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Protection against birds and parasites in some species of tenthredinid larvae

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I. INTRODUCTION

L. TINBERGEN (1949, 1959) has studied, over a number of years, the relative densities of various species of larvae living on pine (*Pinus sylvestris* L.) in a wood near Hulshorst, Netherlands. Simultaneously he determined the composition of the food wild tits in this wood collected for their young. One fact resulting from this study is that, whereas in some prey species a considerable part of the population was eaten by birds, the populations of others, e.g., of sawfly larvae belonging to the genera *Diprion* and *Neodiprion* (Hymenoptera: Diprionidae), were scarcely affected by predation. At Prof. TINBERGEN's suggestion I undertook an investigation on the reason why these larvae run so little risk from birds. As protection by cryptic or by aposematic characters (cf. COTT, 1957) seemed the most likely explanation, I studied the conspicuousness of the larvae on pine needles (chapter III) and of their attractiveness as prey to birds (chapter IV). Chapter II gives experiments and observations on meetings between the larvae studied and birds; in addition, encounters with parasites have been investigated. A final discussion on the nature of the protection against predation by birds follows in chapter V.

I have studied five congeneric species (*Diprion virens* Kl. (syn. *Gilpinia virens* Kl.), *D. frutetorum* F. (syn. *Gilpinia frutetorum* F.), *D. nemoralis* Ensl., *D. simile* Htg., *D. pini* L.) and the closely related *Neodiprion sertifer* Geoffr. (syn. *Diprion sertifer* Geoffr.). *Diprion pallipes* Fall. and *D. pallidum* Kl., also occurring in the Netherlands, have not been studied.

For specific descriptions and life history of the species mentioned I refer to ESCHERICH (1942) and DE FLUITER (1932). Moreover, our

PLATE I

Fig. 1. *Neodiprion sertifer* Geoffr. Larvae in U-bend.
(Photograph by Mr. K. P. VAN KEMPEN.)

Fig. 2. *Diprion pini* L. Responding larva with a mouth drop. (Photograph by "Centrale Fotodienst", University Groningen.)

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PLATE II

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special subject asks for descriptions of the following behaviour patterns.

When disturbed by an enemy, either a bird or a parasite, the larvae perform more or less conspicuous displays. Three types can be distinguished:

U-bend. With a rapid jerk the larva bends its head and thoracic segments backwards, often also raising the end of the abdomen, until the rostral and caudal parts make an angle of about 90° with the rest of the body (Plate I, 1). Moreover, a drop of a whitish liquid appears on the mouth parts (Plate I, 2). As a rule, this mouth drop is withdrawn after some ten seconds; the convulsively bent attitude itself may last for 10 minutes or even more. The form of this activity is almost the same in the six species studied. Intraspecific variations occur in the number of abdominal segments lifted (maximal 4) and in the angle over which the frontal part is raised.

Jerking. Like in the U-bend, the head, the thoracic and in this case also one or more of the rostral segments are lifted from the substratum until they are about at right angles to the attached rest of the abdomen; then they are immediately swept back again. The last abdominal segments remain attached to the needle. The jerking is often repeated rhythmically at a high rate. As an illustration, fig. 1 gives the results of a series of 42 experiments in which a short lasting stimulus (swinging a pencil 2 cm away from the colony) was presented to a *sertifer* colony. The figure shows that in the first 15 second period after stimulation jerking was more than 20 times as frequent as in the preceding control period in which no artificial stimulation was given; these jerkings were due to insects which had passed. In the second 15 second period a rapid decrease followed.

This display which has already been mentioned by ILTIS (1930), ESCHERICH (1942)—who called it “schnippen”—and HUSSON (1952), is restricted to the gregarious species *sertifer* and *pini*. However, these

Fig. 1. Rate of jerking in a *sertifer* colony before and after a visual stimulus.

PLATE II

Fig. 1. *Diprion pini* L. Larvae stretching (×) towards a swinging twig (+).
(Photograph by Mr. K. P. VAN KEMPEN.)

Fig. 2. *Diprion pini* L. Colony in a dense cluster.
(Photograph by Mr. K. P. VAN KEMPEN.)

show some specific differences. *Sertifer* performs jerking at a higher rate than *pini*, it also bends farther backwards than the latter. If in a *sertifer* colony more than one larva have been activated, they as a rule jerk simultaneously, whereas in a *pini* colony the jerking of different members is never synchronized. Characteristic for *pini* is that, during bending backwards, the thoracic legs are detached successively; the tarsus of the second and particularly of the third pair hold on for such a long time that the needle is slightly bent. Consequently, when a moment later also these legs are detached, the needle springs back with a visible quake.

Stretching. The thoracic legs and the first two or three pairs of abdominal legs are detached from the substratum; the fore part of the body is not swept backwards (as in jerking), but on the contrary, the larva stretches it and turns towards the source of the stimulus. This orientation is continuously corrected when the stimulating object moves. Like in the U-bend, the larva produces a mouth drop which, while stretching, it tries to smear on the stimulating object (Plate II, 1).

Like jerking, this activity occurs only in the gregarious species (*pini* and *sertifer*). The form of the activity is similar in both species.

Two completely different kinds of function have been suggested for these displays. RATZBURG (quoted by ESCHERICH, 1942, p. 67) assumes a physiological effect of jerking in facilitating digestion. However, this seems rather unlikely, because, when feeding undisturbed, the larvae never show jerking. It is more generally held that the displays serve to protect the larvae against enemies. This paper is an attempt to deal critically with only the latter aspect of the displays.

With regard to a protective function we can discern the following possibilities:

1. The displays might afford an active defence.
 - a. They might appeal to a disposition in birds and parasites to become startled by sudden movements, and thus act without being actually dangerous to an enemy.
 - b. The displays might mean a real danger for the enemies in causing harm to small attackers, such as parasites.
2. The displays might be part of an aposematic advertisement, based on an association of conspicuousness and unattractiveness.
3. The displays might have the effect of directing an attack to a part of the animal with special defensive properties.

Acknowledgements: I am deeply indebted to the late Prof. Dr. L. TINBERGEN for drawing my attention to the problem and for help, criticism and encouragement. I have often benefited from his extensive theoretical knowledge and from his admirable experience with animals in the field. This study is part of the ecological research in the field station

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II. THREAT AS A FACTOR IN THE PROTECTIVE FUNCTION OF THE DISPLAYS

I. INTIMIDATION OF BIRDS BY THE DISPLAYS

Experiments have been designed to investigate two questions at the same time: viz. (1) can an approaching insectivorous bird release the above mentioned displays in the larvae, and (2) are these displays able to evoke fright responses in the birds.

A. Material and technique

Test birds were two captive Chaffinches (*Fringilla coelebs* L.) and a captive Great Tit (*Parus major* L.). Their cages measured $158 \times 78 \times 78$ cm. Finch R₀ was used in experiment 1, 2 and 9, Finch R₂ in exp. 10 and 11, the Tit in exp. 3, 4, 5, 6, 7 and 8. Some additional observations were made on wild birds visiting feeding trays; for technical details of these experiments I refer to chapter IV.

The Great Tit was reared in captivity from just before the fledgling stage. At the beginning of the experiments it was acquainted with anaesthetized *Diprion* larvae, but not with living specimens. The Finches had been caught four months before they were used in the experiments. During captivity they had not had any experience with the larvae.

Encounters between birds and larvae were arranged as follows. The larvae were presented on a pine twig of about 30 cm length. The twig was laid on the bottom of a cage or on a feeding table for wild birds, very cautiously to prevent disturbance of the larvae. The captive birds were