Influence of the reactions of the prey on the stinging patterns of digger wasps

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Summary. The degree of reactivity of the prey affects the form of behavior subsequently adopted in paralyzing the prey. The mechanism underlying this ontogenetic plasticity is discussed.

In each species of Sphegide, a close correlation can be observed between the form of behavior associated with paralysis of the prey and the nervous system, vigour, etc.[2]. Several mechanisms may be involved in achieving this correlation, and it has even been postulated that a certain somatic plasticity may logically be a prerequisite for phylogenesis[2-3].

The digger wasp *Podalonia hirsuta* hunts the caterpillars of Noctuidae *(Euxoa, Mamestra, Agrotis),* which are vigorous and have a sparsely concentrated nervous system; concomitantly, this wasp produces a higher number of stings than most of the *Sphegides.*

Its stinging pattern can be subdivided[4,5] into 2 successive acts:

- a type 1 attack delivered on the thoracic and cephalic areas according to the basic formula C4 SP (Complete Four Stings Pattern)[6]; – a type 2 attack comprising 2–8 stings delivered on the metathorax and abdomen. This stinging pattern leads in turn to other actions, such as kneading, transportation of prey, and nest-digging, which culminate in the final situation where prey has been procured, provided with an egg, and imprisoned in a closed nest. The collective term 'nesting cycle' (or simply 'cycle') is used to designate the entire sequence of events initiated by the stinging pattern and culminating in the closure of the nest. In the experiments described below, we shall refer to 'experimental cycles' and 'control cycles' in connection with the behavior observed in the course of nesting cycles under experimental and control conditions.

In their natural environment the median number of attacks made by these wasps per nesting cycle was found to be 4, consisting of 1–2 type 1 attacks followed by 2–3 type 2 attacks (the median number of attacks has been systematically chosen in preference to the mean number in order to prevent extreme high values form over-weighting the results).

In the behavior associated with paralysis of the prey, the successive constituent acts correspond to the change in state of the caterpillar (gradual paralysis) and thus to its changing reactions. Any attempt to analyse the organization of the behavior should therefore also take into account the influence of the changing situation. Two series of experiments were thus conducted in order to test the extent of this influence on stinging behavior: these experiments involved delaying and bringing forward the point in the nesting cycle at which the wasp was confronted with a paralyzed caterpillar.

1. *Systematic presentation of normally reactive caterpillars.* After each attack, as soon as the wasp relaxed its hold, the partly paralyzed caterpillar was removed and replaced by a lively caterpillar; the wasp was thus constantly in the presence of a normally reactive caterpillar. The experiment was stopped when the wasp refused a newly presented caterpillar, i.e. remained for an hour without attacking it nor continuing with the subsequent acts associated with nesting behavior.

The experiment was carried out on 22 nesting cycles[7] and compared with 50 control cycles. The following results were observed: a rise in the mean number of attacks per cycle: 10 as compared with 4, with an observed maximum of 47 attacks. This rise mainly reflected an increase in the number of type 1 attacks (8 attacks as compared with 2 on average);

a delay in the onset of type 2 attacks: 7 cycles which were specially investigated in this respect (fig. 1) showed that these attacks gradually increased in proportion, although the state of the prey was stable;

the cessation of all nesting behavior once paralysis of the prey came to an end. None of the usual subsequent acts, such as the kneading or transportation of the prey, were performed. The nesting cycle is thus an abortive cycle, and the wasp enters an extended resting phase.

The motor reactions of the prey thus induce type 1 attacks in particular; the fact that the order of attacks is maintained to some extent points however to some organizing process which cannot be simply explained by the change in the stimulus situation.

2. *Systematic presentation of ready-paralyzed prey.* This experiment was conducted with 2 sets of wasps which in adult life had not yet encountered a caterpillar. Every morning, wasps from the control group would receive a lively caterpillar and those form the experimental group, a paralyzed caterpillar that had been subjected to at least 1 sequence of stings of each type. The experiment lasted 10 days, corresponding to 100 nesting cycles for each set of 10 wasps. It should be noted that the proportion of fully completed cycles was the same for both groups.

a) Stinging pattern inflicted on ready-paralyzed prey. On comparing the 2 groups over the whole experimental period, it was found that the systematic presentation of ready-paralyzed caterpillars brings about the following changes:

a stronger decrease in the median number of attacks with the experimental group than with the control groups; this decrease applied to both type 1 and type 2 attacks so that their relative proportions were unchanged;

a change in the order of occurrence of the 2 types of attack (fig. 2) in a non-negligible number of cases: the 1st attack to be made was as frequently a type 2 as a type 1 attack in the experimental situation, whereas the control cycles were consistently initiated by type 1 attacks; the 2nd attack to be

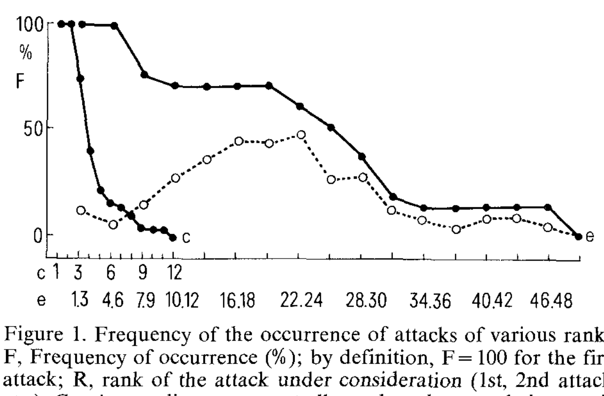

Figure 1. Frequency of the occurrence of attacks of various ranks. F, Frequency of occurrence (%); by definition, F = 100 for the first attack; R, rank of the attack under consideration (1st, 2nd attack, etc.). Continuous lines represent all attacks, whatever their type, in the control situation (c) and the experimental situation (e), respectively. The dotted line represents only attacks of type 2 observed in the experimental situation.

made in the experimental situation was generally (86%) complementary to the first. This tendency to alternate both types of attack was not very strong in the control group.
In the control situation, the end of prey paralysis and initiation of the subsequent event in the nesting sequence mostly occurred after a type 2 attack. In the experimental situation, the change-over pattern depends on the very 1st attack to be made: in cycles initiated by a type 1 attack the change-over to the subsequent nesting event took place, as with the control group, after a type 2 attack. On the contrary, in experimental cycles initiated by a type 2 attack, the change-over was equally frequent after both types of attack.
This experimental situation thus generates 2 different cycles:
form I cycles, beginning with a type 1 attack; these cycles are similar in several respects to those observed in the control situation; form II cycles, beginning with a type 2 attack; these cycles differ both from form I and control cycles.

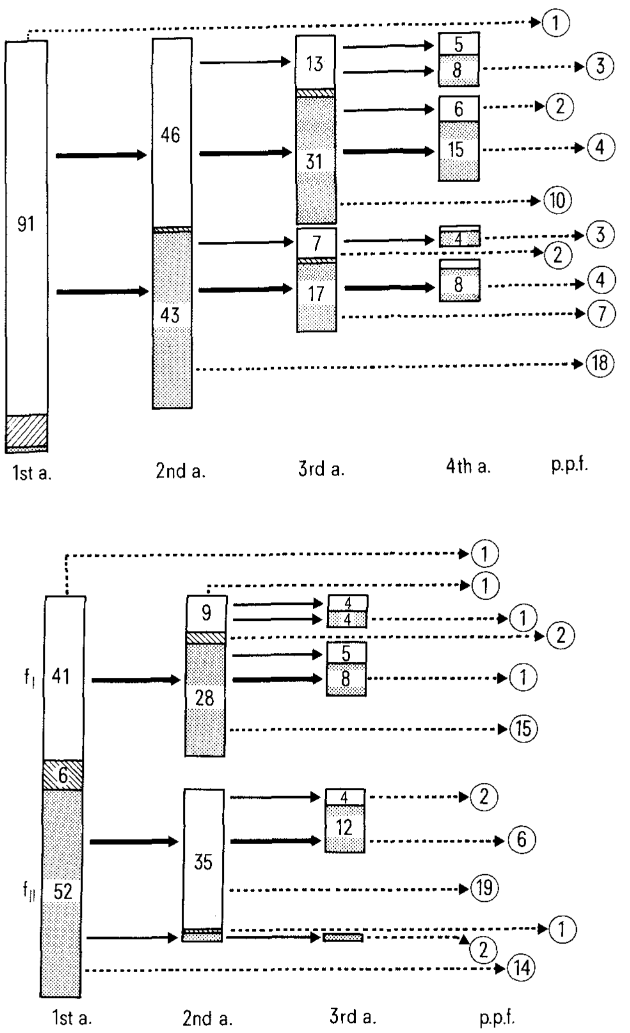

Figure 2. Characteristic sequences of 1st attacks observed in the control situation (upper diagram) and the experimental situation (lower diagram). Only the 1st 4 and the 1st 3 attacks, respectively are shown. □, Type 1 attack; ▩, type 2 attack; ▧, non-classifiable type of attack. Heavy arrows indicate the most frequent sequences. Circles indicate the number of cycles in which paralysis of the prey terminates after the 1st, 2nd, 3rd or 4th attack. Each situation corresponds to a hundred nesting cycles.

b) Ontogenetic regulation of the stinging pattern with ready-paralyzed prey. In order to distinguish between the immediate effects of the experimental situation and the more long-term consequences, the behavioral form of each group was observed from day to day throughout the experiment.
In the control situation, none of the parameters used show any significant variations, while the experimental group displays 2 characteristic changes: on the 1st day of nidification, the experimental cycles begin with a type 1 attack; the proportion of cycles beginning with a type 2 attack tend to increase as from the second day, gradually reaching 50%; the number of attacks per cycle tends to decrease from 1 day to the next; our investigations have shown this decrease to be mainly associated with increase of number of form II cycles: the median number of attacks is 4 per control cycle, 3 per form I experimental cycle, and 2 per form II experimental cycle.

Discussion. These results, which have been analyzed more thoroughly in an unpublished dissertation[8], bring to light a number of links between events which can be described as a set of internal behavioral instructions. According to the particular situation or individual history involved, various possible combinations of these instructions go to shape a given expressed behavioral form. A highly reactive prey tends to generate a type 1 attack; a more inert prey generates either a type 1 or a type 2 attack, or even one of the acts such as kneading or transportation, which are associated with subsequent nesting behavior. Various conditional instructions govern the onset of certain acts. The 1st attack tends to be a type 1 attack; this tendency gradually falls off if the caterpillar encountered at the beginning of the cycle is already paralyzed. The type of attack tends to change from the first attack to the second; this alternation is only clearly apparent, however, when the caterpillars are ready paralyzed.
Type 2 attacks tend to be linked to the subsequent acts involved in nesting behavior.
The particular form in which these instructions are expressed depends on each subject's past history, and particularly on the positive or negative interplay of various instructions together.
In the control group, the direct influence exerted by the situation (i.e. state of the prey) on the stinging pattern does not conflict with the tendency for cycles to be initiated by a type 1 attack. The gradual change in condition of the prey also coincides with a change in the state of the wasp. This double correlation endows the behavioral form with a certain stability.
On the other hand, the tendency for the 2 types of attack to alternate at the beginning of the cycle is less clear-cut in the control group than in the group presented with ready paralyzed prey (cycles of form I and II): this tendency would thus seem to conflict with that imposed by the situation (caterpillar only partly paralyzed) which calls first and foremost for type 1 attacks.
Some conflicts, of variable import, were observed in the experimental groups. The constant presence of highly reactive caterpillars prevented type 2 attacks and the ensuing events from taking place by inducing repeated type 1 attacks until termination of this behavior, so that the nesting cycle was abortive. In this case, the feed-back effect on behavior is bound to be involutive.
On the contrary, a constant supply of ready-paralyzed caterpillars was no bar to normal behavior; here, in the conflict between a stable situation and a tendency for the types of attack to occur in a certain order, the latter tendency was eventually overruled so that form II cycles then took place. Here the feed-back effect consists of

adaptively varying the ensuing behavior with regard to paralysis of the prey. The degree of phenotypic plasticity characteristic of the behavior may be governed by the respective scope allowed be these 2 modes of conflict management.

1 To whom reprint requests should be addressed.

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