An Attempt to analyse the Behaviour of the Larvae of the Hip Fly (*Spilographa alternata*).

By
Niels Bolwig,
Johannesburg, South Africa.

On an excursion to Belfast Castle, North-East of Belfast, during the meetings of the British Association in early September 1952 I picked some hips from a wild rose which were heavily infested with larvae of *Spilographa alternata*. This was done with the intention of analysing the behaviour of the larvae.

Biologically speaking, a hip can be considered as a berry with the "seeds" (fruits) in the centre surrounded by a thick, fleshy layer (formed from the stem of the rose). The "seeds" are hard, packed closely together and covered with minute hairs leaving no space between them, thus forming a hard nucleus into which no fly larva can penetrate. The surrounding fleshy part has a thin inner (facing the "seeds") and a thicker outer epidermal lining.

The fly when laying its eggs, drills a hole through the outer epidermis and inserts its eggs into the fleshy part on which the larvae feed. The larvae remain in the "fruit" until the time of pupation when they rupture the outer epidermis, fall to the ground and pupate, usually after having made their way under some leaves or into the ground itself.

The problems I was interested in solving were:

1. What makes the young fly larva remain in the "fruit"?
2. What makes it leave the "fruit" when mature for pupation?
3. What makes it burrow into the ground or under leaves before pupating?

The possibilities were carefully considered before the experiments were planned, and the following taxi were found as possibly influencing the behaviour of the larvae:

1. Photo-taxis, 2. Thigmo-taxis, 3. Chemo-taxis, 4. Hygro-taxis.

1. **Photo-taxis.**

Young larvae might be expected to avoid light, while full grown larvae might show a positive reaction or be indifferent.

To test the reaction of the larvae to light they were in most cases exposed to the light from the window and their behaviour observed. All the larvae, mature as well as immature, were found sooner or later, to turn away from the light. Their reactions were, however, less pronounced than those I had observed in house fly larvae.

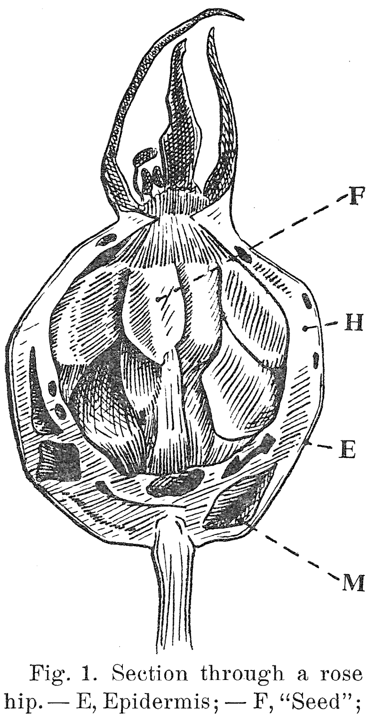

Fig. 1. Section through a rose hip. — E, Epidermis; — F, "Seed"; — H, Parenchyme; — M, Mine formed by a larva.

To get a picture of the exactitude with which the larvae orientate themselves it was tried to register the reactions of some larvae on a sheet of paper. Each larva was placed on the paper in a droplet of stained water and a horizontal beam of light was thrown onto its side. The larva, by crawling over the paper, would draw some stained water after itself and thus register its own movements. Now and then

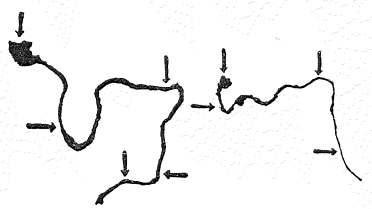

Fig. 2. Tracks drawn by fly larvae showing their reactions to light. The larvae were started at the big blot, and the arrows show the direction of light, and the point at which it was changed. — The left track is of a mature, the one to right of an immature larva.

the direction of the light was changed to one at right angles to the previous beam.

Two examples of tracks of 3rd stage larvae, — one still immature, and one ready for pupation, — are shown in fig. 2. It will be noticed that both larvae turn away from the light and that there are no marked differences with regard to the exactitude and the speed of their orientation. The tracks seem to show that these larvae are slower and less precise in their orientation than those of the house fly.

Judging from these observations one could expect that the migrating larvae would leave the hips mainly under cover of darkness. This assumption was confirmed when I tried to count the number of larvae that migrated during the day as compared with the night. It was found that out of 39 larvae 28 migrated by night and 11 by day.

2. **Thigmo-taxis.**

The young larvae could be expected to show a positive thigmo-taxis, while those ready for pupation might lose their orientation to surfaces and objects touching them.

No satisfactory method was found for testing the thigmo-taxis of the larvae, but observations showed that the larvae would seek out narrow passages in preference to open spaces. If a larva found a small opening with its anterior end, it would try to squeeze its whole body through. Larvae with but few contact-points for their bodies became restless and unwilling to react to other stimuli. It also became clear that the most sensitive part of the larva is its anterior end.

Larvae that got hold of any resisting object with their mouth-hooks seemed to be stimulated to tear the object with increased force until its resistance was overcome, or the larvae for one or another reason lost contact with it. This behaviour was often observed in the observation chambers described below. The movements consisted of a forwards and downwards blow of the anterior end, followed by a backwards scratching with the mouth-hooks until they caught hold of the object which was then pulled up and backwards until the mouth-hooks slipped. The attack was then renewed.

3. **Chemo-taxis.**

The immature larvae could be expected to be attracted by the flesh of the hip, while the larva ready for pupation might be repelled by it. That the state of ripeness or decay of the hip-tissues should play a part in the orientation could be ruled out, since the young larvae remained in the "fruits" already left by the full grown larvae.

To test the reaction of the larvae to their food it was decided to use a method where the conditions resembled those inside the hip as much as possible, so that restlessness caused by lack of contact points was avoided. Small narrow chambers were therefore constructed from washers of a motorcar.

On the one side the opening of a washer was completely covered by à thin slice of hip, on the other by a window of thin cellophane. Cellophane was chosen because its flexibility much resembled that of the hypodermis of the hip. The larva tested was placed in the narrow space formed in the washer between the slice of hip and the cellophane. Two further washers, one each side of the chamber were used to hold the hip-slice and the cellophane in position. The washers were screwed together with small bolts and nuts (fig. 3). — It was important to ascertain that both walls (e. g. the hip and the cellophane) touched the larva. Otherwise it became restless, showing no interest in the food. The chamber was kept in darkness during the experiments and to

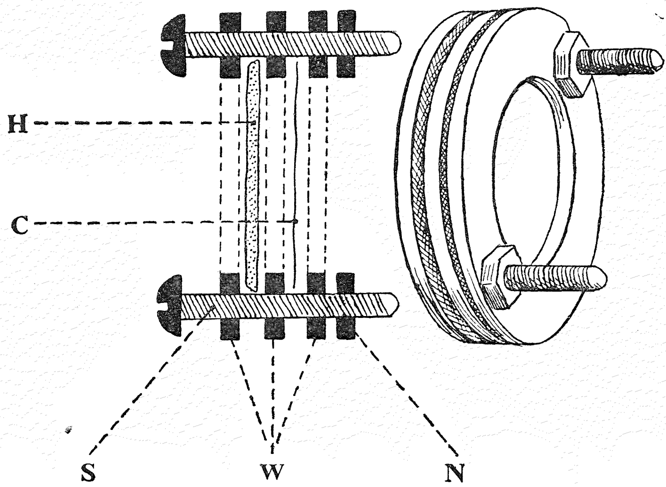

Fig. 3. Observation chamber made from washers. C, Cellophane. — H, Slice of hip. — N, Nut. — S, Screw. — W, Washers.

avoid the reactions being influenced by gravity the chambers were placed on edge. The position of the larva was observed every half hour. In the table 1 on p. 582 "+" indicates that the larva turned towards the hip, "—" that it turned away from it.

It will be seen from the table that it is beyond doubt that the larvae change their reaction to the hip at the time they reach maturity.

4. **Hygro-taxis.**

Young larvae could be expected to have a higher preference for water than full grown larvae.

Table 1.
Reaction to hip.

Immature larvae								Mature larvae							
Larva no.	Number reading 1	2	3	4	5	+	—	Larva no.	Number reading 1	2	3	4	5	+	—
1i	+	+	+	+	+	5	0	1m	+	—	—	—	—	1	4
2i	+	+	+	+	+	5	0	2m	—	+	—	+	—	2	3
3i	+	—	—	+	—	2	3	3m	+	—	+	—	+	3	2
4i	+	+	—	+	+	4	1	4m	+	—	+	+	+	4	1
5i	+	+	+	+	+	5	0	5m	+	—	+	—	+	3	2
6i	+	+	+	+	+	5	0	6m	—	+	—	+	—	2	3
7i	+	+	+	+	+	5	0	7m	—	+	+	—	—	2	3
8i	+	+	+	+	—	4	1	8m	—	—	+	—	—	1	4
9i	+	+	+	+	+	5	0	9m	+	+	+	—	—	3	2
10i	—	+	—	+	+	3	2	10m	+	—	—	—	+	2	3
						43	7							23	27

For testing the larvae's reaction to water, a similar method was applied as that for testing their reaction to the flavour of hips, but the hip-tissue was replaced by moistened filter paper. As before, the readings were half

Table 2.
Reaction to water.

Immature larvae								Mature larvae							
Larva no.	Number reading 1	2	3	4	5	+	—	Larva no.	Number reading 1	2	3	4	5	+	—
1ih	—	—	+	+	+	3	2	1mh	+	—	—	+	+	3	2
2ih	—	+	+	—	—	2	3	2mh	—	+	+	+	+	4	1
3ih	—	—	—	+	+	2	3	3mh	+	+	—	—	—	2	3
4ih	+	+	+	—	+	4	1	4mh	+	—	+	—	—	2	3
5ih	+	—	+	—	+	3	2	5mh	+	+	—	—	+	3	2
6ih	—	—	—	+	+	2	3	6mh	+	+	+	+	—	4	1
7ih	+	+	+	+	—	4	1	7mh	+	+	—	+	—	3	2
8ih	+	+	—	+	—	3	2	8mh	+	—	—	—	+	2	3
9ih	—	+	—	—	—	1	4	9mh	—	+	+	—	—	2	3
10ih	—	+	+	—	—	2	3	10mh	+	+	—	+	+	4	1
						26	24							29	21

hourly. In the table "+" indicates that the larva at the time of reading turned towards the filter paper, "—" that it turned away from it.

The figures in the table show no marked difference between the reactions of the mature and the immature larvae.

To test if the pupating larvae had any preference for humidity, a number of mature larvae were placed in the middle of a small, open, rectangular tin filled with shavings of plastic material. At one end of the tin was a roll of cotton wool which was kept wet. After the pupation, the tin was divided into one cm. wide zones parallel to the cotton wool, and the number of pupae in each zone was counted.

Table 3.

Number of pupae touching wet cotton wool	2
Number of pupae .1—1 cm. from wet cotton wool	5
" " " 1—2 cm. " " " "	4
" " " 2—3 cm. " " " "	3
" " " 3—4 cm. " " " "	1
" " " 4—5 cm. " " " "	2
" " " 5—6 cm. " " " "	1

The table shows that the pupating larvae have a preference for moisture.

Summing up the results of these experiments, it can be concluded that several factors influence the behaviour of the larvae of *Spilographa alternata*, and that there is a hierarchial order in which the stimuli act as releasers of reactions and thus bring about orientation. Without a slight pressure causing a deformation of the body wall the larva will not react normally to other stimuli. The importance of the other stimuli will depend on the strength of the stimulus and the physiological condition of the larva. The larvae will always avoid light, and show, at least at the time of pupation, a preference for humidity, but their reaction to food will change from a positive one to one of indifference at the time they are ready for pupation and stop eating. The humidity does not appear to serve as an orientating stimulus as long as the larva is still in the hip, but on the ground, where there can be a wider range of choice the larva will seek moist places although it seems to avoid soaking wet soil.

There is no evidence that the mature larvae are forced out of the hip by any stimulus. Having stopped eating it will tear any tissue within its reach without discrimination. Before that time it will be attracted by the parenchymatic tissue of the hip and tear that only with its mouth hooks. The mature larva's lack of discrimination between the tissues will sooner or later cause a rupture of the epidermis. Having once got its mouth hooks through the epidermis the resistance will stimulate the larva to tear the edges of the hole with increased force. Eventually the hole becomes so big that the larva misses its edges. Being without contact points for its anterior end it will move forwards, and next time it thrusts its anterior end downwards it will usually slip and pass through the opening. Once through the opening the larva's failure to obtain any hold with its mouth hooks will induce restlessness and further forward movements. The result is that the larva will make its way out and fall to the ground.

As will be seen it is no interior repellant or exterior attractant that forces the larva out of the hip. It happens incidentally as a result of the larva's general activity.

During daytime the larvae will orientate themselves away from the light towards the dark interior of the hip. Hence the small number of larvae that make their way out by day.

On the ground the tendency of the larvae to make their way through narrow passages will force them down into the soil. This burrowing reaction will in the day-time be supported by the negative reaction of the larvae to the light. Once in the soil the larvae will seek out a moist, but not wet place where they will pupate.

Answering the three questions set at the beginning it can be said:

1. The larva stays in the hip as long as it eats because it is attracted by the flavour of the tissues on which it feeds.

2. The mature larva leaves the hip incidentally because it is no longer attracted by the surrounding tissues, and works with its mouth hooks in all directions, eventually causing ruptures in the epidermis. In the ruptures the larva is without contactpoints for its anterior end. This stimulates it to move forward, the result being that it falls through the hole.

3. Having fallen to the ground the larva is drawn down into the soil as a result of its positive thigmotaxic orientation. This tendency to burrow in the ground can be supported by a negative photo-taxis and a positive hygro-taxis.

Anmeldelse.

Herbert Weidner: **Bestimmungstabellen der Vorratsschädlinge und des Hausungeziefers Mitteleuropas.** Jena (Gustav Fischer) 1953. 8° 234 Sider. Pris indb. 14.50 DM.

En nyttig Bog ikke blot for Praktikeren, men ogsaa for den almindelige Entomolog blot han gør sig klart, at Bestemmelseskaraktererne er valgt under Hensyn til det ringe Artsantal. Der er megen Forøgelse fra 1. Udg. (1937), bl. a. i Larvetabellerne. Udmærkede Billeder, hvoraf dog de færreste er nye. Foruden Tabellerne er der en Indledning om Præparations- og Undersøgelsesteknik, en Tabel over Trægnav og et Register ogsaa over en Del engelske og enkelte franske Navne paa Skadedyr.

S. L. Tuxen.