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Citation	北海道大學理學部紀要, 13(1-4), 214-217
Issue Date	1957-08
Doc URL	https://hdl.handle.net/2115/27229
Type	departmental bulletin paper
File Information	13(1_4)_P214-217.pdf



On the Releasing Mechanism of the Behaviour System of Some Hunting Wasps (Hymenoptera)¹⁾

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(With 1 Text-figure)

The solitary Hymenoptera generally known as hunting wasps exhibit a complicated system of behaviour at the time when they prepare the nests for their progeny. It has a certain innately determined pattern characteristic of each species. Despite its prescribed and inflexible action tendency, however, the admirable adjustment of their behaviour to every probable happening under the natural condition seems rather astonishing. High degree of complication and automatism, therefore, appear at first sight to refuse every attempt to analyse this system in terms of the stimulus physiology. From the point of view of the behaviourism, however, it is not always impossible to approach this by analysing the system into units and by taking the situation as stimuli-complex. Indeed, when observed widely and in detail, it can be perceived that the system consists of several units of behaviour that are combined linearly one after the other in manifestation. Moreover, it seems that each unit of behaviour possesses a particular situation to enable itself to release and the accomplishment of a certain unit comes to create a new situation which in turn releases the succeeding unit of behaviour, as if they were interlocked with each other. But the situation is usually a complex of several stimulating factors, including both the internal and external. Among them some rule over a range of several units, some relate to a part of the range and others concern with only a single unit as a mere sign stimulus. Therefore, the ruling or releasing factors are considered arranged in a hierarchical organization, although I dare not say in the nervous system of the animals, as postulated by N. Tinbergen (1951). In the present paper, one of the simplest cases of such a behaviour system was discussed.

The case of the spider wasp that preys on a single victim

According to the method of Iwata (1942), the behaviour system of the Pompilids of the genera *Batozonus*, *Episyron*, *Cyphononyx*, *Pompilus*, *Anoplius*, etc.

1) Dedicated to Professor Tohru Uchida in commemoration of his 60th birthday. Contribution No. 26, from the Biological Laboratory, Fukui University, Japan.

Jour. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. 13, 1957 (Prof. T. Uchida Jubilee Volume).

that have a habit of making several nests within a restricted area (base ground) can be formulated as follows :

HT (BE)ⁿ T S O C

In this formula symbols stand for the units of behaviour : H Hunting, T Transportation of the prey, B Burrowing of the nest, E Examination of the prey, S Storing of the prey in the nest, O Oviposition, C closing of the burrow. The arrangement of the symbols indicates that the behaviour system progresses from left to right, (BE)ⁿ showing that the combination of B and E is repeated several times.

The first releasing factor of the Hunting is considered a positive egg pressure (meaning all the physiological states caused by the maturation of the egg) and this seems to rule over the system as far as the Oviposition. According to my consideration, T can be released by the presence of the paralyzed spider, together with the sense of distance which will be acquired during the course of the Hunting and may be strengthened by the change of the environment. The chief releaser of the Burrowing is regarded as the presence of the paralysed spider. But it will also be supported by the contact with the base ground (memory of the nesting site). However, in order to release this unit, extinction of the sense of distance is not necessarily needed. Hence units T and B are sometimes appear at the same time and carried out alternately. The Examination of the prey seems to be called forth by the sense of distance (aided probably by the sense of time after the preceding contact with the prey).

As the results of behaviour B, two qualitatively different releasing factors emerge anew. One is a simple releaser or sign stimulus of the subsequent unit, namely the appearance of the burrow (an optimum condition for the oviposition) and the other is an internal releasing factor, that is to say, the sense of the negative equilibrium which has been given rise to by digging the equilibrated ground. The appearance of the burrow, the presence of the paralysed spider and the sense of distance (though much reduced by this time in degree) act upon the wasp as a new situation and bring about the succeeding unit of behaviour, the Storing of the prey. Then, released by the stimuli-complex of the positive egg pressure, contact with the burrow and with the spider (including the extinction of the sense of distance), the Oviposition occurs. That the above mentioned process of HT (BE)ⁿ T S O is ruled over by the positive egg pressure is easily verified by the following experiments: 1) Deprivation of the prey at any unit of the system. (Result : Reverse of the behaviour to H.) 2) Shift of the prey away from the nest. (Result : Reverse to T.) 3) Destruction of the burrow. (Result : Reverse to B.) 4) Taking the spider out of the burrow before oviposition and placing it on the experimentally closed nest. (Result : Reverse to B, sometimes to T.) 5) Deprivation of the spider from the burrow after the egg is laid. (Result : Automatic progress of the behaviour system to unit C.) 6) The same as above, but

with the spider placed on the nest which was closed experimentally. (Result: The spider is usually indifferently dealt with, as if it were an inanimate object, but even when the wasp shows some concern about it, it is sooner or later discarded.)

Among the above mentioned experiments, the results of experiments 1-4 indicate that the reverse of the behaviour system is always possible up to that nearest unit upon which the releasing factors are still completely working at that moment. While the last two are very clear-cut in exhibiting that a fundamental change of the releasing system occurs at the point of O, and the behaviour of the wasp can not be reversed across this bordering point. The so-called non-adaptability or blind progress of the instinctive behaviour can partly be attributed to the irreversibility in such a case. Thenceforth, the behaviour of the wasp comes to be ruled over by the negative egg pressure, that is, all the physiological conditions resulted from the rejection of the maturated egg. At the same time, however, another releasing factor is also united to this. It is the sense of negative equilibrium stated in the foregoing page. This factor acts upon the wasp to request the recovery and re-equilibration of the ground. The sign stimulus accompanied in this case is the presence of a hollow or any non-equilibrated states of the ground. These stimuli-complex awakens the Closing behaviour in the wasp. The behaviour of Closing comes to an end by leveling the ground most elaborately. Sometimes such a behaviour as accumulating rubbish follows the Closing behaviour. But this is considered also only an extension of C and is led by the sense of negative equilibrium. Because, in such a case the presence of rubbish on the nest forms a complete equilibrium against its surroundings.

It must be specially mentioned here that the sense of negative equilibrium appears as soon as the wasp begins to break the equilibration of the ground. Therefore, it sometimes compels the wasp to close the half-dug burrow when it must be abandoned, quite independently of the egg pressure at that time. Somewhat similarly the immediate external releasing stimulus acts usually so strongly on the wasp that she often begins to show a reaction of a determined type against it, irrespective of the governing internal factors. In these cases, however, the released reaction is usually vanished sooner or later, on account of the lack of its leading factor.

According to the consideration above described, the releasing mechanism of the behaviour system in the spider wasps mentioned can be illustrated as set out in Fig. 1.

As regards the units of behaviour, each of them consists of several parts of behaviour, for instance the Closing includes a) carrying the spider just in front of the burrow, b) penetrating the burrow empty-handed head first to inspect the interior, c) coming out head first, and d) catching the spider and backing with it into the burrow. These parts of the behaviour within a unit are apparently more innately, accordingly more mechanically, determined in combination than between

the units. Therefore, once the first step is released, each part is automatically developed in succession up to the end of the unit without cease. Hence it is regarded as an interlocking system. On this account, in order to change the procedure, a considerable series of learning trials is usually required.

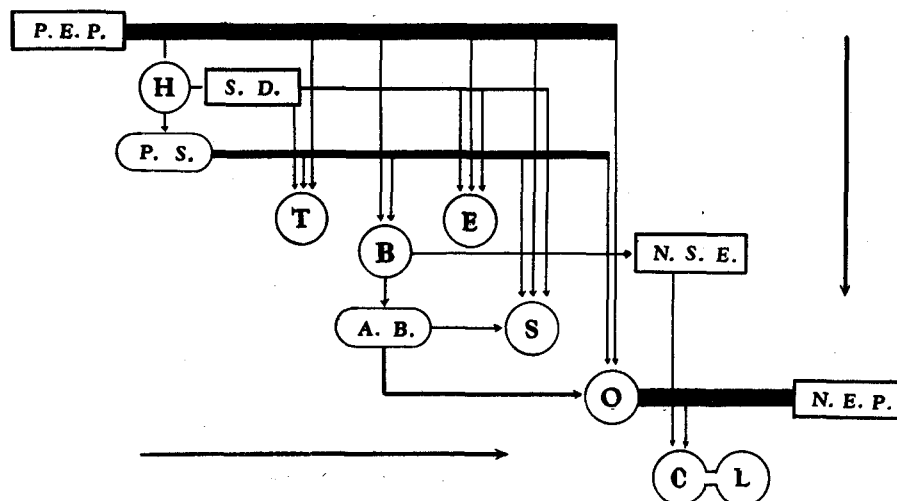


Fig. 1. The releasing mechanism of the behaviour system in the spider wasp. The rectangles stand for the internal releasing factors, the ellipses the external releasing stimuli and the circles the behaviour released. The horizontal lines show the ranges ruled over by certain factors and their thickness the power of the leadership. *Abbreviation* : P. E. P., positive egg pressure. N. E. P., negative egg pressure. S. D., sense of distance. P. S., paralysed spider. N. S. E., negative sense of equilibrium. A. B., accomplished burrow. Other symbols in text.

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