Comparative Physiology. — *On the Life-History of Ammophila campestris Jur.* By G. P. BAERENDS. (Communicated by Prof. H. J. JORDAN.)

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The reproductive activities of the females of *Ammophila campestris* a digger wasp belonging to the *Sphecidae,* consists of coition, digging one cell nests, and capturing and paralysing caterpillars (and occasionally larva of Tenthredinidae), which they store in the nests as food for the larva. Observations made by ADLERZ (1903, 1909) in *Sweden* and by CRÈVECOEUR (1932) in *Belgium* have shown that *campestris* does not store all caterpillars before the hatching of the egg, as digger wasps usually do, but that she brings only one caterpillar before, and the rest after the larva has hatched. Moreover, some of ADLERZ' observations seem to suggest that *campestris* might, at least occasionally, be occupied with more than one nest at the same time.

These peculiarities had never been observed before in any digger wasp. If ADLERZ' suggestion were right, it would imply such a highly organised behaviour as could hardly be expected in any insect. The wasp would have to remember the localities of her different nests, not only for a single day, but sometimes for nearly a fortnight, for, during the nights and bad weather periods, the wasps stay out in the heather and do not visit the nests. In the Dutch climate bad weather may continue for some weeks.

In addition, there must be some regulatory system that guarantees an equal food distribution among the different nests; presumably the wasp can be stimulated somehow to start or to stop provisioning a certain nest.

These questions induced me to make a closer study of the life-history of this species.

To get an exact knowledge of the course of events of the wasp's activities, it was in the first place necessary to observe individual wasps during a series of consecutive days. Individual identification of each wasp was possible by a system of coloured markings.

Twenty wasps were continuously watched during about a fortnight each. My observations of these wasps cover the activities at the nesting places as completely as possible. I did not, however, follow them on their foraging and hunting excursions in the heather. As I could be sure, however, that none of the marked wasps had a nest outside the observed area, I can assume that none of their nesting activities escaped my attention.

Here follows a brief account of the most important results of these observations.

During the first bright days in June the males leave the cocoons. The

females appear some days later. Mating takes place within a few hours after the female has hatched. Shortly after coition the female begins to dig her first nest (nest A). As nesting sites flat, sandy areas with a compact soil are selected. The nest consists of a vertical shaft about 2½ cm long and one elliptical cell about 2 cm in length. Having finished the nest, the shaft is temporarily closed by loosely filling it up with some clods, and the wasp then disappears into the heather. She usually returns within a few hours, carrying a paralysed caterpillar. She reopens the nest, carries the caterpillar down and lays an egg. Then she closes the nest with much more care than before. After she has finished, it is impossible for the human eye to distinguish the entrance from the surroundings. She now leaves nest A and it may be some days, before she provisions it again.

Soon afterwards the wasp begins to dig a new nest (B).

It appeared to be a general rule that once a nest was begun, the work at this nest was continued without interruption, until an egg was laid.

The first series of activities, therefore, constituting the first stage of the care for every nest made, will be called the first phase.

After completing the first phase of nest B, which takes her one or more days, dependent on the amount of sunshine, the wasp returns to nest A and, before fetching a caterpillar, opens the nest. After a brief visit, she closes it again and flies off to the heather. Such a visit, in which no caterpillar is brought, will be called a "solitary visit", in contrast to "provisioning visit". As a rule the wasp, after this solitary visit brings one or more fresh caterpillars, before she leaves the nest alone for the second time. This phase I shall call, therefore, the second phase; it consists of a solitary visit followed by storing 1—3 caterpillars. Occasionally this phase consists of a solitary visit only, namely when the egg has not yet hatched at the time of this visit.

After having finished this second phase in nest A, the wasp carries through the same phase in nest B. Now she again pays a solitary visit to nest A and there enters into the third and last phase, consisting of one or more solitary visits and the storeage of another 3—7 caterpillars. This phase is concluded by closing the nest in an especially careful manner, the wasp pressing down the contents of the shaft with her head, during which a loud humming sound can be heard.

She now goes to nest B to accomplish the third phase here. After having finally closed this nest she begins to dig a new nest.

As we see from the above, in each nest provisioning occurs in three phases. During every phase the wasp is occupied with one particular nest exclusively, interrupting work at the nest only for foraging on her own behalf, for hunting caterpillars or for sleeping, but never for any work concerning another nest.

Having finished one phase she goes to another nest and works through an entire phase there. If there is no other nest to provide for, she makes a new nest. Occasionally, in very favourable weather, the wasp, after

having completed the second phase in nest A, digs a new nest C before beginning the second phase of nest B. In this way a wasp sometimes has three nests under her care.

The second and the third phase always begin with a solitary visit; sometimes a phase consists of even no more than that one solitary visit. This may occur when the nest has been disturbed shortly before this visit, or, in the case of the second phase, when the egg has not yet hatched. This suggests that the solitary visit serves as an inspection, that is to say that the wasp during this visit receives stimuli from the contents of the cell which determine whether she will leave the nest alone or go and fetch fresh caterpillars.

An experimental test of this hypothesis is possible on the following basis. If the solitary visit actually has a regulating function, it should be possible to influence the wasp's subsequent behaviour by changing the contents of the nest just before the solitary visit. This could not be done in the real nests but it appeared that the wasps did not interrupt their provisioning activities, when I replaced their nests by artificial nests, provided certain precautions were taken. These nests were made of gypsum and consisted of a lower part, containing the cell, and a lid that could easely be lifted so that I could reach the cell and change its contents at will.

I carried out the following experiments:

1. Nests, which according to preceding observations, should be provisioned immediately after the solitary visit, were disturbed by removing the larva just before that visit. The result was that the nest was abandoned after the first solitary visit.

2. In similar nests, I replaced the larva by a paralysed caterpillar with an *Ammophila's* egg, taken from another nest. Now the wasp did not start provisioning immediately after the solitary visit (as she should have done), but she waited until the egg was hatched.

3. Before the wasp paid her first solitary visit of the third phase to the nest I added some paralysed caterpillars to the contents of the nest. The result was that the wasp either stopped provisioning altogether, or at least brought less caterpillars than the smallest amount ever stored under normal conditions.

4. In nests containing one caterpillar with an *Ammophila's* egg, nests, therefore, that should not be provisioned immediately, I replaced the egg by a larva. In these cases the wasp brought fresh caterpillars soon after the solitary visit.

5. Occasionally a wasp pays a solitary visit when the third phase is halfway concluded. A few times I succeeded in taking all caterpillars away just before the visit. Normally the wasps should have brought only a few more caterpillars, but now they again stored a considerable number of caterpillars, making the total amount of stored food larger than ever observed under normal conditions.

The same experiments were carried out just before provisioning visits.

Under these circumstances the wasps did not react to any change in the contents of the cell. They even continued provisioning when the larva was removed together with the food.

These experiments conclusively show, therefore, that the solitary visit is a real inspection, during which the wasp learns how to act in the following hours or even days.

Apart from having a function as a regulatory principle, the solitary visit also demonstrates a most remarkable psychological fact: although the external stimulating situation is exactly the same at a solitary visit as at a provisioning visit, the wasp's behaviour is profoundly influenced by it at the first occasion, whereas at the second occasion not the slightest influence can be traced.

In one case, however, the contents of the nest does influence the wasp's behaviour during a provisioning visit. When I put certain objects into the cell just before the wasp would pay her very first visit, during which she had to lay her egg, the wasp did react. If the object was a caterpillar with an *Ammophila's* egg or a cocoon, the wasp pulled it out of the cell and threw it away. If it was a larva, she immediately brought in her caterpillar but failed to lay an egg. Often she even captured some more caterpillars and stored them, still postponing the laying of the egg. It appeared that the presence of a young larva stimulated the wasp to bring 1—3 caterpillars (corresponding with the second phase) and that an older larva stimulated the wasp to bring 3—7 caterpillars (corresponding with the third phase).

Whereas, as we have seen, it is, the amount of food present at the solitary inspection visit which determines the wasp's behaviour in the second and third phase, the wasp is stimulated at her first visit by the age of the larva.

Now the two series of experiments that served to investigate the part played by the solitary visit revealed the regulatory system, at work within the second or the third phase. They did not answer the questions as to the factors that bring the wasp from one phase into the next phase in the same nest.

Here the third series offers a suggestion. The age of the larva, which the wasp happens to find in her nest at her first visit, determines whether she will be brought into the second or into the third phase. This and other arguments, which cannot be treated in detail here, render it probable that the age of the larva has the same influence during the solitary visits.

The following may be illustrated by the narrative of the activities of wasp GO (fig. 1).

The wasp was marked shortly before she finished the third phase in nest A. After having closed this nest she paid a solitary visit to nest B. As the egg had not yet hatched, she closed this nest again without bringing a caterpillar and began to dig a new nest C. Next morning she brought in a caterpillar and laid an egg in this nest. Then she paid a solitary visit to B again where the larva had just hatched. Provisioning, therefore, is

started (third phase) and is continued for 2 days. After she has finally closed nest B, the wasp pays a solitary visit to C. The egg in C has not yet hatched whereupon the wasp leaves C alone and starts digging (D). As this was begun at a late hour, nest D was not completed before the end of the day. Next morning the wasp brought a solitary visit in C, nest D apparently being abandoned. In C, the larva has hatched and the

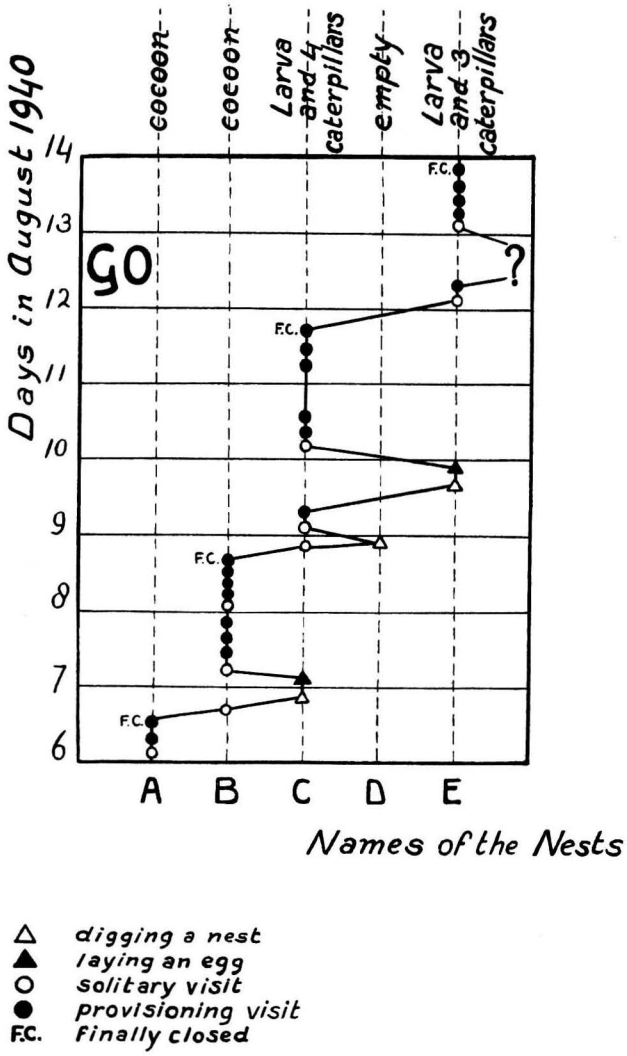

Fig. 1. Diagram of the activities of the wasp GO from August 6—14. All evidence about one nest is given in a vertical column at the top of which the condition of the brood on August 14 is given.

wasp brought one caterpillar. Then a new nest E was started, an egg was laid, whereupon, next day, the third phase in C is completed, which took 2 days. Next morning a solitary visit was paid to nest E where the larva had hatched. As a consequence one caterpillar was brought soon after-

wards. After that the wasp again began a new nest which is not taken into account here, because of incompleteness of my observations. Next day the third phase in nest E was completed.

Summary.

1. *Ammophila campestris Jur.* is able to look after 2 or even 3 nests at the same time.

2. The provisioning of each nest occurs in three phases, during each of which the wasp works at one nest exclusively.

The first phase consists of digging the nest, capturing and storing the first caterpillar and laying an egg. During the second phase 1—3 caterpillars are brought and during the third phase the wasp stores 3—7 caterpillars.

3. Both the second and the third phase begin with a solitary visit at which no caterpillar is brought.

4. Experiments show that these solitary visits have the function of an inspection, that is to say the quantity of food present at a solitary visit determines the wasp's subsequent provisioning behaviour, while absence of the larva causes the nest to be abandoned. During all provisioning visits except the first, the wasp is entirely insusceptible to the contents of the nest.

The behaviour of this species reveales a highly developed psychological organisation. The wasp must have an excellent memory for the different nest sites and, in addition, must be able to react to stimuli, received during an inspection-visit, which has taken place several hours or even more than a day before.

LITERATURE.

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