At 3.30 p.m., I examined the nest and knew that the mother wasp did not enter since I put the arrangement. The subsequent day it was a bad weather. On a 3rd day at 11.50, I opened the cells. Larva B had been transported in cell A and was with larva A, keeping some distance between them. Meanwhile the wasp returned from her excursion carrying a prey. She came in the exposed glass-tube at once. She proceeded without showing any confusion under the broad daylight and came in the left branch. In cell A, she touched both the larvae one after the other, turned round and went

in the tunnel. She emerged from the nest but at once returned in the burrow. She came smoothly through the left tunnel in cell A, touched one of the larvae that located at the entrance portion (probably B) and returned in the dark tunnel. Then she stayed there for some minutes. While she was absent, I examined the cells and found that no victim had been added in either of the cells.

Then cells A and B was interchanged. After a while the wasp came in through the glass tunnel. At the bifurcation she entered the left branch without hesitation, but after thrusting her anterior body in the direction, she retreated in the main tunnel, turned her way a little and then proceeded in the right branch. There she touched the larvae one after the other and went back in the main tunnel. Once more she came in. She thrust her head in the left branch as before, but at once retreated a little and entered the right branch. She touched the anterior larva with her antennae and returned in her own tunnel. When she came in sight in the glass tube for the 3rd time, she entered straight the right-hand branch, took up the anterior larva with her mandibles and went back in the main tunnel with it. Then she came again empty-handed, entered the right cell (A), turned round and proceeded in cell B. But as soon as she entered the cell she turned round and went back in the main tunnel. The next time she entered the right branch up to the entrance of the cell, but without coming in, went back. For the 6th time she came backing with a small quantity of sand, placed it at the entrance to cell A. She then emerged from the entrance of the nest, but at once entered the burrow. She came sweeping as usual in the main tunnel, but without entering either of the branches, returned from the forking point. Again she came in sight in the glass tube, this time proceeded a little in the right branch but at once went back. In her 9th visit she came backing with the larva. entered straight in the left branch, put it in the centre of the empty cell and then returned in the main tunnel. She then emerged from the nest, but at once returned in the tunnel. But without coming in sight, went out of the entrance, Again she entered the burrow, came to the bifurcation, thrust her head first in the right, then in the left, but without entering either of the branches, returned up to the orifice. At once she turned round, but the next moment she went out. Again she entered and came this time in cell A, touched the larva, returned at once. She then went out of the nest, flew about a little, alighted in front of the nest and again crept in. The wasp came in cell A, touched the larva and went back. She showed her head at the entrance and was closing there. But instantly she stopped her work, came in the tunnel of glass. At the bifurcation the wasp thrust her head first in the left and then in the right branch. But, without entering either of them went back. At the entrance she began to close there, gathering sand actively. But again she stopped the work, returned in the tunnel.

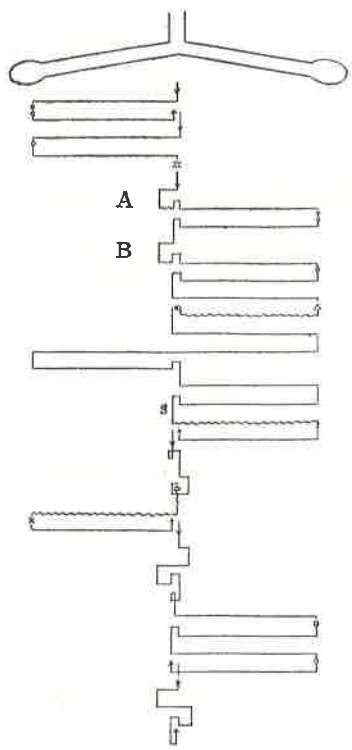


Fig. 42. Behaviour diagram of Wasp No. 68 (B) in a Y-maze. Method of presentation is as in Fig. 36. S — carrying an armful of sand, * — change of position of the larvae. Circlet — touch the larva.

without coming in sight in the glass tube however, she returned to the entrance. At last the strange manoeuvre of her ingress and egress came to the end. She completed the closure of the tunnel, made a simple orientation flight and flew away.

The above described behaviour of the wasp can be shown diagramatically in Figure 42.

In this figure, the behaviour of the wasp marked with A is especially suggestive. At that moment, the larvae which had been in the left chamber were just transported to the right chamber. The fact that the wasp came straight to the left branch and thrust her anterior body in the direction without showing any hesitation indicates evidently that she had already learned the direction of the tunnel leading to the brood-cell. On the other hand, another fact that the wasp, nevertheless, stopped suddenly to enter the branch and at once retreated to go to the right branch shows also obviously that the wasp can be aware of the presence or absence of the larva without directly touching it, probably through the sense of smell. The behaviour marked with B will probably shows the similar process. But this behaviour is not so decisive as that of A, since at this time the wasp has had an experience of entering the right cell.

After that, the wasp worked as follows : At 2.00 of the same day in the left chamber had been added one fly, while in the right cell nothing. I removed all the remains from both bottles, leaving in the left cell the larva and one fly, and in the right cell the larva alone. At 2.47, 2 more flies had been added in the left cell, while in the other none. Then the bottles were interchanged, but the nest was invaded by small red ants.

This experiment seems to show that the wasp has a sort of memory regarding the direction of the original tunnel. At the same time it seems to give a suggestion that she becomes aware of the presence or absence of the larva some distance away from it, probably through the sense of smell.

(3) Wasp No. 85. Aug. 9, 1948. At first this experiment was conducted to know whether or not the wasp makes discrimination between the larva of her own and the cabbage caterpillar (p. 37). I put a caterpillar with a fly in cell A and a larva of the 3rd instar in cell B, placing A on the left and B on the right. About 3 hours later, at 2.40 p.m., I found that the caterpillar had been discarded out of the nest, while in cell B one victim had been added. Then both the cells were interchanged. Two days later at 6.25 a.m., the results of the wasp's work of the previous day was examined. In the empty cell (A) 18 flies had been accumulated (in total 19), while in the larval cell (B) there were remains of only 4 flies, indicating that only one of them had been added on the previous day.

I removed all the fly and the remains from each cell, but I put 4 intact flies in cell B and placed the bottles as before (A on the right and B on the left). At 2.30 p.m., bottle A remained empty, while bottle B was supplied with 3 new flies. The subsequent day at 11.25 a.m., when I examined the nest it had permanently been closed and in both cells no victim had been brought anew.

This instance indicates that in the course of the busy work of the final provisionment the wasp carries in the victims quite mechanically without examining the larva, since if she examined she might retransport the flies that had been dragged in the wrong chamber. It shows also that there is a certain habitualness in taking a direction even in her backing progress, apart from the connection with the first visit. To my regret, the direction of the original tunnel of this nest was unknown.

(4) Wasp No. 102. Aug. 14, 1948, at 9.20 a.m. The form of the nest and experimental arrangement were shown in p. 164 of Part I of this paper. In the brood-cell were a larva of the middle stage of the 4th instar and 12 flies, of which only one was intact. I put in bottle A 2 flies without a larva and in B the larva and 1 fly. A was supposed to have an advantage for the automatic provisionment. At 9.37 the wasp came back without carrying a prey. She came in the tube without hesitation. At the forking point she thrust her head dashingly in the branch leading to A, but suddenly she stopped and retreated and turned her way towards B. But after proceeding by half of her body, she turned round and went back in the main tunnel. She then emerged from the entrance but at once returned in the tunnel. At the bifurcation she came by a step in the branch leading to A, but stopped as before, turned her way, entered the branch to B and walked up to the end of the cell. Then she went back in the main tunnel. The subsequent behaviour was described in Part I (l. c.)

In this instance we can perceive at least that the wasp has a sort of memory about the original direction of the tunnel. The greater part of the behaviour shown by this wasp seems to represent only the confusion caused by the change of the structure and illumination in the nest.

(5) Wasp No. 120. Aug. 17, 1948. The nest and the experimental arrangement were as shown in Figure 43. In the brood-cell was a larva of the 3rd instar still attaching to the pedestal. The victims stored were 5 in number of which 3 were half eaten. I put in bottle A the larva and 3 flies and bottle B 3 flies without a larva. It was at 2.00 p.m. At 2.15, the wasp was in the nest. At 2.20 a flower fly was thrown out of the nest. Probably it was the prey that was carried in a short time before. At 3.25, the entrance was opend and the wasp was in the nest. I uncovered the arrangement and found that not a single fly had been brought in either of the cells. The wasp was in the tunnel. The next day at 9.40, the wasp was carrying the dirts out of the entrance but soon she flew away. In the nest the larva had grown into the final instar. In cell A there were 4 intact and 3 eaten flies and in B 13 intact flies. Careful examination of the species of the flies in each cell revealed that one of the flies was transported from B into A. In cell B no larva was placed, but the cell was situated in the same direction as the original tunnel.

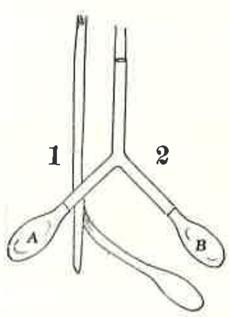


Fig. 43. The nest and the experimental arrangement of Wasp No, 120.

I removed all the flies except one from each cell. At 0.12 p.m., the wasp was already closing the nest permanently. In the burrow, cell A remained as before, while in cell B one fly was added.

This is one of the instances in which the backward progress dragging a fly is comparatively well controlled in connection with the original tunnel, but at the same time without connecton with the actual larval cell.

b. Experiments using a T-maze

(1) Wasp No. 114. As for the form of the nest and the first experiment conducted upon the wasp, I have already described (p. 70, Fig. 35). As for the

behaviour of the wasp on that occasion, the confusion shown in her repeated going and coming between the two cells (Figs. 36 and 37) can be explained, from the standpoint of the memory of the direction, by supposing that the wasp could not easily find the exit towards her own tunnel. The wasp, after touching a larva, might intend to bring a victim from the tunnel, or after depositing the fly in one cell, might intend to go out of the nest. In both cases she failed to take the correct direction in turning in the middle of the way through 90°, and went straight to the other cell. There she found a fly and brought it to the larva of the previous cell (shown by numerals 5 and 13 in figure 36) or there she found a larva and received a fresh impulse to bring food to it (shown by numerals 4, 7, 10 and 12 in the same figure). Only in 3 cases (2, 10 and 14) she acted in correct. Case 8 seems somewhat doubtful. That is to say, in the case of a T-tube, learning of the correct way toward the entrance of the nest that turns on the way through 90° is more difficult than in the Y-tube. In the graphic representation of her next behaviour (Fig. 37), the part shown by 1 is evidently a mistake of the wasp, since in this case both the larvae were gathered together in cell A. While those shown by 5 and 7 may be the same error as explained above, namely, the failure of finding the exit to her own tunnel.

c. *Experiments using a triple Y-maze*

(1) Wasp No. 114. Aug. 19, 1948. This experiment is a succession of the previous instance. After the observation of gathering the 2 larvae in one of the cells (the behaviour shown in Figure 37), I changed the method of the experiment into a more complicate sort, using a triple Y tube of glass. The instruments used in the present experiment was as shown in Figure 44. The basal stalk of the tube is 10 cm in length, while each branch half of its length. The cells are similar in form with one another, bearing the length of 5 cm. Cell C was the same bottle that was used in the preceding experiment. It involved, therefore, 2 larvae and 13 flies, of which 7 had already become remains, Other cells were all empty. In order to avoid as far as possible the confusion caused by the light, I covered the instruments with sand excepting for each bifurcation and the entrances to each cell. These sand cleared spaces served as observation windows.

In the following I used some symbols to abbreviate the description. A solid line shows the forward progress of the wasp without sweeping the floor, a dotted line the same but with the sweeping

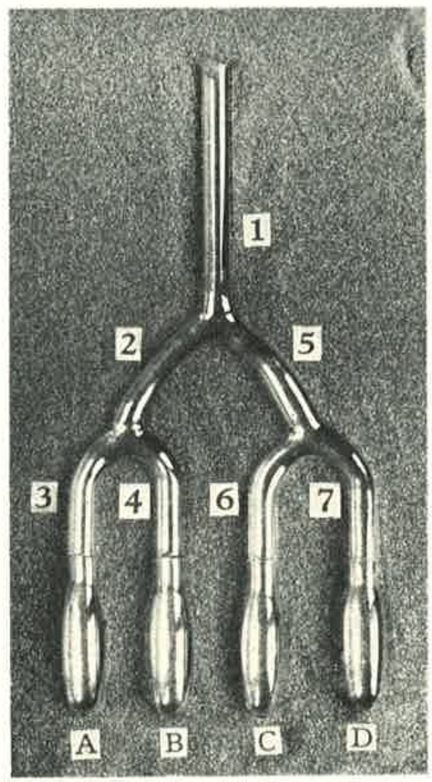


Fig. 44. The triple Y maze. Numerals show the numbers of each branch tunnel.

movement, while a waved line the backing progress. Each numeral shows each branch of the tunnel represented by the corresponding number in Figure 44. Number 1, however, includes the natural tunnel of the wasp, in addition to the basal axis of the instrument. Numerals within parentheses show the behaviour of thrusting only the head (or abdomen, in the case of backing progress) in the corresponding branches. (c.f.) stands for "caught the fly", (p.f.) for "placed the fly", (t.r.) for "turned round", and (t.l.) for "touched the larva".

I set the arrangement at 9.15 a.m. At 9.35, the wasp entered the nest with a prey. Her movements in the nest were as follows :

The 1st time : 1 ··· 2 ∼ (1) ··· 5 — (6) — 7 — D — (7) — D — 7 — 5 — 1 — emerged from the entrance but at once entered again.

The 2nd time : 1 ··· 5 (t.r.) ··· 2 ∼ (1) — 2 ∼ (1) — 2 ∼ 1 — 2 — 3 — A — 3 — 4 — B — 4 — 2 ··· 4 — B — 4 — 3 — A — 3 — 2 — (5) — 1 — emerged and was frightened at the observer, flew about a little, alighted in front of the nest and entered again.

The 3rd time : 1 ··· 2 ··· 3 — A — 3 — 4 — B — 4 ··· 2 ··· 5 ··· 6 — 7 — 5 ··· 2 ··· 3 — 2 ··· 5 ··· 6 — (7) — 5 ··· 2 ··· 3 — 2 ··· 5 — 7 — D (stayed for 50 s.) — 5 — 1 — emerged, at once entered again, but soon reappeared at the entrance, swept the sand a little, flew up, landed, swept the surface and came in the tunnel.

The 4th time : (At 9.47) 1 ··· 2 ··· (4) ··· 3 — A — 3 — 4 — B — 4 ··· 2 ··· 5 — 6 — C — 6 — (7) — 5 — 1 — went out but at once came in. (The wasp found the brood-chamber for the first time.)

The 5th time : 1 ··· 5 ··· 6 ··· C (stayed for about 40 s., probably in examining the larva) — 6 — 7 — D — 7 — 5 — 1 (c.f.) ∼ 5 ∼ 7 — D (p.f.) ··· 7 ··· 5 ··· 1 — went out but at once entered the nest. (The wasp appeared to intend to bring the victim in C, but it resulted in taking it in D.)

The 6th time : 1 ··· 5 ··· 6 ··· C (stayed for about half a minute) — 6 — 7 — D (c.f.) ∼ 7 ∼ 5 (p.f.) — (1) — 5 (c.f.) ∼ 1 — went out but at once entered the tunnel again.

The 7th time : 1 ··· 5 ··· 6 ··· C — 6 — 5 — 1 ··· 5 ··· 6 — C — 6 — 5 — 1 — 5 — 6 — C — 6 — (7) — 6 — C — 6 — 5 — 1 (c.f.) ∼ 5 ∼ (the prey became reverse in its bodily orientation; the wasp captured it by the tip of the abdomen, but the wings of the fly unfolded and obstructed by the wall of the tunnel; so the wasp dragged it with great difficulty at the bifurcation of the tunnel) ∼ 5 ∼ 7 ∼ D (p.f.) — 7 — (5) — 7 — D — 7 — 5 — 1 — emerged, swept a little and penetrated again. (Again she failed in bringing the prey in C.)

The 8th time, at 9.58 : 1 ··· 5 ··· 6 — C (stayed for 20 s.) — 7 — D (c.f.) ∼ 7 ∼ 5 ∼ 1 (dragging it in a reverse orientation of the body , capturing it by the tip of the abdomen) ∼ went out with the prey. She carried it backwards for about 25 cm from the entrance, turned it round and captured as usual, flew to a distance of 7 m away from the nest, took a short rest and returned with the fly to the nest. She then entered the tunnel with the prey.

The 9th time : 1 — 2 (t.r.) — 5 — 6 — C — 6 — 5 — 1 (t.r.) — 5 — 6 — C — 6 — 7 — 5 — 1 — went out, but at once came in. (This time the wasp did not show the sweeping movement.)

The 10th time : 1 — 5 — 6 — C — 6 — 7 — D — 7 — 5 — 1 (c. f.) ∼ 5 ∼ 7 ∼ D (p.f.) — 7 — 5 ··· 1 — emerged, at once entered again. (Again she failed to carry the fly in cell C.)

The 11th time : 1 ··· 5 ··· 6 ··· C — 6 — 7 — D (c.f.) ∼ 7 ∼ 5 ∼ 1 (p.f.) — 5 — 6 — C — 6 — 7 — 5 — 1 — (2) — (5) — 1 — (2) — 1 — emerged from the entrance, but at once returned in the tunnel.

The 12th time : 1 — (2) — 1 — (2) — 1 — went out of the burrow, at once turned round and came in.

The 13th time (at 10.06) : 1 ··· 5 ··· 6 — C — 6 — 7 — D — 7 — 5 — 1 (c. f.) ∼ 5 ∼ 7 ∼ D (p.f.) ··· 5 ··· 1 — emerged from the nest, but at once came in again.

The 14th time : 1 ··· 5 — 6 — C — 6 — 7 — D (c.f.) ∼ 7 ∼ 5 ∼ 1 (p.f.) ∼ went out of the entrance with the fly. It was reverse in its bodily orientation, since it was dragged out by the apex of the abdomen. The wasp altered the manner of capture as in usual case, then flew up, but soon alighted in front of the entrance and penetrated again carrying the fly.

The 15th time, at 10.09 : 1 ··· 5 ··· 6 ··· C — 6 — 7 — 5 — 1 ··· 5 ··· 6 — C — 6 — 7 — D — 7 — 5 — 1 (c.f.) ∼ 5 ∼ 7 ∼ D (p.f.) ··· 7 ··· 5 ··· 1 — then she closed the glass tube with a small quantity of sand and went out of the nest. But at once she turned round and came in again. But without coming in sight in the glass tube, emerged again, flew about a little and at last went far a way, leaving the entrance opened.

The above behaviour of the wasp was shown graphically in Figure 45.

In this figure, the behaviour of the wasp represented from the 1st to the 4th entrances will certainly show the search of the wasp for her larval cell. During the course, the wasp made 8 trials from the main tunnel to go in the first branch-tunnel. In these cases it seems especially of interest that the wasp invariably entered first the left hand pathway of the first branches, excepting for 2 cases. This fact will give evidence that she has a memory or the learning effect of the direction of her pathway to her larval cell, since it was situated on the left side in her last visit in the preceding experiment. Besides, as for the 2 exceptional cases we may be able to explain them also by assuming the intervention of the odour factor coming from the brood-cell. That is, we suppose that there are two potential factors that guide the wasp to her larval cell under the natural condition. One may be the memory (probably kinesthetic in nature) of the direction of the curvature of the tunnel and the other the odour coming forth from the larval cell. Under the natural condition the two sources of stimuli always agree in direction with each other. They are never spatially separated. While in the present state of the nest they are spatially divided through the experi-

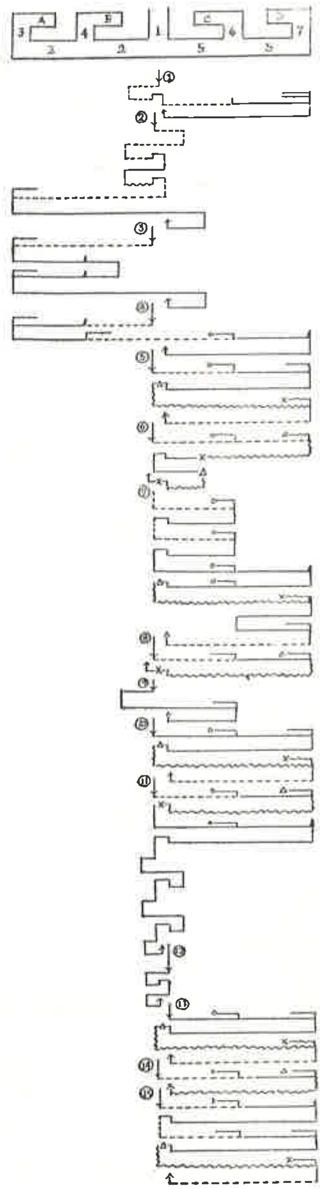
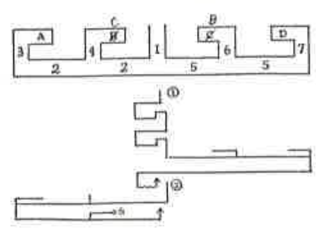


Fig. 45. Behaviour diagram of Wasp No. 114 in the triple Y maze. Solid line — forward progress. Broken line — forward progress with sweeping movements. Waved line — backing progress carrying a fly. △ — captured a fly. × — placed the fy. Circlet — touched the larva.

mental technic. The one, the inner factor, guides the wasp in the left direction, while the other, the outer factor, guides her in the right direction. The two exceptional cases wherein the wasp first entered the right-hand branch might be those in which the wasp was tempted much by the actual stimulus coming forth from the larval cell. However, the fact that in other 6 trials the wasp invariably first went in the left direction should be said to indicate that the inner factor, the memory, exerts a stonger influence upon the behaviour of the wasp than does the outer factor, the direct odour.

In her last trial of the 4th entrance the wasp succeeded in finding out the brood-cell. And it is a great surprise to us, judging from the subsequent behaviour of the wasp, how correctly and surely she has learned by a single visit the way to the larval cell — the maze that has 2 forking points on the way. But this conclusion is open to the question as to whether the wasp has directly learned the way to the larval cell or merely she has learned the fact that she should follow the outer stimulus only to go correctly to the larval cell. This problem will be solved by the subsequent experiment. Whichever explanation may hold true, it is invariably a surprise to us how easily the wasp has acquired the method of going to the brood-cell. However, this is only related to her forward progress. In her backing progress carrying a prey, things become quite different. The wasp can not control her course as she wants. Indeed, all the behaviour of the wasp after she has learned the correct way to the larval cell is nothing but an expression of her effort to lead her backing progress to the larval cell. Prior to the actual transportation of the prey, the wasp always ascertained the correct way to the chamber by her forward progress. Nevertheless she never succeeded in carrying it correctly to the brood-cell until the last moment of her efforts. The reason for this seems to lie merely in that the way to the empty cell (D) has a mechanical easiness to enter at thd 2nd bifurcation. However, in this case it is the 2nd surprise to us that things did not come to the end by mere automatic completion of the work of transportation of the fly to a certain cell. By some reason or other, the wasp became aware of her failure of the transportation and then she recommenced the work from the beginning. She retransported the fly to the entrance gallery of her own tunnel, the starting point of her work, and resumed the same manoeuvre as before. Five times she tried and five times she failed. No one will be able to deny the presence of something in the nervous system of the wasp that cannot be stabilized unless she can ascertain the presence of the carried prey by the side of her larva — something like the will, endeavour and even judgement (recognition of the failure and an effort for its emendation) in the human beings. At the same time, however, we must not overlook the fact that it was impossible for the wasp to carry the fly simply from cell D to cell C. It seems that the wasp is able to recognize the actual states of things and be aware of the failure of her work and even repeat some part of the subunits within the behaviour unit, storing, in order to emend the wrong result. But she is unable to correct her failure directly at its very spot. This is probably due to the interlocking system of the acts wihtin a behaviour unit. It will be also worthy of notice that, although she thus failed to carry the victim correctly to the larval cell, it is related only to the 2nd bifurcation. At the 1st bifurcation the wasp took invariably the correct direction.

In order to ascertain the reserved problem concerning the leading power of the larval cell, I made the following experiments: I removed all the victim including remains from bottle C and placed instead 3 fresh flies, the larvae being untouched. I then exchanged B and C for each other. As a result the arrangement of the bottles and each contents became, from the left side, as follows: A (empty), C (2 larvae and 3 flies), B (empty) and D (one fly). After the arrangement of the bottles, I waited for the wasp coming back. But she did not return for 30 minutes thereafter. So I left the place to examine another nest, placing a pebble on the entrance. Less than 2 minutes later, when I saw the nest, the pebble was moved and the wasp was already in the tunnel. I hurriedly uncovered the arrangement and exposed all the portion of the tube to the direct rays of the sun, so as to impede the entrance of the wasp to the apparatus. Soon the wasp came in sight in the glass tube but retreated in hesitation. I covered the arrangement again with sand excepting the branching points, placing the whole nest under my big umbrella and then let her come in. Judging from the condition of the time and also from the usual behaviour of the wasp I convinced that she had not yet enter the arrangement when I found her in the nest. She then showed the following behaviour in the arrangement: 1 — 2 (t. r.) — 1 — 2 (t. r.) — 1 — 5 — 6 — B — 6 — 7 — D — 7 — 5 — 2 ∼ 1 — appeared at the entrance, closed there and flew away (Fig. 46).



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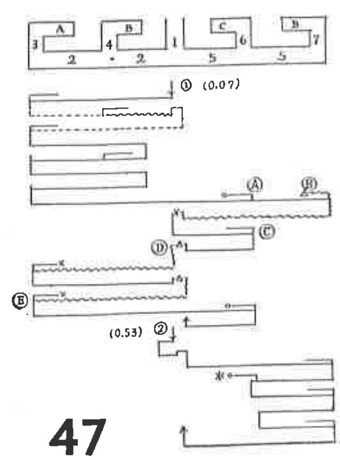

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Figs. 46 and 47. Behaviour diagram of Wasp No. 114 in the triple Y maze, the 2nd and 3rd experiments.

In the wasp's behaviour at this moment we can perceive the same sort of hesitation at first at the first forking point of the tube as observed in the preceding experiment. The wasp appeared to be tempted much to go in the left direction. Nevertheless, at her 3rd attempt she went straight to the previous position of the larval cell. This seems to be one important evidence that the wasp is more strongly guided by her memory regarding probably the direction and the curvature of the tunnel than by the actual influence of the odour of the larval cell, although the latter has apparently some leading power upon the behaviour of the wasp. This is also a definite proof that the wasp has learned the way to the larval cell by her single visit to it and not learned the relation that she has only to follow the olfatory stimulus coming forth from the larval cell in order to reach there correctly.

Ten minutes later, at 11. 40, she returned without a fly as before and entered the tunnel. This time she succeeded in finding the larvae after the following procedure: 1 — 2 — 4 — 3

— A — 3 — 4 — C (t.l.) … 4 … C (t.l.) … 4 … C (t.l.) … 4 … C (t.l.) … 4 … C (t.l.) … 4 … C (t.l.) … 4 … 2 … 1 — went out and flew away (Fig. 46, ②; * means the repetition of the same behaviour). In this case the wasp came in the left-hand branch from the first. Probably the result of her preceding visit exerted some influence upon her.

As it became clear that the wasp came to know the exact position of her larval cell, I exchanged again the positions of cells C and B for each other, in order to confirm the procedure of her learning once more. Thus, the larvae came to be in the 3rd bottle from the left end. At 0.07 p.m., the wasp returned carrying a fly. She entered the tunnel at once and showed the following behaviour in the arrangement :

1 … 2 … 3 … A (stayed for about 40 s.) … 3 — 4 — B — 4 — 2 — 1 … 2 … 3 … A … 3 — 2 (t. r.) — 4 — B — 4 — 3 — 2 (t.r.) — 3 — A — 3 — 2 (t,r.) — 3 — 2 — 5 — 6 — C — 6 — 7 — D (c.f.) ∼ 7 ∼ 5 ∼ 1 (the fly being dragged in its reverse bodily orientation) ∼ (p.f.) — 5 — 6 — C — 6 — 5 — 1 (c.f.) ∼ 2 ∼ 3 ∼ A (p.f.) — 3 — 2 — 1 — (c.f.) ∼ 2 ∼ 3 ∼ A (p.f.) — 3 — 2 — 5 — 7 — D — 7 — 5 — 2 (t.r.) — 1 — went out (at 0.17) and flew about and then flew away (Fig. 47).

In figure 47. the wasp found the larvae for the first time at the point marked with Ⓐ. The behaviour before arriving at Ⓐ represents the search for the larval cell, undoubtedly basing upon the memory acquired by her preceding visit. The behaviour Ⓑ - Ⓒ is nothing but the preliminary activity that usually precedes the transportation of the prey. Those Ⓓ - Ⓔ show the error of direction in her backing progress. By this experiment it was clarified that the wasp had acpuired by her single visit a fixed memory regarding the left-hand way, associated with the existence of the larval cell. But in this case she showed an error at the second bifurcation in entering branch 3 first, though the error was at once corrected. Moreover, it must also be noticed that this time, though the wasp attempted to transport the victim twice to the brood-cell, she committed an error in both cases at the first forking point of the tunnel in carrying it in the left branch.

While she was absent the contents of each bottle were examined. In A were 2 flies, one of which was transported from bottle D, in B and D nothing. At 0.53, the wasp returned empty-handed. Her behaviour in the glass tunnel was as follows : 1 — 2 (t.r.) — 5 — 7 — D — 7 — (5) — 7 … 6 — C (t.l.) ∼ 6 ∼ (5) … 6 … C ∼ 6 ∼ (5) … 6 … C (repeated the same behaviour as many as 21 times in total, always touching one or both of the larvae in the cell) — 6 — 7 — D — 7 — 5 (t.r.) — 7 — D — 7 — 5 — 1 — emerged and flew away (Fig. 47). In this case, the persistently repeated entrances and exits to and from cell C may be of the same nature of behaviour as observed in the case of the first change of the position of the brood-cell. The subsequent behaviour may represent the search for a victim to be transported.

I then interchanged bottles B and C once more, placing C in the 2nd position from the left end. At 0.30, the wasp returned with a prey. She entered the tunnel and moved about as follows :

The 1st time : 1 — 2 — (4) — 3 — A (not c.f.) ∼ 3 ∼ 2 (t.r.) — 1 — emerged from the entrance, but at once entered again.

The 2nd time : 1 — 2 — 3 — A (touched the prey and appeared to be searching for the larva) ∼ 3 — A ∼ 3 — A (repeated the same behaviour 6 times and then) — 3 — (4) ∼ 2 (t.r.) — 1 — went out and at once came in the nest.

The 3rd time : 1 — (2) (5) ∼ 1 — 5 — (6) ∼ 5 (t.r.) — 1 — 2 — (3) ∼ 2 — 3 ∼ 2 (t.r.)

—1—emerged, but at once reentered the tunnel.

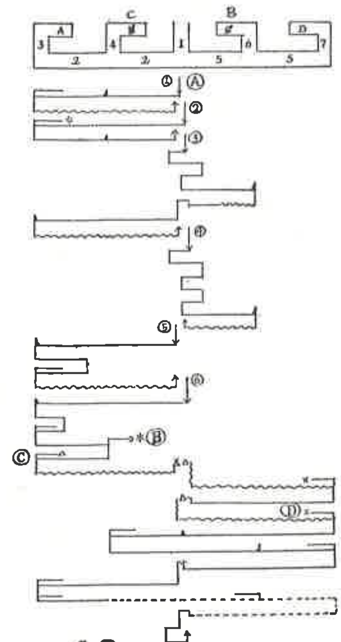
The 4th time : 1—(2) (5) ∼1—(5) ∼1—5 ··· 6 (not went in B) ∼5∼ (t.r.) — (2) — 1—crept out but at once returned in the nest.

The 5th time : 1—2—(3) ∼2—3∼A (only to the entrance) ∼2—1—went out and at once came in the tunnel.

The 6th time : 1 — 2 — (3) ∼ 2 — 3 — A (repeated several times the forward and backward progress) — 3 — 4 — C ∼ 4 — C (t.l.) ∼ 4 — C (caught one of the larvae and carried it to the interior) — 4 — 3 — A (c.f.) ∼ 2 ∼ 1 (p. f. and at once c.f.) ∼ 5 ∼ 7 ∼ D (p.f.) — 7 — 5 — 1 (c. f.) ∼5∼7∼D (p.f.) — 7—5—1—2—4—C (t.l.) — 4 — 2 — 5 — (6) — 7 — D — 7 — 5 — 1 — emerged out of the nest, but at once came in the tunnel.

The 7th time : 1 ··· 2 ··· 3 ··· A — 3 — 4 — C (t.l. repeatedly) — 4 ··· 2 ··· 5 ··· 6 ··· (7) ··· 5 ··· 1 — 2 — 1 — went out and flew away (at 0.43 p. m.).

The above behaviour of the wasp are shown in a graphic representation in Figure 48. In this figure, the behaviour of the wasp shown from A to B may be done in search of the larva. But the psychic relation between this and the previous visit is uncertain, because, this time the wasp did not follow the result of the previous experiment. However, it might happen that the repeated changes of the situation of the brood-cell rendered her follow only the external factor (smell) among the stimuli that can guide her to the larval cell. Moreover, the presence of 2 flies in cell A might delay the discovery of the larva (see the 1st entrance). While the 3rd visit seems to show the presence of the memory upon the previous way to the larval cell. In her 6th entrance, C - D, the wasp tried to carry flies to the larval cell, but this time, too, she failed to control her backing progress. The behaviour below D may be done to ascertain the result of the previous transporation. But it is unknown why she did not attempt this time to correct the erroneous transportation of the previous work.



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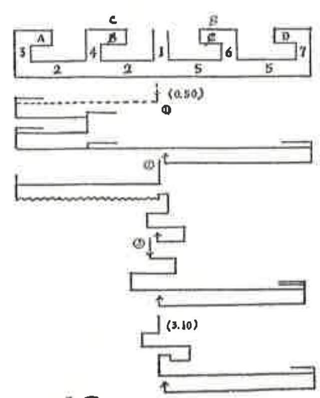

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Figs. 48 and 49. Behaviour diagram of Wasp No. 114 in the triple Y maze, the 4th and 5th experiments.

At that time, in bottle A was 1 fly, in D 2 flies. In C a fight had been broken out between the 2 larvae and one of them was wounded at the 4th segment.

At 0.50, the wasp returned without carrying a fly. She behaved in the glass tunnels as follows :

The 1st time : 1 ··· 2 ··· 3 ··· A — 3 — 4 — C (t. l. then repeated several times the forward and backward progress) — 4 — 3 — A — 3 — 4 — C (examined especially the larva located at the interior portion which was wounded) — 4 — 2 — 5 — 7 — D — 5 — 1 ⇝ went out of the nest, but at once returned in the tunnel.

The 2nd time : 1 — 2 — 3 ⇝ 2 (t.r.) — 1 — (2)(5) — 1 — emerged but at once crept in.

The 3rd time : 1 — (5)(2) — 5 — 7 — D — 7 — D (rested a while) — 7 — 5 — 1 — emerged from the burrow and flew off.

At 3.10, she came back empty-handed. She took an alarming attitude at the first forking point for about a minute and then entered the branch-tunnel : 1 — (2)(5) — 5 — 7 — D (rested a while) — 7 (rested a short time) ··· (6)(5) ··· 5 ··· 1 ··· went out. She entered the tunnel again, swept out the sand a little from within, turned round, closed the entrance roughly, rested a while at the entrance, rubbing her antennae with a front leg and at last flew up. But she soon alighted on the neighbouring ground, rested a short while and then began to flew about low over the ground. She did not alight on the ground when she came near the nest. It appeared that she was searching for the nesting place to dig a new burrow. The closure of the entrance of the nest was very rough, half-opening and it seemed that the nest was abandoned. I closed the entrance and placed a pebble on it. It remained without change for 2 subsequent days. I examined the arrangement and found both larvae dead and rotten.

According to Figure 49, it is presumable that the wasp lost her interest to provision this nest, although it is unknown whether the cause may be some uncertainty she might feel, or the wounded larvae she might know. Indeed, she did not bring a victim to her nest in her last 2 returns at 0.50 and 3.10 respectively and abandoned the nest at last. Therefore, the behaviour of the wasp shown in her last 2 returns (Fig. 49) is considered abnormal.

According to the results of the above experiments it seems evident how exactly and how promptly (by a single visit !) the wasp can learn the correct way to her brood-chamber in a mazy tube. Indeed she can follow the correct way in the triple-Y-tube already in her 2nd visit. Moreover, it was also made clear that the result was not effected by following some external factor that guided the wasp automatically to her larval cell, although such a factor, probably the smell of the larval cell, is confirmed to exert some influence upon the behaviour of the wasp. This astonishing result is, therefore, doubtlessly effected by the fact that the wasp was guided by the internal factor of that memory regarding probably the direction and the curvature of the pathway which was, no doubt, acquired in her previous experience. This memory becomes so rapidly established that the word "learning" can not be applied here in its usual sense. The above accounts, however, can be applied only within the scope of the forward progress. In her backward walking carrying a fly, the wasp con not always take a correct way. The direction to be progressed at the branching point of the tube seems to be determined rather by the mechanical easiness of the way, although it seems to be controlled more or less by the wasp. Hence all the attempt of the wasp to take victims to the larval cell completely failed in the end and she could not supply even a single victim to the larvae.

The most remarkable fact obtained here is the astonishing mode of learning of the wasp regarding the correct pathway in her branched tunnel. But this mode of learning seems to stand upon the common basis prevailing in the life of the hunting wasps in general. A wasp, during her transportation of a prey from afar to her nest, usually lays it aside from time to time on the way to go to visit her nest. But when she comes back to the prey, she shows the same astonishing memory as met with here regarding the exact position of it, although her experience to the place is restricted to a single visit. This phenomenon which occurs in the broad daylight, however, relates in the main to the memory of the direction of the sunlight as well as of the distance between the two points*. Nevertheless, the easiness of the process of learning in reference to the necessary objects seems to be fundamentally the same as in the case of our *Bembix*.

2. Learning of the short way

Wasp No. 105. Aug. 14, 1948. I saw a wasp carrying in her nest a fly at 1.55 and 2.06 p.m. respectively. On digging open the brood-chamber I found in it a larva of the middle stage of the last instar supplied with 15 flies, of which 7 were remains. I set an experimental arrangement at the end of the tunnel as shown in Figure 50. The left-hand branch was 15 cm in length, while the right-hand one twice as long as it. I put in the centre of the cell the larva and an intact fly. At 2.40 I saw the wasp return without a prey and entered the nest, but I could not observe her behaviour. The next day, at 10.25 a.m., the wasp carried in a fly. At 11.34 ditto. On examining the brood-cell I knew 5 flies had been added in it. Judging from their bodily orientation it was evident that all of them were carried in through the left-hand branch, the short path. Thus, the wasp, in opposition to the original direction of her own tunnel, took the short way. However, on account of the lack of the direct observations, it was uncertain whether the results were due truly to her selection or merely effected by chance. I then turned the brood-cell through 180°, so that the victims stored in it might come as if they had been brought in from the right-hand branch, the long path. At 11.45, the wasp took in another fly. I uncovered the cell and waited for her coming in. After spending 2 minutes the wasp came sweeping the tunnel through the right-hand branch and made a fricative near the cell (a phenomenon occasionally observed in such a case). She trampled over the victims to go to the larva and touched it with the antennae. Then she returned to the victims, caught one of them with her mandibles and brought it by the side of the larva. She then passed over the larva, went to the exit to the left-hand branch, opened the sand-stoppage (formed casually by the fallen sand) and went in the tunnel. Two minutes later the wasp returned backing with the fly through the right-hand branch. She placed it as usual in the entrance portion of the cell and rested motionless thereafter in the tunnel for about 5 minutes. thrusting her abdomen in the cell. I covered the cell with sand. Ten minutes later she emerged from the

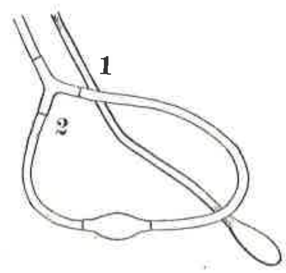


Fig. 50. Experimental equipment for the learning of the short way. 1, natural tunnel.

* Tsuneki, K. 1950. Experimental analysis of the sensory cues working in the return to the nest of the Pompilidae. Annot. Zool. Jap., 23, (3), pp. 75 – 84.

entrance and flew away. At 0.30 p.m. the wasp returned capturing a prey. After 3 minutes from her entrance, she came in the cell through the left-hand branch and touched the larva. But the next time when she brought the fly, she came through the right-hand branch. Passing over the accumulated victims, the wasp brought the fly to the larva, then turned round and went back in the right-hand tunnel. At 0.38 she flew away.

I then removed all the victims but one decapitated fly from the brood-cell. At 1.13, a new victim was brought in. The wasp came through the left-hand branch and returned from the cell at once without touching the larva through the same tunnel. But, curious enough, thenceforth she did not come in sight for about 5 minutes. I uncovered the glass tube, but she was not there. I covered the tube again. Soon, the wasp came in the cell through the left-hand tube. She touched the larva, caught it between her mandibles as if intended to carry it somewhere, but after a while she released it. She then returned to the exit to the left-hand tunnel and penetrated in it. But only a few seconds later she came back and strided on the larva, caught it between the jaws. Probably it was on accunt of the brightness of the chamber. But soon she laid down the larva, left it *in situ* and went in the right-hand tunnel. However, after a moment she returned again, caught the larva once more from in front by its neck or by its 3rd or 4th segment and pulled it backward. The larva turned and twisted its body and struggled violently. So I covered the brood-cell with sand excepting a small observation window, through which I could see the wasp started in the right-hand tube. Soon after, she came dragging the prey through the right-hand tunnel and placed it in the cell. She then went to the larva, caught it again and moved it a little. Next moment she laid it down and went to the left-hand tube and entered it. But at once she came back and again caught the larva. The larva resisted and struggled furiously by twisting and turning its body. The wasp released it at last and went in the right-hand tunnel. Then she came retreating with the sand and swept it backward in the cell. So the larva was half covered with it. It twisted the body and came out of the sand. The wasp went in the tunnel. But she came backing once more through the same tunnel, but this time without the sand and at once returned. At 1.37, after spending 20 minutes in the tunnel she departed on the next foraging excursion.

At 1.47, the wasp returned with a prey. She came to the cell through the left-hand branch and returned without examining the larva. But later she did not come in sight until 2.05, so I covered the cell and left her alone. At 2.40, again she took in a fly. This time she came and went twice through the left-hand branch in order to examine the larva as well as to transport the fly. She flew off at 2.47. At 3.15, she took in another fly and at 3.27 flew away*. At 3.39, she came back empty-handed and 4 minutes later went off. I examined the brood-cell and found 6 victims in the cell, including the fly that I placed in it. Out of the 5 flies newly added, 3 were transported from the left-hand branch, while the remaining 2 from the right-hand. I removed 4 flies from the cell, leaving 2 in it. At 3.47, the wasp carried in a fly. She came out at 3.53, but after flying about a while, entered the nest again, probably for the night. The subsequent day (the 16th) when I arrived at the place at 10.00 a.m., the wasp was about to carry in a fly. In the cell had been added 2 flies, both of which were brought in through the left-hand branch. At 10.48, I saw the wasp take in another fly. On examining at 10.58, I found 2 more flies had been carried in the cell through the left-hand tunnel. I removed all the victims but 2. At 10.55 the *Bembix* entered her nest with a

* At this time of the day no wasp was engaging in the provisioning work. The activity of this wasp, therefore, is entirely compensatory in nature and is markedly accelerated by the removal of the prey from the nest.

prey. She came through the left-hand tunnel, touched the larva, hurriedly returned and then came again dragging the prey, put it in the chamber and went out. All her passages were carried out through the left-hand branch. At 11.00, she came back carrying a fly. This time I left the whole tunnel of glass uncovered. She entered the left-hand branch, but returned from the millde of the way; again she came in through the same tunnel up to the entrance of the cell, but went back without entering the cell, this time with the backward progress. Next she came in till the middle of the same tunnel, but at once retreated in her own dark tunnel. I covered the tunnel of glass with sand. Soon she came backing with the fly, placed it at the entrance of the cell and went out, after making in vain the closing movement in front of the cell.

I then exchanged the tunnel of both side for each other, thus making the left-hand branch the long way and the right-hand tunnel the short way. The brood-cell was placed as before. At noon, the wasp came back with a booty and entered the nest. At 1.00 p.m., when I examined the brood-cell 2 flies had been added in it, of which one that was first taken in had been-carried through the left-hand branch, while the other that was taken in in the 2nd time had been transported through the right-hand branch. During the time when I was examining the contents of the nest, the wasp was resting in her own tunnel and soon came through the right-hand tunnel in the cell. She touched the larva, caught it by the neck or by the thorax and moved and dragged it about. Soon, however, she released the larva, trampled on it and the prey to go in the left hand tunnel. But at once she came back from the tunnel in the cell, passed over the larva and went in the right-hand tunnel. She returned again in the larval cell and caught the larva between her mandibles. Soon she laid it down and went in the left-hand tunnel. But at once turned round, gathered the sand from in the cell and closed there, packing the material with the tip of her abdomen. After the work finished the wasp went in the right-hand tunnel. At once she turned round, thrust her head in the cell, but returned without entering. The same behaviour was repeated several times. At last she turned round and went in her own tunnel. At 1.40, the wasp was making the permanent closure in the entrance tunnel. The passages she walked during the course of the experiment were shown diagramatically in Figure 63.

Out of 8 cases that were directly observed, 7 were those in which the fly was dragged in through the same tunnel as was passed in the first visit empty-handed. Only a single case made an exception wherein the wasp dragged in the victim through the different tunnel from the first one. Judging from the fact it may be allowed in this individual to infer that in other cases which were not directly observed by me, things might pass in like manner. Now, if we arrange the number of

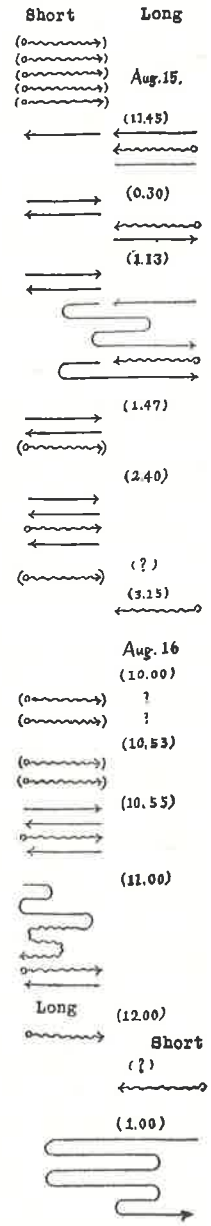


Fig. 51 Behaviour diagram of Wasp No. 105 in her learning of the short way.

prey transported through each side of the tunnel in the first series of experiment (before the exchange of the tunnels), the number of the prey carried through the left-hand tunnel (the short way) comes to 14, while that through the right-hand tunnel only 4. That is to say, the flies carried to the brood-chamber through the short path are 3.5 times as many as those carried through the long path, the former occupying 78 % of all. This is by no means an accidental result, since, as examined above, the direction of the backward progress in this wasp is in fair accordance with that of the first visit carried out head first. Moreover, the instances in which the prey were transported through the long path concentrate comparatively in the earlier portion of her activity. Besides, after the tunnels were interchanged in position, the wasp used to pass the tunnel through the short way, despite of its locating on the different side. Only in one occasion (at noon of the 16th) she transported the victim through the long way. But this occurred at her first return after the rearrangement was performed. The fact shows that the wasp, in this case, passed the left-hand tunnel either owing to the memory of the direction or owing to the memory of the short way. Whereas, the results of her succeeding passage seem to give a proof that the latter was the case.

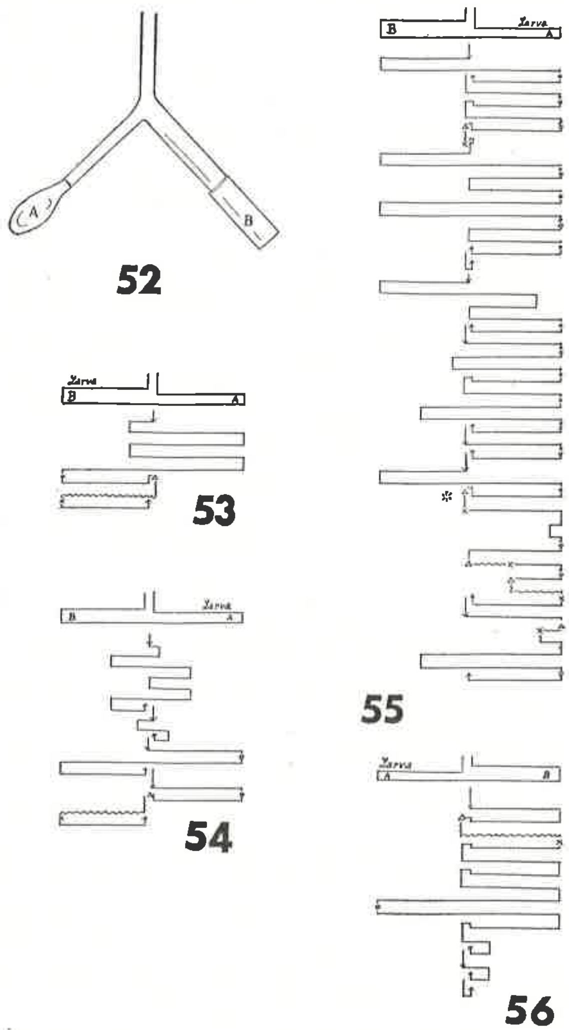
In conclusion we can say as follows : *Bembix*, if given two sort of the ways that lead respectively to the same brood-chamber, one the short way and the other the long way, she has a marked tendency of learning to pass through the short way.

3. Learning of the broadness of the path

1) Wasp No. 136. Aug. 26, 1948. I saw the wasp carrying in a fly to her nest at 9.02 and 9.12 a.m. respectively and dug the brood-cell at 10.20. The nest was of the simple type and in the brood-cell was a larva of the early middle stage of the 4th instar supplield with 15 flies, of which 9 were already eaten. I placed at the end of the tunnel a Y-tube of glass, attached with a bottle at the apex of each branch. The branches were different in diameter, one placed on the left side being 10 mm, while the other put on the right side 20 mm, both bearing 7 cm in length. Bottle A placed at the end of the left-hand narrow branch was an ellipsoidal cell of glass, while the other (B) put to the broad branch of the right side was a normal tube bottle of the same diameter as the branch, both being 7 cm in length (Fig. 52). I placed the larva of this nest alone in the right-hand broad cell without supplying a victim, while the left-hand narrow bottle was left empty.

At 10.43 the wasp came back with a large flower-fly (*Eristalomyia tenax*) and was escaped at the entrance. She succeeded in recapturing it in her pursuit and entered the nest with it. At 9.50, she came out and flew away. The fly was in bottle B, namely by the side of the larva. At 11.20, she took in one more fly, at 1.29 p.m., ditto. I examined the cells at 4.13. Within cell B were 2 flies and in the broad tube just in front of the cell were placed 3 flies, while cell A remained empty. I removed again all the victims from the nest. The next day, I examined the arrangement at 9.45 a.m. Cell A remained empty as before, while cell B contained 3 flies.

I turned the arrangement through 180° so as to place the broad branch together with bottle B on the left side and the narrow tube with bottle A on the right side. While I was engaging in the rearrangement, the wasp came back with a booty and was flying about around the nest. At times she alighted in front of the entrance and attemted to enter the burrow. But every time she was driven away by my hand. At last she dropped the fly and flew away. But 4 minutes later she returned carrying another fly and entered the nest. I uncovered the arrangement and waited for her coming in. She appeared as usual empty-handed and entered without hesitation the left-hand branch, but before arriving at the cell, turned round and came in the right-hand (now, narrow) branch. she entered up to the interior of the cell. turned round and went in the left branch. But this time too, she returned from the middle of the branch and came in the right branch. Again she entered the empty cell and returned to the left-hand branch. This time she entered the cell, touched the larva and then went back in the main tunnel. At once she came backing with the fly and carried it in the left branch. She placed it at the entrance of the cell, went back at once (without examining the larva) in the main tunnel and after making a closing behaviour in the glass tube, flew away. Her behaviour at this time was shown graphically in Figure 53.



Figs 52 - 56. Fig. 52 — Experimental equipment for the learning of the broadness of the path. 52 - 56 — Behaviour diagram of Wasp No. 136 in the apparatus.

In this experiment, among 3 factors that can be inferred to guide the wasp to her larval cell, namely, as an internal factor the memory of the direction of the way and as external factors the odour of the larval cell and the broadness of the way, only the direction of the way underwent a change. Whereas, the wasp in her first two attempts, although apparently attracted much by the left-hand branch, came in the right-hand passage in the end. That is to say, she appeared to have been guided more strongly by the memory of the direction of the passage than by others.

In order to test the effect of odour of the larval cell, I replaced the left-hand bottle with another new one of the same size and shifted the larva and the 2 flies in the right-hand cell. At 10.12, she came back with a fly. After opening the closure of the cell (which was formed in the main tunnel) she came to the forking point. There she thrust her head in the right-hand branch, but at once returned and entered the left-hand tube. She did not come in, however, until the cell, turned round from the middle of the way and went back toward the main tunnel. She stopped, however, at the bifurcation, turned round again and entered the right-hand branch. This time too, she returned before arriving at the cell and came in the left-hand branch. There she turned round from half of her way, and at last went back in the main tunnel. In this case, among the 3 factors, 2 underwent a change, namely the direction of the way and the broadness of the path. Accordingly, if the wasp be guibed by either of the two or by both, she would go in the left-hand branch without hesitation. Whereas she showed a manner of uncertainty at the dichotomous point and after trying to enter this or that branch, returned in the basal tunnel in the end.

Soon the wasp came in again. She thrust her head first in the left and then in the right branch, proceeded a little in it, but at once turned round and returued in the basal tube of glass. For the third time of her trial, she came in the right-hand tunnel up to the interior of the cell and touched the larva. But when she went back to the bifurcation of the tunnel she entered the left-hand tunnel also and reached the interiormost wall. Probably her entrance in the left branch at this time may be a mistake for going to the basal tube to bring the fly. She returned and went in the main tunnel. Soon she came in, but without carrying the fly. She entered the right-hand branch without hesitation and in the cell touched the larva. Possibly the disturbance occurred in her return to the victim drived her to come to the larva once more. Then she went back in the main tunnel and at once came backing with the fly. But she happened to drag it in the left-hand broad tnnnel and placed It in the empty cell. At last she flew away, without making the reexamination of the fly just before taken in.

According to the result (Fig. 54) it is presumable that the odour of the larva takes a considerable part in guiding the wasp to the larval cell, But at the same time it shows that the odour alone can not be decisive to lead the wasp to the larval chamber, since she showed repeatedly a confusion in the entrance to either of the branches. In the end, however, odour factor acted more strongly upon the behaviour of the wasp than other factors did. However, we must take into account in this case that the wasp has had only a single experience regarding the previous conditions of the nest and that she have probably been influenced more or less by the remaining memory on the first experimental condition of the nest associated with the odour factor coming forth from the same direction. At any rate, it will be able to say that her confusion shown at the bifurcation of the tunnel occurs through the separation of the guiding factors that must firmly be conbined together under the normal state of the nest.

I left the arrangement without any change. At 10.35, the wasp came back capturing a white banded flower fly (*Megaspis zonata* Fabr.). Her behaviour in the nest was shown in Figure 55. In the figure, a small black spot stands for "touched the fly", other symbols and lines were as in the foregoing figures. The behaviour of the wasp below * in the figure was as follows : She came dragging the fly to the forking point and laid it down to come in the right-hand branch. There she touched the prey (which were at the entrance of the cell) and the larva (which was in the interior) alternately. She then went to the laid-down fly which had half slipped into the left-hand broad branch, captured it by the tip of the abdomen and dragged it backward. As the bodily orientation of the fly was raversed, the wings and the legs came to be extended and hindered greatly the wasp's progress. The wasp pulled it sometimes by the tip of a wing, or sometimes by one of the legs. But the prey could not easily be transported. Nevertheless she continued to pull it eagerly with great effort and succeeded in carrying it till the middle of the way. There she laid it down and came in the brood-cell, touched the prey and the larva in turn and returned to the flower fly to resume the transportation. This time she caught it by the waist and pulled it violently with the stridulating sounds. The prey became more and more difficult to move and the wasp's legs slipped vainly on the glass floor. The wasp stopped her work and came again to the larva. But soon she returned to the prey, caught it by the leg or by the wing or sometimes by the tip of the abdomen and at last barely succeeded in pulling it in the cell. There she laid it down and *began to gnaw its body**. Soon she ceased to gnaw the victim and went back in the main tunnel. Once she emerged from the entrance but at once returned in the burrow. She came straight in the right-hand cell, caught one of the prey that had been placed there by the tip of the abdomen and attempted to drag it out. However, on account of its revesed bodily orientation the work was very difficult. So she ceased to drag it backward and *began to carry it by the forward progress*. But of course the attempt ended in failure. At last she gave up the work and returned to the main tunnel empty-handed. At the bifurcation she turned in the left-hand tube but returned from the middle and came in the larval cell again. There she touched the larva and went back, this time staright in the main tunnel and soon after flew away.

During the course of the experment shown in Figure 55, the wasp entered straight from the main tunnel in the left-hand broad branch as many as 4 times. But judging from her behaviour directly, observed these entries seem to be mistaken or rather forced by the structural character of the tube. As a mechanical result of the connection of the broad tube with the narrow basal one, the way to the broad branch can more easily be entered than the way to the narrow branch. When the wasp apparently intended to go in the narrow branch she was observed every time taking care not to slip in the broad branch. However, despite of such a care, once her front legs happened to enter in the direction, she used to follow the passage without hesitation. We can perceive here the weakness of the leading power of her memory of the direction upon her behaviour.

As the wasp seemed to have an adequate experience on the altered conditions of the nest, I then exchanged the position of both the branches and the cells of either sides for each other, putting in the left-hand narrow bottle the larva and one fly, while leaving the other broad bottle empty. At 11.20, the wasp returned with a booty. This time she behaved in the nest as shown in Figure 56. The subsequent day when I arrived at the place at 8.40 a.m., it began to rain. In the nest, in the left-hand bottle there was remains of a fly and in the right-hand bottle 2 intact flies. The larva attained the later stage of the last instar and was in the right-hand branch. Probably it moved forward for itself to spin the cocoon. The tunnel had been permanently closed. In the last experiment, if the wasp remembered the broadness factor of the branches more strongly than the direction factor, she might have

* This is a very abnormal behaviour and makes us suppose the manner of manipulation given upon the pedestal fly.

gone to the left-hand branch to meet the larva. Whereas the results were opposite to our expectation. Moreover, the manner of provisionment was alreadly of the automatic nature of the final activity. So that the leading power of her memory regarding the character of the tunnel, whatever may be the true nature of it, must appear more clearly than usual.

Generally speaking, this experiment seems to show that the direction factor of the pathway acts more strongly upon the behaviour of the wasp than either of the broadness- and odour factors. However, the result shown in Figure 54 seems to give a strong suggestion that the broadness factor of the tunnel exerts also some influence upon her behaviour.

2) Wasp No. 150. Sept. 5, 1949. At 10.30 a.m., I dug the nest. It was of the simple type, having a straight tunnel of 23 cm in length. In the brood-chamber was a larva of the later stage of the 4th instar supplied with 19 flies, of which 13 were intact. It was supposed that the nest was completed soon. I left the entrance tunnel by 10 cm untouched and placed at its end the same arrangement as used in the preceding experiment (Fig. 52). On the left-side were located the narrow branch-tunnel and a cell of bottle (A), while on the right side the broad branch and an usual tube bottle (B). In A were put a larva of the middle stage of the 4th instar taken out of another nest and 3 intact flies and in B only a single fly without a larva. At 10.55, the wasp returned with a fly. At 11.03 ditto. Her behaviour in the arrangement in both cases was as shown in Figure 57. From her behaviour observed at 10.55, we can perceive that the wasp was already in the course of the final provisionment. But when she entered the nest at 11.03, she became aware of that the larva was not present in the broad cell and after searching for it in the other branch-tunnel found it in the end-chamber of it. Neverthelass, in her next journey carrying the fly, she failed to bring it to the larva, owing to theb ackward progress and, morever, to the charcter of the tunnels. From that time until 10.13 of the subsequent day I left the experimental arrangement without giving any change, only removing from time to time the victims stored in the nest. During the period the wasp brought a victim no less than 27 times to her nest. But of which 2 recovered and fled away from between her legs at the entrance to the burrow, 3 escaped from my direct observation*. As for the remaining 22 cases, I have shown the principal matter in Table 12 and the behaviour of the wasp graphically in Figure 58. Now, I will give some interpretations on the behaviour of the wasp.

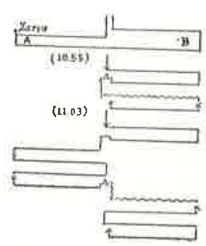


Fig 57. Behaviour diagram of Wasp No. 150 in the apparatus shown in Figure 52.

a) It was very frequently observed that the wasp appeared to take care not to slip into the broad branch that led to the empty (sens non-larval) cell. In such cases the wasp wended her head toward the narrow branch from the first and proceeded along the lateral wall of that side as closely as possible. Such a behaviour is represented by ⊙ in the Figure. Nevertheless, she often slipped into the broad branch and once slipped in, she proceeded indifferently in that branch up to the

* After 2.05 p.m. of the 5th I awaited until 2.30, but the wasp did not return. I stopped the observation of the day. The next day at 8.20 a.m. I examined the nest, and found 1 fly added in A and 2 flies in B. The wasp did not yet begin to work on the morning. So that it became that the wasp brought 3 flies further after 2.30 p.m. of the previous day. I removed all the flies from B, but cell A was left untouched, with remains of 3 flies and the larva.

end cell. This sort of her behaviour is also represented in the figure by ●. Such a behaviour is to be refered to that the wasp had a definte intention to go to the direction of the narrow branch at least at first, apart from the reason of such selective activities.

b) Out of 22 times of the provisionments, only 5 times (instances observed at 11.18, 11.40, 0.05, 9.22 and 10.12) are those in which the wasp took in the prey without examining the larva. In all the remaining cases the wasp carried it in the cell after the examination of the larva. Even in the exceptional cases, however, she could not omit the behaviour of visiting the cell, only omitting the actual contact with the larva.

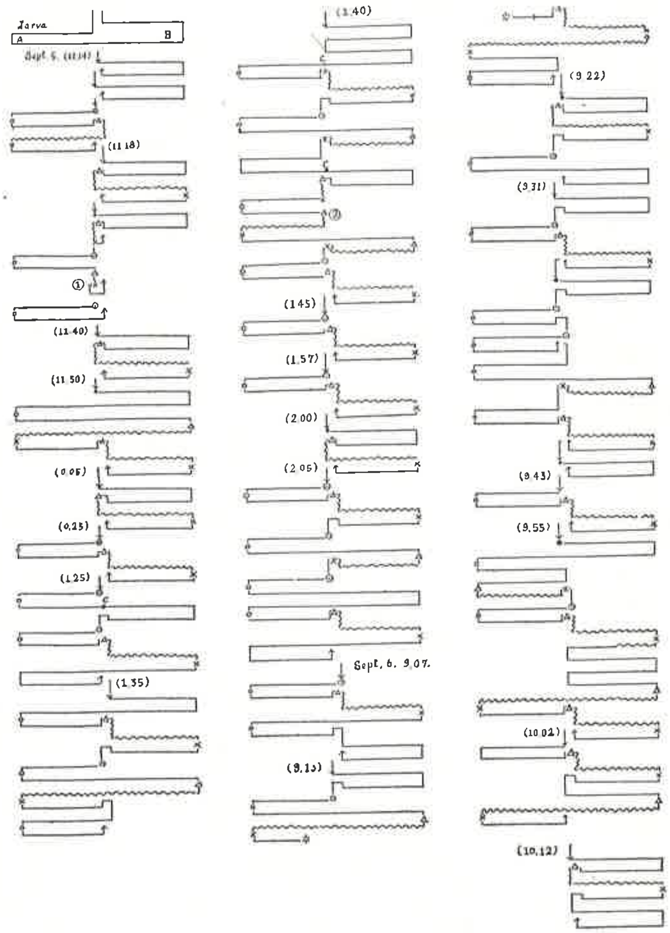


Fig. 58. The same as in Figure 57.

c) Even when the wasp carried the victim in a cell after the examination of the larva, it was impossible for her to lead her backing progress as she wants. In her backing progress, no special behaviour that makes us think of the *intention* of the wasp could be observed. So that all the prey but 3 were transported in the uninhabited cell that located at the end of the broad branch which could more easily be entered than the other.

d) However, the wasp, after the first transportation, attempted in 10 occasions to correct the error of the preceding transportation. Among these retransportations, 7 times she succeeded in correcting the error and carried flies in the larval cell. But in the remaining 3 cases she has commited an error again and carried them once more in the empty cell. Moreover, it is worthy of notice that out of the 7 correct retransportations, 6 were those in which the prey was directly transported from the right (broad) cell to the left (narrow) one, without any intervention of the basal main tunnel. It is not necessarily certain, however, that such a direct retransportation is in reality effected by the intention of the wasp. Because, we can also consider that such a case is resulted from the following procedure : "The wasp progressed backward with the intention of going to the main tunnel, as usually she does when intended to retransport a victim to another cell, but through the error caused by the backing progress she went to the other cell". Moreover, in the case when she came to the empty cell after the vitit of her larva and retransported the fly found there directly to the larval cell, it may be possible to regard that she might come there erroneously, with the intention of going to the main tunnel to take the fly just carried in. On the other hand according to the detailed examination of the behvaiour of the wasp, sometimes it seems also considerable that the wasp was aware of the divided condition of the tunnel as well as the presence of a non-larval cell at the end of one of the branches. Under such conditions it may be possible to occur that the wasp intends to carry a victim directly from the non-larval cell to the larval chamber. The instances observed at 9.13, (especially in the 2nd time), 9.55 and 10.02 a.m. of the 6th seem to belong to such a case. According to the considerations, there seems to be 2 possible cases in the direct transportation of the prey from one cell to the other. One is effected through the error, the other is intended by the wasp from the first.

e) In case the wasp proceeded head first from one cell to the other, there can be admitted also the same 2 cases as were given in the above consideration In the behaviour shown in Figure 58, those marked with *c* are the instances of non-intended entrance toward the branch. In these cases the wasp was proceeding in the bifurcation with the evident appearance of going to the main tunnel. This was supposed from her manner of sweeping the floor and from the direction of her head facing the main tunnel. Moreover, in such a case she used to enter somewhat in the basal tube. Whereas, at some moment her body happened to incline toward the other branch and then she became to proceed on in the direction, sometimes with the continued sweeping movement. Other instances of going from one cell directly to the other were all carried out smoothly with the distinct appearance of the wasp's intention of going to the cell.

f) In one occasion (the observation made at 9.55) the wasp retransported a fly that was placed correctly in the larval cell. According to the procedure of her behaviour at that time, however, it seems that the mistake of the wasp lies in her 2nd entry to the cell preceded to the transportation, and not in the very act of carrying away the victim from the larval cell. That is to say, when she entered the branch, she seemed to take it for the other branch and therefore she seemed to take the larval cell for the other empty cell. So that, apart from the result effected, there is no mistake in the act of the wasp excepting that she erroneusly reentered the same branch-tunnel. Or, it seems more probable that the preceding contact with the larva stongly releases the prey bringing activity in the wasp and this makes her search for a fly in the tunnel (though she did not bring in a fly from the field in this case) and the contact with the fly drives her to carry it away, with no connection with the direction or the nature of the tunnel.

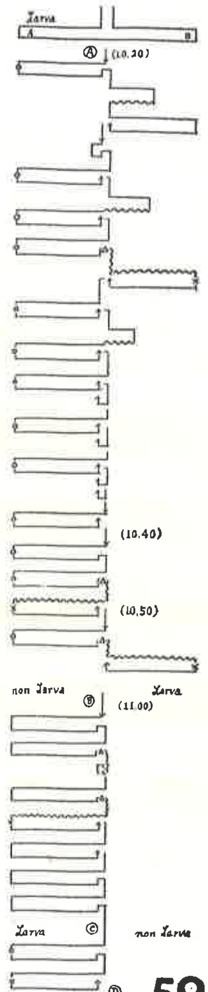
g) In 2 occasions, namely those at 11.23 and 1.40, the wasp used a very ingenious method of carrying-in of the prey. After the usual examination of the larva the wasp did not drag in the victim from the main tunnel at a stretch to the cell, but she carried it first up to the forking point and then entered empty-handed the narrow branch leading to the brood-chamber to examine the larva. She then returned to the bifurcation to take the victim, captured it without going out of the branch and dragged it backward into the larval cell. Thus, by keeping the tip of her abdomen in the narrow tunnel, she was able to avoid the error of slipping into the broad branch that leads to the empty cell. The behaviour observed at 1.40 p.m. (Sept. 5) is especially of interest in this connection. In that occasion the wasp carried a fly first erroneously to the empty cell by the usual non-stop method of transportation. But she then corrected the error by retransporting the fly first to the main tunnel and then to the larval cell. And in that occasion she showed the one-stop method above related. However, when she subsequently attempted the retransportation through the same course, she did not use that ingenious method and transported the fly once more erroneously to the empty cell (Fig. 58, notice ② !).

At first sight, this behaviour appears as an ingenious adjustment to avoid the error of transportation. But this behaviour bears in itself no important learning significance whatever. It will be explicit not only from the fact described above, but also from the subsequent behaviour of the wasp wherein no such ingenious method could be observed again.

In the course of the above observations I renewed my impression that the wasp possesses the memory of a considerable solid nature regarding the direction of the tunnel leading to the larval cell, and that the frequent entrances of the wasp toward the broad branch are dependent merely upon the mechanical easiness of the branch to enter. In order to make sure this question I made the following experiments continuously on Wasp No. 150 :

I exchanged the Y-tube of glass bearing the branches of different broadness for another of the same form but with the branches of the equal diameter (1 cm) and put in the left-hand bottle the larva and a fly, while the right-hand bottle was left empty. At 10.20, the wasp brought in a fly. At 10.40 ditto, at 10.50 ditto. The behaviour of the wasp in each case was as shown in Figure 59, A – B. According to the results it is clear that the dominancy of the left-hand branch in the number of times of being entered by the wasp does not depend upon the result of her learning on the difference of the broadness of the branches associated with the situation of the larval cell. If so, she should enter both the branches with nearly equal frequency to each other. However, we must not forget that there is another external factor that can lead the wasp directly to the larval cell. That is the odour of the larval cell. According to the results of experiments conducted up to now, it still remains uncertain whichever of the two acts more strongly upon the behaviour of the wasp. Therefore, in order to investigate the question once more, I exchanged the positions of both the branches and the cells for each other. As a result the larval cell came on the right side. At 11.00, the wasp came back carrying a booty and entered the nest. She moved about in the nest as shown in Figure 59, B-C. The result showed clearly that in this case the wasp followed decisively the learning effect or the memory of the direction of the branch-tunnel leading to the larval cell. As the wasp continued to visit the left-hand empty cell in vain, I changed the larval position as before, lest the wasp should abandon the nest. At once she found the larva in the left-hand cell, touched it with her antennae and returned in the main tunnel. Once more she came back in the larval cell, touched the larva once more and soon after flew away (Fig. 59, C-D).

By the above described experiments it became certain that in this individual and under the above conditions, the learning effect of the direction of the larval cell acted more strongly upon the wasp than that of the broadness of the tunnel did. On the other hand, not a single experiment ever described has denied positively the presence of the discrimination ability on the broadness of the pathway in the wasp. At the same time, however, no experiment undertaken up to now has positively given a proof on the presence of such an ability. Therefore, to make sure once more whether such an ability is endowed to the wasp or not, I altered the arrangement as before, but this time arranging the broad tube so as to come on the left side and placing the larval cell (contained the larva and one fly) at the end of the right-hand narrow branch. The wasp has long learned to pass through the left-hand branch to go to the larval cell and at the same time she has learned to pass through the narrow branch to go to meet the larva. In the new arrangement the direction of the larval cell was altered, but the broadness of the tunnel leading to the larval cell remained unchanged. So that if the wasp came through the right-hand narrow branch to the larval cell she might be guided either by the memory of the broadness of the tunnel or by the odour coming forth from the larval cell, save the case wherein she entered the branch by chance. Therefore, if such a result effected it will give some support in favour of the concept that the wasp can recognize the difference of the broadness of the tunnel in association with the position of the larval cell. Because, in this individual it has been made clear that she used to be guided more strongly by the memory of the direction than by the direct odour of the larval celll.



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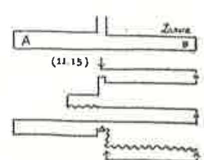

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Figs. 59, and 60. Behaviour diagram of Wasp No. 150.

At 11.15, the wasp came back with a fly and entered the burrow. Her behaviour in the nest was as shown in Figure 60. The result appears to be advantageous toward my expectation. However, the fact that she entered the branch without showing any hesitation makes me doubt as to whether the entering was made selectively or not. And indeed, the behaviour of the wasp in her subsequent provisionment seems to justify my doubt (Fig. 61). The wasp continued to provision and brought home 16 flies until 1.20 p.m., of which 2 could flee away from between her legs. During the time I left the arrangement unchanged, excepting that the larva, having become nearly full-grown, was exchanged at 11.30 for another 3rd instar one and that the victims were removed from time to time from the brood-cell. The behaviour of the wasp in the nest in each of her return was shown in Figure 61. During the course, the following behaviour of the wasp will be worthy of record :

a) In her first return she entered very smoothly the left-hand broad branch and she repeated the same manoeuvre once more before she went in the correct direction. This behaviour is quite contrary to the result of the preceding observation (Fig. 60).

b) Out of 14 instances of entering the nest with a prey, the first 8 were the cases in which the wasp came invariably first in the left-hand broad branch, though sometimes she appeared to slip in that direction from the bifurcation. While the last 6 were cases wherein the wasp came always in the right-hand correct path. This result may show the process of her new learning of the way to the larval cell. But it is also uncertain what is the chief object of her learning among the 3 leading factors.

c) Nevertheless, the direction of her backing progress did not undergo any improvement. All the prey but 4 were transported in the erroneous direction.

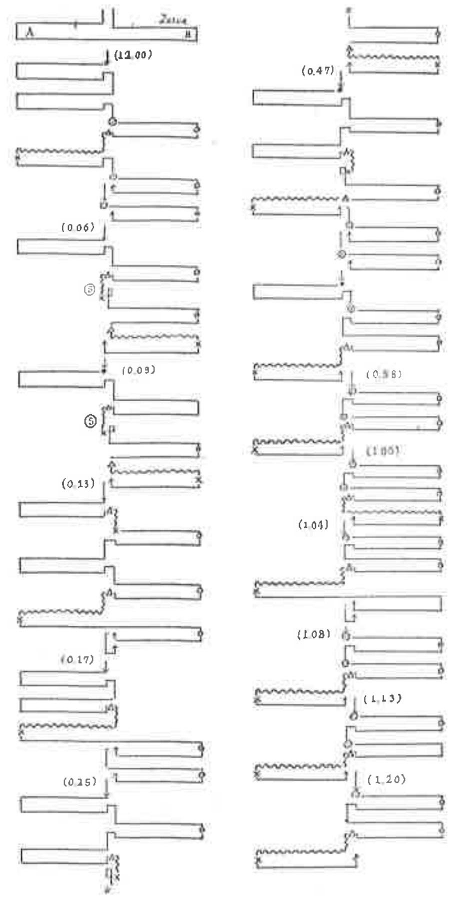


Fig. 61. Behaviour diagram of Warp No. 150.

d) In 5 occasions she showed the one-stop method of transportation of the prey. However, in 2 occasions, when she caught the fly placed temporarily near the bifurcation, the tip of her abdomen went out of the branch-tunnel and she happened to slip in the broad branch to carry the fly in the empty cell (observations at 0.13 and 0.47).

e) The occurrence of the one-stop method of transportation is concentrated in a general way in the middle of the process. But it is also uncertain whether the procedure depends upon the intention of the wasp or not.

f) Throughout the whole procedure, retransportation of the prey did not occur. This is a curious contrast to the results of the foregoing experiments.

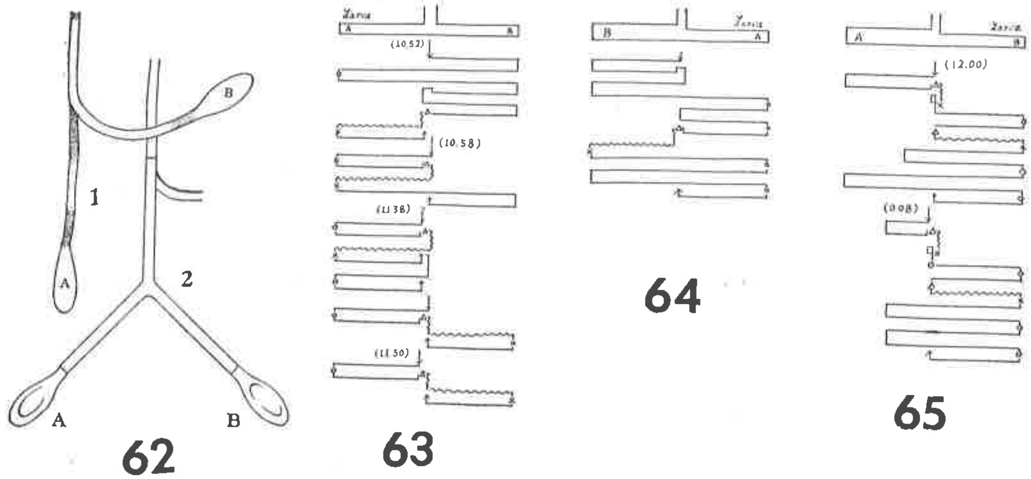
Having had the wasp become to enter first the right-hand narrow branch as a rule, I changed the arrangement so as the broad branch with the empty cell to come on the right side and the narrow branch with its larval cell on the left side. But the wasp did not return until 2.40. So I stopped the observation. rearranging the tube and the bottles as before, The next day, when I arrived at the place, the surface of the nest had been seriously disturbed by the passage of several wagons. It was so extraordinarily disturbed that I could not find the exact position of the nest. But I found a wasp digging the sand, probably in search of her missing nest. I approached her and knew that she was the very wasp of No. 150, carrying a painted marks on her propodeum. At once I examined the arrangement. It was also disarranged by the trample of horses and the cells were detached several centimeters from the ends of the branch-tunnels. I examined the cells. The left-hand broad chamber remained empty, while in the right-hand narrow bottle were added 2 flies. Of course they were brought in on the previous day. I rearranged the tube and the bottles as planned the previous day and covered them with sand. The wasp continued to work and at last succeeded in finding the entrance to the arrangement. After staying several minutes inside the cell she flew away on the foraging excursion. She soon came back carrying a booty, but unfortunately enough the nest was abandoned by the wasp through an accident caused by a curious passer-bye. With great regret, I was obliged to stop my experiment.

From a series of experiments made with this wasp I could not obtain any conclusive result regarding whether the wasp can learn the difference of the broadness between the 2 branches of her tunnel. But I could obtain some indirect, but positive evidence for the problem. That is the behaviour of the wasp shown in the case when she intends to go in the narrow branch-tunnel. That particular behaviour seems to suggest that the wasp has the ability of recognizing the difference. However, it was certainly confirmed that even if such an ability is really endowed to the wasp, the power of its influence on the wasp's behaviour at the forking point of her pathway is exceedingly smaller than that of either the memory of the direction of the way, or the odour of the larval cell. Moreover, in the present experiments an inadequacy of considerable importance was involved in my arrangement. That is that the branch-tunnel of each side was too short to enable the wasp to learn the difference of the broadness of the path. Accordingly, in order to clarify this point, I made another experiment with another individual :

3) Wasp No. 157. Sept. 7, 1949. I saw a wasp carring in a victim to her nest twice in the morning and dug the nest at 9.30. It belonged to the compound type, including forking tunnels and two cells within (Fig. 62). In one of the cells was a cocoon, in the other were a larva of the early stage of the 4th instar and 6 flies, of the latter 4 were already eaten or half-eaten. I connected a Y-tube of glass having branches of equal diameter (1 cm.) with the end of the natural tunnel of the entrance gallery and placed a glass bottle at each end of the branches (Fig. 62, 2). In the left-hand bottle (A) were put the larva and one fly, while in the other nothing. From 10.52 a.m. until 11.50 the wasp carried in 5 flies. The behaviour of the wasp in the nest in each of her return was graphically shown in Figure 63. In her first return the wasp appeared to show distinctly the memory of the direction of her own tunnel which had already broken. However, once she became aware of the exact position of her larva in her searching for, the accuracy of her entrance towards the correct direction is quite astonishing (in so far as the forward progress is concerned).

I then altered the arrangement as in the preceding instance, placing the broad branch

(20 mm in diameter) with an empty bottle at its end on the left and the narrow branch (10 mm in diameter) with a bottle containing the larva and a fly on the right. At 11.55, the wasp returned with a booty. Her behaviour in the nest at that time was as shown in Figure 64. According to the direct observation of the wasp's behaviour, it seemed clear that she was perfectly guided by the learning effect of the direction at the forking point of the tunnel, and not by the easiness of the way to enter.



Figs. 62–65. 62 — Nest and experimental arrangement of Wasp No. 157. 63–65 — Behaviour diagram under experimental conditions.

I then inserted a glass tube of the corresponding diameter between the end of the branch and the bottle cell of each side, with the result of lengthening both branches to 30 cm respectively. At just noon and 8 minutes later, the wasp came back with a victim and entered the nest. Her behaviour in both occasions was as shown in Figure 65. In her return at noon she entered 3 times in the left-hand broad tube and both in the first and in the last entrances she came up to the end-wall of the bottle. But in her middle entrance she returned from the middle of the way. Whereas, in her 4 visits of the right-hand narrow tube always she came up to the brood-cell and touched the larva. In her 2nd retnrn at 0.08, her behaviour was much more characteristc than in the preceding case. Although she moved herself in much the same manner as in the preceding case, not a single occasion did she come up to the end-chamber of the broad tunnel, but invariably she returned from the middle of the way. Now, is this the result of the lack of the odour of the larval cell in that path ? If so, the same behaviour might have appeared in the first entrance observed at noon. Moreover, the 2nd and the 3rd entrances to the broad path in both observations seem to me representing errors of the way that was taken for the main tunnel to go out of the nest. If truly so, in these cases the question of the odour of the larval cell should be placed out of dispute, since both the broad branch and the main tunnel of the wasp do not bear the larval odour. Notwithstanding, the wasp returned from the middle of the way in the broad branch. Such a question regarding the larval odour must be applied rather to the case of her erroneous entrance to the branch-tunnel leading to the larval cell. Because, in such cases (the 3rd and the 4th entrances to the larval cell), if she can perceive from afar the presence of the larva by odour, she must become aware of the error of the way and must turn round half-way. Whereas the fact that such a behaviour was not observed even in a single time, seems to depend upon the fact that both the main tunnel and the narrow branch were guite equal in diameter.

The results obtained here can be summarised as follows:

1) In case a forking tube of glass bearing the branches of different diameter is connected with the end of the natural tunnel of the wasp and a larva is placed in one of the end-bottles of the branches, the wasp can learn the way to the larval cell very promtly. Indeed she can learn the correct way to be followed by a single visit to the cell.

2) In this case, the objects of learning involved are inferred to be 3 in kind, namely, the direction of the way, the odour coming forth from the larval cell and the broadness of the tunnel.

3) Generally speaking, among the 3 objects, the direction of the way can most easily be learned, usually by a single trial. On the other hand, the broadness of the tunnel appears to be most difficult to learn.

4) Indeed, the effect of learning of the broadness of the tunnel can not make its appearance even under the controlled conditions, when the tunnel is comparatively short. However, when it is of a considerable length, the learning effect more or less clearly appears upon the behaviour of the wasp.

Judging from the characters of the objects to be learned, the results obtained seem to be quite natural. Because, the learning of the direction is regarded in this case as secured through the sense of motion. And this capacity is extraordinarily developed in Hymenoptera. They can learn the direction of the way usually by a single trial. The effect is kinesthetic. Therefore, at any turning point, it can rather mechanically and automatically make its appearance, without any connection with the external stimuli. Therefore, apparently its effect has a predetermined nature. Therefore, at the bifurcation it does not need to select this way or that. On the other hand, the learning effect of the odour of the larval cell always needs an actual stimulus. At the bifurcation, it must select this or that way through the sense of smell. While, the learning effect of the broadness of the tunnel is based upon the sense of contact in this case and, therefore, it is necessarily needed to walk some distance along the tunnel before the recognition becomes established.

(to be continued)

Behaviour of the amputated wasps It will naturally be thought of by every person who read the above accounts that if the individuals of wasps from which the antennae are cut off are used in the maze experiments the result will be more simple, since by such means the odour factor at least can be excluded from the leading elements. In reality, however, such is only an utterly vain device. The amputated wasps completely lose their interest in rearing their larvae and no such fervent activities as mentioned can be observed upon them. The following will give the general attitudes of such wasps :

Wasp No. 141. Aug. 26, 1948, at 10.10 a.m. A wasp who had been eagerly provisioning her nest was cut off her both antennae from the base. When released, she flew off madly to somewhere. Twenty minutes later, however, she came back empty-handed, easily found the site of her nest and entered the tunnel. During her absence, I dug open the brood-cell. It was simple in structure, having the gallery of 18 cm in length and contained a big larva of the later middle stage of the 4th instar supplied with 14 flies of which 10 had been already eaten.

As the larva was too big to use for my purpose, I replaced it with another smaller one (early stage of the final instar), put it in the glass cell with 2 green bottle flies and connected it with the end of her tunnel. When the wasp entered the nest, the bottle was unearthed to see her behaviour inside the brood-cell. She did not come, however, in the larval chamber, but went out and eagerly sept the sand at the entrance for a long while. I covered the bottle with sand. Soon she entered and when I uncovered the glass-cell at once, she was in the bottle, trampling on the larva and the flies indifferently, but at once fell into confusion by illumination. I covered the cell again. When I examined the cell after 3 minutes, she was resting quitely at the end of her own tunnel, showing the tip of her abdomen. She did not come in the glass cell while I was observing for 10 minutes thereafter.

The next day at 8.30, the wasp came out of the cell for the first time. She was in a state of discouragement. She did not close the opening. She tried to fly up, but could not (partly owing to the coolness of the morning), only turning somersault repeadedly. She rubbed her face with a front leg and abdomen with the hind pair of legs, walked to a distance of 40 cm and rested still. One hour later, when I saw the place she was not there and I could not see her throughout the day. Two days later, when I examined the nest, no trace at all of the wasp could be found there.

In two other instances things passed in much the same manner. The wasps would not catch the fly that was placed in front of them when they came out of their nests. They would not touch the larva in the cell, only resting still in the tunnel when they were in the nests. They could return to their nest on the manupulated day, but did not on the following day. The reason for this, howerver, remains uncertain.

(to be continued)

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第 1 集

Tsuneki, K. —— Ethological studies on *Bembix niponica* Smith, with emphasis on the psychobiological analysis of behaviour inside the nest II. Experimental part pp. 1-116

第 2 集

小野寺正二 —— トチカガミ根毛の生理学的研究 Ⅰ 細胞質の 2, 3 の物理的及び化学的性質 pp. 117-125

(Onodera, M. —— Physiological studies on the root hair cells of *Hydrocharis* plants I. Some physical and chemical characters of the cytoplasm)

第 3 集

Minabe, M., Naniwa, I., Yachi, Y. and Takeuchi, K. —— On the effects of spraying vitamin B_1 upon forming the soft rice pp. 127-135

第 4 集

斎藤吉明 —— トマトパウダーの研究（第1報） トマトの熟度別，部位別ビタミン類の含有量並にピューレー減圧濃縮物中ビタミン類の消長について pp. 137-147

(Saito, Y. —— Studies on the tomato powder (Part 1) On the vitamin contents in different maturity degrees and in different parts of the tomato fruit, with the change of vitamin contents during the course of the vacuum concentration)

第 5 集

三浦 静 —— 福井県加越台地の地質 —第1報— （特に新第三系の層序について） pp. 149-161

(Miura, S. —— Geology of the Ka-Etsu upland, Fukui Prefecture (Part 1) With special reference to the Tertiary formations)