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Superparasitism in *Trichogramma evanescens minutum* RILEY, an egg parasite of sugarcane and maize borers in India

II. Causes of superparasitism

(Hymenoptera: Trichogrammatidae)

It has been reported by NARAYANAN & CHACKO (1957) that superparasitism was of common occurrence in *Trichogramma evanescens minutum* RILEY when mass multiplied in the laboratory, and that the progeny that resulted from superparasitism was defective since their fecundity and longevity, their mating habits, vigour, etc., were adversely affected. Such parasites were of little value in the biological control of insect pests. The present investigation was carried out to find out the factors that led to the occurrence of superparasitism in this parasite.

Several workers have studied the nature of the distribution of parasite progeny. FISKE (1910) observed that the distribution of the progeny of the parasites among the available hosts was governed by the laws of chance. Working with the parasites of the gypsy moth, he came to the conclusion that the faculty which enabled the female parasite to select healthy hosts for her offspring was, as a rule, non-existent. THOMPSON & PARKER (1927) stated that the number of eggs laid by a parasite in a host was roughly proportional to the amount of food material available, as the parasites possessed an instinct which regulated the oviposition in any given case.

The existence of discriminative powers in *Trichogramma* was pointed out by SALT (1932); while studying the nature of parasitism in *Collyria calcitrator* (GRAVENHORST), and *Trichogramma evanescens* WESTWOOD, he observed that these parasites did not distribute their progeny at random. He (1934) further observed that *Trichogramma* discriminated between healthy and parasitised eggs of *Sitotroga cerealella* (OLIVIER). According to ULLYETT (1943) the degree of discriminative ability varied among the different species, and under certain conditions this ability would break down under the influence of more powerful factors. LLOYD (1938) reported that *Ooencyrtus kuwanai* (HOWARD) was able to exercise a remarkable degree of discrimination between host eggs which were attacked previously and those which were not. HARTLEY (1922) had reported that *Aphelinus semiflavus* HOWARD possessed a very high degree of discriminative ability even when parasitisation of its host approached 100 percent.

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It is clear from the brief review of the published literature given above that many hymenopterous parasites, including *Trichogramma*, possess a discriminative ability. But in spite of this ability superparasitism occurs to a considerable extent when *Trichogramma* is mass multiplied in the laboratory. During the course of the present investigation the nature of the distribution of the progeny by *Trichogramma*, when various densities of eggs of *Corcyra cephalonica* STAINTON were exposed for different periods of time, has been studied in detail.

Experiments

Experiments were conducted to find out the nature of parasitism when 60, 50, 40, 30, 20, 10, and 5 eggs of *Corcyra cephalonica* were exposed to a mated female *Trichogramma* for 1, 2, 4, 8, 16, and 24 hours.

Materials and Methods

A separate culture of *Trichogramma* started with a single mated female was maintained for the experimental purposes. The eggs of *C. cephalonica* were pasted on small strips of cards and exposed to a single freshly emerged mated female parasite in a specimen tube which had the mouth covered by a double layer of muslin held tight by an India rubber band. In arranging the host eggs on the card care was taken to see that there was enough space between the eggs for the parasite to move about freely. A male parasite was also introduced into the specimen tube as mating took place more than once.

After exposing the eggs to varying periods of time they were removed from the card by dissolving the gum in a droplet of water. To observe the nature of parasitism each egg was dissected in a drop of water on a microslide under a stereoscope and the number of parasite eggs laid in each of the host eggs was counted.

Each experiment was repeated 4 times. The experiments were conducted at a temperature of 25 °C., and at a relative humidity of 75 percent.

Observations

Experiments A and B: It is clear from Table 1 that very little superparasitism occurred when 60 or 50 host eggs were exposed for 1 to 24 hours.

Experiments C and D: A slight increase in superparasitism was recorded when the number of host eggs was brought down to 40 and 30.

Experiment E: When only 20 eggs were available the incidence of superparasitism increased considerably.

Experiments F and G: Heavy superparasitism was observed when the host density was brought down to 10 and 5, and when the time of exposure was increased.

Statistical analyses of the data indicated that the differences in the degree of superparasitism for the different timings were significant only when 10 host eggs were exposed.

Discussion

From the data collected during the course of the present investigation it can be seen that very little superparasitism occurs if sufficient number of host eggs are available for *Trichogramma* for oviposition. When a large number of hosts are available it lays only one egg in each host, thus avoiding superparasitism. In Experiment A out of 750 host eggs parasitised only 2 were superparasitised. This shows that this parasite is able to discriminate between healthy and parasitised eggs, and that it has a high degree of discriminative ability. These obser-

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Table 1

Experiment no.	No. of eggs exposed	Time of exposure in hours	No. of host eggs parasitised (in 4 replications)	No. of host eggs parasitised with (in 4 replications)				% age of superparasitism based on no. of eggs (in 4 replications)	
				2 eggs	3 eggs	4 eggs	5 eggs	exposed	parasitised
(1)	(2)	(3)	(4)	(5)				(6)	
A	60	1	102	0	0	0	0	0.0	0.0
		2	98	0	0	0	0	0.0	0.0
		4	117	1	0	0	0	0.4	0.9
		8	162	0	0	0	0	0.0	0.0
		16	137	0	0	0	0	0.0	0.0
		24	134	1	0	0	0	0.4	0.8
B	50	1	96	1	0	0	0	0.5	1.0
		2	123	1	0	0	0	0.5	0.8
		4	113	0	0	0	0	0.0	0.0
		8	162	3	0	0	0	1.5	1.9
		16	134	1	0	0	0	0.5	0.8
		24	145	5	1	0	0	3.0	4.1
C	40	1	79	5	0	0	0	3.1	6.3
		2	102	0	0	0	0	0.0	0.0
		4	135	2	0	0	0	1.3	1.5
		8	121	4	0	0	0	2.5	3.3
		16	119	4	0	0	0	2.5	3.4
		24	101	4	0	0	0	2.5	4.0
D	30	1	96	0	0	0	0	0.0	0.0
		2	100	3	0	0	0	2.5	3.0
		4	79	1	0	0	0	0.8	1.3
		8	98	6	0	0	0	5.0	6.1
		16	94	2	0	0	0	1.7	2.1
		24	91	0	0	0	0	0.0	0.0
E	20	1	70	8	0	0	0	10.0	11.4
		2	73	9	0	0	0	11.3	12.3
		4	71	5	0	0	0	6.3	7.2
		8	71	1	0	0	0	1.3	1.4
		16	75	8	2	0	0	12.5	13.3
		24	71	6	0	0	0	7.5	8.5
F	10	1	35	0	0	0	0	0.0	0.0
		2	39	4	0	0	0	10.0	10.3
		4	39	7	1	0	0	20.0	20.5
		8	38	4	0	0	0	10.0	10.5
		16	39	7	0	0	0	17.5	18.0
		24	40	15	5	1	0	52.5	52.5
G	5	1	20	0	0	0	0	0.0	0.0
		2	20	4	3	1	0	40.0	40.0
		4	19	3	1	2	1	35.0	36.8
		8	20	5	0	0	0	25.0	25.0
		16	20	4	1	0	0	25.0	25.0
		24	19	5	3	0	0	40.0	42.1

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vations corroborate those made by SALT (1936), and LAING (1938) in *Trichogramma evanescens*, and by JONES (1937) in *Trichogramma lutea* GIRAULT. It is astronishing that no other published literature is available on this aspect of insect parasitism relating to *Trichogramma* which is probably the most controversial parasite utilised for the biological control of insect pests. It has been emphasized by NARAYANAN & CHACKO (1957) that there are two schools of thought, one holding that *Trichogramma* is a beneficial parasite, and the other holding that *Trichogramma* is of no use in controlling insect pests of agricultural and horticultural importance in the field. SALT (1936) observes that the ability of *Trichogramma* to discriminate between parasitised and unparasitised eggs is perfect. The factors that enable it to exercise this ability, according to SALT (1937), are an external odour left by the parasite as it walks about the host eggs or as it oviposits, and an internal difference which it feels when it thrusts its ovipositor in the host egg. Though it is evident that *Trichogramma* is gifted with a well developed discriminative ability, yet superparasitism occurs and this can be explained on a scientific basis as discussed below:

When the density of the host eggs is reduced and when the time of exposure is increased, the degree of superparasitism increases. This increase in the incidence of superparasitism is not on account of the inability of *Trichogramma* to discriminate between healthy and parasitised host eggs, but because a complex of factors such as the scarcity of the host eggs, the longer periods of exposure to a limited number of eggs, and the physiological urge to oviposit comes into play, and the restraint exercised by the parasite breaks down. When the restraint, or the ability to withhold oviposition when there is a scarcity of host material, breaks down the parasite accepts unsuitable hosts for oviposition, and this results in superparasitism. The parasite has, in fact, no choice but to accept host eggs which it recognises as unsuitable for her offspring. It is forced to lay 2, 3, or even 4 or 5 eggs in an individual host egg. ULLYETT (1936) states that the physiological urge to oviposit experienced by the gravid females is probably the basic cause of superparasitism. LLOYD (1940) is of the opinion that the discriminative faculty of a parasite seems to be easily countered by other overriding factors in the laboratory and in the field.

SALT (1936) reports that the restraint exercised by *Trichogramma* is limited and in a longer period of time the restraint breaks down resulting in superparasitism; he also states that the degree of restraint is found to be proportional to the scarcity of the host eggs and is maintained for 8 hours only to the deposition of 5 percent of its available eggs when only a few host eggs are available. However, during the course of the present investigation it has been observed that while in certain individual parasites the restraint breaks down even within one hour, in others it is maintained upto 24 hours. This shows that the ability to maintain the restraint varies considerably from individual to individual. The statistical analyses of the data also show that the increase in the degree of superparasitism is not uniform or significant. Thus we see in *Trichogramma evanescens minutum* a condition which is intermediate between the hypothesis of ran-

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dom distribution as enunciated by FISKE(1910), and SALT's (1936) observations. This could perhaps be attributed to the difference in the two strains of the same species. It has been shown by ULLYETT (1943) that the distribution of the progeny by the parasite *Horogenes* (*Angitia*) *cerophaga* GRAVENHORST among the larval population of *Plutella maculipennis* (CURTIS) does not conform to the theory of random distribution; nor does it agree with the hypothesis that the female can and do discriminate perfectly between hosts which have been parasitised previously and those which have not. He states that the degree of superparasitism is intermediate between the two conditions. Thus the theory of intermediate conception of superparasitism on account of the interplay of different factors stands. In the case of *Trichogramma* these factors are perfect discrimination and imperfect restraint.

Thus it is seen that the discriminative ability of *Trichogramma* is perfect, but it is coupled with imperfect restraint. The scarcity of host eggs, the longer periods of exposure to a limited number of host eggs, and the physiological urge to oviposit cause the breakdown of the restraint exercised by this parasite and this results in superparasitism. When superparasitism occurs there is a considerable wastage of progeny. Therefore, superparasitism is, undoubtedly, one of the factors that reduces the efficacy of *Trichogramma* in the biological control of insect pests.

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Summary

1. Experiments were conducted to find out the factors that resulted in superparasitism in *Trichogramma evanescens minutum* RILEY when mass multiplied on the eggs of *Corcyra cephalonica* STAINTON under laboratory conditions. — 2. Very little superparasitism occurs if a sufficient number of host eggs are available for oviposition. *Trichogramma* has a well developed discriminative ability. — 3. When there is a scarcity of host eggs, and when the parasite is exposed to a limited number of eggs for long periods, the restraint breaks down and the physiological urge to oviposit results in superparasitism. — 4. The restraint exercised by *Trichogramma* is not perfect, and the ability to maintain it varies from one individual to another.

Zusammenfassung

1. Es wurden Versuche angestellt, um die Faktoren zu ermitteln, die zu Hyperparasitismus von *Trichogramma evanescens minutum* RILEY bei Massenvermehrung auf Eiern von *Corcyra cephalonica* STAINTON unter Laborbedingungen führen. — 2. Wenn eine genügende Anzahl von Wirtseiern zur Eiablage zur Verfügung steht, tritt sehr wenig Hyperparasitismus auf. *Trichogramma* hat ein gut entwickeltes Unterscheidungsvermögen. — 3. Wenn ein Mangel an Wirtseiern herrscht und der Parasit sich längere Zeit einer begrenzten Zahl von Eiern gegenübersieht, wird die Zurückhaltung durchbrochen, und der physiologische Drang zur Eiablage führt zu Hyperparasitismus. — 4. Die von *Trichogramma* geübte Zurückhaltung ist nicht vollkommen, und die Fähigkeit dazu schwankt bei den einzelnen Individuen.

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Резюме

1. Делаются опыти, чтобы определить факторы, которые ведут к гиперпаразитизму у *Trichogramma evanescens minutum* RILEY при массовом выращивании на яйцах *Corcyra cephalonica* STAINTON под лабораториыми условиями. — 2. Если имеется достаточное количество яйц хозяина, возникает только мало гиперпаразитизма. *Trichogramma* имеет хорошо развитию способность различения. — 3. Если имеется недостаток яйц и паразит имеет через длительное время ограниченное количество яиц, ведёт физиологическая нужность к откладке яиц к гиперпаразитизму. — 4. Сдержанность у *Trichogramma* не полная и способность к ней колебает у отдельных особей.

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