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The phenomenon of superparasitism in *Trichogramma evanescens minutum* RILEY — I[1]

(Hymenoptera: Trichogrammatidae)

Trichogramma evanescens minutum RILEY is an important parasite that is used as a biological control agent against many insect pests. According to METCALF et al. (1951) the most elaborate attempts to bring about pest control by rearing large numbers of an entomophagous insect and releasing them have been with *Trichogramma*. The genus *Trichogramma* is world wide in distribution. It is parasitic on the eggs of many orders of insects, mainly Lepidoptera. The sugarcane shoot borer *Chilo infuscatellus* (SNELLEN), the jowar stem borer *Chilo partellus* (SWINHOE) (= *Chilo zonellus* SWINHOE), the sugarcane root borer *Emmalocera depressella* SWINHOE, and the paddy stem borer *Tryporyza incertulas* (WALKER) are some of the pests for the control of which *Trichogramma* is used in India.

However, opinion is divided as to the utility of this parasite in the control of insect pests. *Trichogramma* is a very important factor in the control of *Diatraea saccharalis* FABRICIUS in Louisiana (HOLLOWAY & LOFTIN 1919, HINDS & SPENCER 1929), in the Rio Grande Valley of Texas (HOLLOWAY & LOFTIN 1919), and in Barbados (TUCKER 1932). EVANS (1930), on the other hand, states that ovipositing many times in the same host egg, and ovipositing even in foreign bodies cause a dissipation of its doubtful beneficial effect. BOX (1932) has recorded that even a high degree of parasitism by *Trichogramma* does not appreciably affect the sugarcane borer population in Antigua. According to TUCKER (1932, 1933), the objections raised against *Trichogramma* are its limited range of operation, its random search for host, and its non-specificity. The author's (1957) own observations have led him to believe that possibly superparasitism, which affects the fecundity and longevity of *Trichogramma*, is another important factor that limits the efficacy of this parasite.

NARAYANAN & CHACKO (1957) have pointed out that when *Trichogramma* is mass multiplied in the laboratory superparasitism is of common occurrence. Only very little information is available on the fecundity and longevity of *Trichogramma* that emerge from superparasitised eggs. The present investigation was, therefore, undertaken to study in detail the effect of superparasitism on these aspects as well as on size.

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Materials and Methods

Two strains of *Trichogramma evanescens minutum*, viz., IARI strain and Ajmer strain, and the crosses between them were used for the experiments.

IARI Strain

A culture of this strain is maintained at the Parasite Laboratory of the Division of Entomology, Indian Agricultural Research Institute. For the present studies a few eggs of *Corcyra cephalonica* Stainton parasitised by this strain of *Trichogramma* were selected, and kept in specimen tubes (2″ × $^1/_2$″), one egg in a tube. When the adult parasites emerged a healthy male and female were selected and introduced into a larger specimen tube (4″ × 1″). The mouth of the specimen tube was covered by a double layer of muslin, held in position by a rubber band. About fifty eggs of *Corcyra cephalonica*, which were used as the laboratory host, were pasted on a rectangular strip of card and exposed to this pair. About twenty four hours later the card was taken out and kept in another specimen tube for the development of the parasite eggs that were laid within the eggs of *Corcyra cephalonica*. Batches of fresh eggs were exposed daily to this pair for ten days, and the exposed eggs were kept in specimen tubes for the development of the parasites.

When the adults emerged, host eggs were supplied for parasitisation. Thus a separate culture, started with a single pair, was built up and maintained for the present studies.

Fecundity and longevity of *Trichogramma* that develops and emerges singly from a host egg, i. e., without superparasitism:

About one hundred eggs of *Corcyra cephalonica* were pasted on a strip of card in such a way that there was a little space around each egg. These eggs were exposed to a few *Trichogramma* in a specimen tube for about two minutes, after which all the parasites were taken out. On the fourth day the card was cut around each blackened (parasitised) egg, so that each egg could be kept in a separate tube for the development and emergence of the parasites. When the adults emerged, only those that emerged singly were selected and the others discarded. Eight pairs were formed for studying the fecundity and longevity, and the rest were used for getting the second generation. Each of the eight pairs was introduced into a small specimen tube along with a supply of host eggs pasted on a card strip. Each succeeding day, till the death of the females, fresh host eggs were given, and the exposed eggs were taken out and kept in separate tubes. The fecundity was calculated by counting the number of host eggs that turned black. The longevity of the female was also noted.

From the remaining adults that emerged singly, as many pairs as possible were formed, and each pair was introduced into a specimen tube. About fifty host eggs were supplied to each pair. When the host eggs turned black, each was kept in a small specimen tube. When the adults (second generation) emerged, all those that emerged singly were selected. Eight pairs were formed, and studies on their fecundity and longevity were made as in the previous generation.

The third generation was obtained from the remaining adults of the second generation. Eight pairs were formed, and the fecundity and longevity were studied as in the first and second generations.

Fecundity and longevity when two apparently normal parasites, a male and a female, emerge from the same host egg:

In order to obtain apparently normal male and female parasites, about one hundred eggs of *Corcyra cephalonica* were exposed to a number of parasites for about ten minutes, and the parasite eggs allowed to develop. When the host eggs turned black, each parasitised egg was kept in a small specimen tube. When the adults emerged, only those which were apparently normal (i. e., without any apparent ill-effect), and whose development was such that a male and a female emerged from the same egg, were selected. Studies were made on the fecundity and longevity of eight females after selecting eight pairs.

To the remaining pairs host eggs were exposed, ten to fifteen eggs to each pair. When the eggs turned black, each was kept in a separate tube. When the adults (second generation)

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emerged, eight pairs were selected and studies on the fecundity and longevity were made as in the first generation.

From the remaining pairs of the second generation the third generation was obtained. Eight pairs were selected, and the fecundity and longevity studied as in the first and second generations.

Fecundity and longevity when two apparently normal female parasites emerge from the same host egg:

The same method as in the previous case was adopted, but here only those which were apparently normal and whose development was such that two females emerged from the same host egg (and also two males from the same host egg) were selected. Eight pairs were formed from eight such females and eight males, and the fecundity and longevity studied. Studies on the fecundity and longevity of the second and third generations which developed similarly were also made.

Fecundity and longevity when two defective parasites, a male and a female, emerge from the same host egg:

In order to get defective forms, about fifty eggs of *Corcyra cephalonica* were exposed to a large number of parasites for about fifteen to twenty minutes. When the eggs turned black, each parasitised egg was kept separately, and when the adults emerged, only those which were defective (having ill-developed wings), and whose development was such that a male and a female emerged from the same egg were selected. The fecundity and longevity of eight such females were studied.

No defective second generation was procured. The progeny of the first generation were either normal, or if two developed in an egg they were apparently normal. So studies on defective second and third generations were not possible.

Fecundity and longevity when two defective females emerge from the same egg:

The same method as in the previous case was adopted, but only those which were defective, and whose development was such that two females emerged from the same egg (and two males from the same egg) were selected. Eight pairs were formed, and studies were made on their fecundity and longevity.

As in the previous case the progeny of the first generation were either normal or apparently normal, and, therefore, studies on the succeeding generations were not made.

Ajmer Strain

This strain of *Trichogramma evanescens minutum* was obtained from the eggs of *Chilo partellus* collected at Ajmer. A culture of this parasite was built up on the eggs of *Corcyra cephalonica*. The culture was started with a single pair as in the IARI strain.

The fecundity and longevity of this strain were studied for three successive generations of the various types of development.

Ajmer Male × IARI Female

This was started with a male from the Ajmer strain and developed singly in a host egg, and a female from the IARI strain also developed singly in an egg. As in the IARI and Ajmer strains, the culture was built up and studies on the fecundity and longevity were made.

IARI Male × Ajmer Female

This cross was started with a male from the IARI strain, and a female from the Ajmer strain. The fecundity and longevity were studied as in the previous cases.

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All the experiments were conducted at a temperature of 25 °C., and at a relative humidity of 75%. A temperature of 25 °C. was maintained at the Parasite Laboratory of the Indian Agricultural Research Institute. The relative humidity was maintained by keeping a supersaturated solution of sodium chloride in distilled water in a desiccator.

The adult parasites were given 10% sucrose solution as food. It was applied daily on the inner walls of the specimen tubes in thin streaks with the aid of a fine brush.

Every third day the tubes in which the parasites were kept for experimental purposes were changed, and clean tubes substituted.

Experiments

During the course of the present investigation the effect of superparasitism on the fecundity and longevity of three successive generations of *Trichogramma evanescens minutum* was studied in detail. Two different strains of *Trichogramma*, viz., IARI strain (the strain that is maintained at the Indian Agricultural Research Institute), and Ajmer strain (obtained from the eggs of *Chilo partellus* collected at Ajmer), and the crosses between them (Ajmer male × IARI female, and IARI male × Ajmer female) were used for the experiments. The fecundity and longevity of parasites with the following types of development were studied:

(1) a normal female in a host egg (the term 'normal' is used to refer to a parasite that has developed singly in a host egg without any superparasitism)

(2) two apparently normal parasites, a male and a female, in the same host egg ('apparently normal' refers to a parasite that has developed along with another parasite, but does not show any visible ill-effect of superparasitism except in size)

(3) two apparently normal females in the same egg

(4) two defective parasites, a male and a female, in the same egg ('defective' refers to a parasite which has developed along with another parasite, and which shows the ill-effects of superparasitism, such as malformed wings or absence of wings)

(5) two defective females in the same egg.

Studies were also made on the effect of superparasitism on the size of the adult parasites.

Observations

The following abbreviations are used to refer to the various types of development:

Nf — a female developing alone in an egg
ANfm — two apparently normal parasites, a female and a male developing in an egg
ANff — two apparently normal parasites, both females
Dfm — two defective parasites, a female and a male
Dff — two defective parasites, both females.

The mean fecundity and longevity (of eight replications) of the three generations of the two strains, and their crosses, and the results of the statistical analyses are given in Tables 1—4.

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Table 1

Fecundity and longevity of inbred IARI strain

Nature of development	Mean fecundity I generation	II generation	III generation
Nf	185.38 ± 21.91 (A)	209.88 ± 70.77 (B)	180.50 ± 20.79 (C)
ANfm	33.38 ± 4.59 (D)	34.13 ± 5.20 (E)	34.75 ± 8.90 (F)
ANff	116.25 ± 5.60 (G)	74.00 ± 14.10 (H)	79.63 ± 6.23 (I)
Dfm	10.13 ± 2.09 (J)		
Dff	10.38 ± 1.68 (K)		
	Mean longevity of the female		
Nf	11.85 ± 1.17 (A)	9.13 ± 1.09 (B)	7.75 ± 0.75 (C)
ANfm	2.75 ± 0.37 (D)	3.38 ± 0.32 (E)	3.38 ± 0.26 (F)
ANff	9.63 ± 1.38 (G)	10.50 ± 1.45 (H)	10.75 ± 0.56 (I)
Dfm	2.14 ± 0.22 (J)		
Dff	2.00 ± 0.19 (K)		

Table 2

Fecundity and longevity of inbred Ajmer strain

Nature of development	Mean fecundity I generation	II generation	III generation
Nf	41.13 ± 1.58 (A)	48.50 ± 3.27 (B)	48.50 ± 4.90 (C)
ANfm	21.88 ± 2.48 (D).	25.13 ± 2.09 (E)	24.13 ± 2.09 (F)
ANff	31.63 ± 3.71 (G)	35.38 ± 2.10 (H)	32.13 ± 3.57 (I)
Dfm	2.00 ± 0.19 (J)		
Dff	3.00 ± 0.87 (K)		
	Mean longevity of the female		
Nf	3.00 ± 0.33 (A)	3.75 ± 0.16 (B)	5.38 ± 0.32 (C)
ANfm	3.00 ± 0.33 (D)	2.50 ± 0.19 (E)	2.25 ± 0.25 (F)
ANff	3.13 ± 0.29 (G)	3.63 ± 0.26 (H)	3.38 ± 0.26 (I)
Dfm	1.13 ± 0.13 (J)		
Dff	1.50 ± 0.19 (K)		

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Table 3

Fecundity and longevity of Ajmer male × IARI female

Nature of development	Mean fecundity I generation	II generation	III generation
Nf	128.25 ± 21.58 (A)	138.88 ± 19.65 (B)	145.63 ± 33.83 (C)
ANfm	34.38 ± 5.12 (D)	37.00 ± 7.90 (E)	34.38 ± 3.66 (F)
ANff	50.00 ± 6.54 (G)	49.63 ± 5.12 (H)	51.63 ± 4.92 (I)
Dfm	4.63 ± 0.86 (J)		
Dff	5.38 ± 0.53 (K)		
	Mean longevity of the female		
Nf	10.38 ± 0.94 (A)	9.25 ± 1.25 (B)	11.25 ± 2.11 (C)
ANfm	5.66 ± 0.80 (D)	5.25 ± 1.03 (E)	4.63 ± 0.32 (F)
ANff	5.88 ± 0.97 (G)	5.38 ± 0.46 (H)	5.38 ± 0.65 (I)
Dfm	1.38 ± 0.18 (J)		
Dff	1.63 ± 0.18 (K)		

Table 4

Fecundity and longevity of IARI male × Ajmer female

Nature of development	Mean fecundity I generation	II generation	III generation
Nf	239.88 ± 24.17 (A)	226.75 ± 9.61 (B)	238.13 ± 6.37 (C)
ANfm	55.63 ± 10.79 (D)	65.13 ± 5.16 (E)	57.25 ± 5.08 (F)
ANff	85.25 ± 12.34 (G)	88.25 ± 9.30 (H)	85.00 ± 5.73 (I)
Dfm	12.13 ± 1.51 (J)		
Dff	13.00 ± 1.46 (K)		
	Mean longevity of the female		
Nf	18.50 ± 2.24 (A)	18.88 ± 0.40 (B)	17.63 ± 1.16 (C)
ANfm	5.88 ± 0.95 (D)	6.75 ± 0.59 (E)	6.25 ± 0.70 (F)
ANff	9.50 ± 1.28 (G)	11.38 ± 1.48 (H)	10.00 ± 0.46 (I)
Dfm	2.13 ± 0.23 (J)		
Dff	2.25 ± 0.25 (K)		

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Table 5

Results of the statistical analyses of the data

Combinations	Significance: Fecundity				Significance: Longevity			
	IARI strain	Ajmer strain	Ajmer male × IARI female	IARI male × Ajmer female	IARI strain	Ajmer strain	Ajmer male × IARI female	IARI male × Ajmer female
1	2	3	4	5	6	7	8	9
A & B	NS	NS	NS	NS	NS	NS	NS	NS
A & C	NS	NS	NS	NS	*	**	NS	NS
A & D	**	**	**	**	**	NS	**	**
A & E	**	**	**	**	**	NS	**	**
A & F	**	**	**	**	**	NS	**	**
A & G	**	*	**	**	NS	NS	**	**
A & H	**	*	**	**	NS	NS	**	*
A & I	**	*	**	**	NS	NS	**	**
A & J	**	**	**	**	**	**	**	**
A & K	**	**	**	**	**	**	**	**
B & C	NS	NS	NS	NS	NS	**	NS	NS
B & D	*	**	**	**	**	NS	*	**
B & E	*	**	**	**	**	**	*	**
B & F	*	**	**	**	**	**	**	**
B & G	NS	**	**	**	NS	NS	NS	**
B & H	NS	**	**	**	NS	NS	*	**
B & I	NS	**	**	**	NS	NS	*	**
B & J	*	**	**	**	**	**	**	**
B & K	*	**	**	**	**	**	**	**
C & D	**	**	**	**	**	**	*	**
C & E	**	**	**	**	**	**	*	**
C & F	**	**	**	**	**	**	**	**
C & G	**	*	*	**	NS	**	*	**
C & H	**	*	*	**	NS	**	*	**
C & I	**	*	*	**	**	**	*	**
C & J	**	**	**	**	**	**	**	**
C & K	**	**	**	**	**	**	**	**
D & E	NS	NS	NS	NS	NS	NS	NS	NS
D & F	NS	NS	NS	NS	NS	NS	NS	NS
D & G	**	*	NS	NS	**	NS	NS	*
D & H	*	**	NS	*	**	NS	NS	**
D & I	**	*	*	*	**	NS	NS	**
D & J	**	**	**	**	NS	**	**	**
D & K	**	**	**	**	NS	**	**	**
E & F	NS	NS	NS	NS	NS	NS	NS	NS
E & G	**	NS	NS	NS	**	NS	NS	NS
E & H	*	**	NS	*	**	**	NS	*
E & I	**	NS	NS	*	**	*	NS	**
E & J	**	**	**	**	**	**	**	**
E & K	**	**	**	**	**	**	**	**
F & G	**	NS	NS	NS	**	*	NS	*
F & H	*	**	*	*	**	**	NS	**
F & I	**	NS	*	**	**	**	NS	**
F & J	*	**	**	**	**	**	**	**

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Table 5 (continued)

1	2	4	5	6	6	7	8	9
F & K	*	**	**	**	**	*	**	**
G & H	*	NS	NS	NS	NS	NS	NS	NS
G & I	**	NS	NS	NS	NS	NS	NS	NS
G & J	**	**	**	**	**	**	**	**
G & K	**	**	**	**	**	**	**	**
H & I	NS	NS	NS	NS	NS	NS	NS	NS
H & J	**	**	**	**	**	**	**	**
H & K	**	**	**	**	**	**	**	**
I & J	**	**	**	**	**	**	**	**
I & K	**	**	**	**	**	**	**	**
J & K	NS	NS	NS	NS	NS	NS	NS	NS

NS = Not Significant
** Significance at 1% level
* Significance at 5% level

Fecundity

A consolidated account of the data on the fecundity of the three generations of the crosses and the inbred forms is given in Table 6.

Table 6

Consolidated account of the fecundity of three successive generations of the two strains and the crosses between them

Type of development	Strain or cross	First generation	Second generation	Third generation
Nf	IARI strain	185.38 ± 21.91	209.88 ± 70.77	180.50 ± 20.79
	IARI male × Ajmer female	239.88 ± 24.17	226.75 ± 9.61	238.13 ± 6.37
	Ajmer male × IARI female	128.25 ± 21.58	138.88 ± 19.65	145.63 ± 33.83
	Ajmer strain	41.13 ± 1.85	48.50 ± 3.27	48.50 ± 4.90
ANfm	IARI strain	33.38 ± 4.59	34.13 ± 5.20	34.75 ± 8.90
	IARI male × Ajmer female	55.63 ± 10.79	65.13 ± 5.16	57.25 ± 5.08
	Ajmer male × IARI female	34.38 ± 5.12	37.00 ± 7.90	34.38 ± 3.66
	Ajmer strain	21.88 ± 2.48	25.13 ± 2.09	24.13 ± 2.09
ANff	IARI strain	116.25 ± 5.60	74.00 ± 14.10	79.63 ± 6.23
	IARI male × Ajmer female	85.25 ± 12.34	88.25 ± 9.30	85.00 ± 5.73
	Ajmer male × IARI female	50.00 ± 6.54	49.63 ± 5.12	51.63 ± 4.92
	Ajmer strain	31.63 ± 3.71	35.38 ± 2.10	32.13 ± 3.57
Dfm	IARI strain	10.13 ± 2.09	No defective forms procured	
	IARI male × Ajmer female	12.13 ± 1.51		
	Ajmer male × IARI female	4.63 ± 0.86		
	Ajmer strain	2.00 ± 0.19		
Dff	IARI strain	10.38 ± 1.68	No defective forms procured	
	IARI male × Ajmer female	13.00 ± 1.46		
	Ajmer male × IARI female	5.38 ± 0.53		
	Ajmer strain	3.00 ± 0.87		

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Normal parasites (*Nf*):

It is seen from Tables 1—4, and 6 that the parasites from the cross IARI male × Ajmer female have the highest fecundity in all the generations. The next best result is shown by the IARI strain; this is followed by the Ajmer male × IARI female; the Ajmer strain has the least fecundity. Within the same strain or cross no significant difference in the mean fecundity of the three generations has been observed (Table 5).

Apparently normal female that develops with apparently normal male (*ANfm*): Here again the maximum fecundity has been observed in the IARI male × Ajmer female, and it is about one-third to one-fourth that of *Nf* (of IARI male × Ajmer female). The Ajmer male × IARI female shows the next best reproductive capacity, the fecundity being one-third to one-fourth that of *Nf*. This is followed by the IARI strain with a fecundity of one-sixth to one-fifth that of *Nf*. The least fecundity is obtained in the Ajmer strain, and it is about half that of *Nf*.

Within the same strain or cross there is no significant difference in fecundity from generation to generation. However, the reduction from all the three generations of *Nf* is significant at 1% level in both the crosses and in the Ajmer strain. In the IARI strain, the reduction from the first and third generations of *Nf* is significant at 1% level, while the reduction from the second generation is significant at 5% level only.

Apparently normal females that develop together (*ANff*):

The IARI strain shows the highest fecundity in the first generation, but in the succeeding generations it has dropped down to less than that of any generation of the cross IARI male × Ajmer female. The difference in fecundity between the first and second generations is significant at 5% level, and between the first and third generations at 1% level; there is no significant difference between the second and third generations. The fecundity is less than that of *Nf*; the reduction in any generation from the first and third generations of *Nf* is significant at 1% level, while the reduction from the second generation is not significant at all. The fecundity is more than that of *ANfm*; the increase in the first and third generations is significant at 1% level, and in the second generation at 5% level.

In the IARI male × Ajmer female the difference in fecundity in the three generations is not significant. The fecundity is only one-third that of *Nf*, and the reduction is significant at 1% level. Although the fecundity is more than that of *ANfm*, the increase in the first generation is not statistically significant; the increase in the second generation is significant at 5% level; the increase in the third generation is significant at 5% level with the first and second generations, and at 1% level with the third generation of *ANfm*.

In the Ajmer male × IARI female the difference in the fecundity of the three generations is not significant. The fecundity is less than that of *Nf*, and is about one-third to two-fifths; the decrease from the first and second generations of

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Nf is significant at 1% level, while the decrease from the third generation is significant at 5% level only. The increase in fecundity from that of *ANfm* is not significant except in three instances, viz., between the third generation of *ANff*, and the first as well as third generation of *ANfm* (all at 5% level); and between the second generation of *ANff* and the third generation of *ANfm* (again at 5% level only).

In the Ajmer strain too there is no significant difference in the fecundity of the three generations. The fecundity is less than that of *Nf*; the difference from the first and third generations is significant at 5% level, while the difference from the second generation is significant at 1% level. The fecundity is more than that of *ANfm*; the increase in the second generation is significant at 1% level; the increase in the first and third generations from the first generation of *ANfm* is significant at 5% level, but the increase from the second and third generations of *ANfm* is not significant.

Defective female that develops with defective male (*Dfm*):

The maximum fecundity has been observed in the cross IARI male × Ajmer female. The IARI strain shows the next best fecundity, and is followed by the Ajmer male × IARI female and the Ajmer strain.

In the two strains and their crosses the fecundity is much less than that of *Nf*, *ANfm*, and *ANff*. The difference is significant at 1% level, except in two cases of the IARI strain (i. e., from the second generation of *Nf*, and from the third generation of *ANfm*) where the difference is significant at 5% level only.

(As the progeny of the first generation were not defective, observations on the fecundity of the succeeding generations were not made.)

Defective females that develop together (*Dff*):

Here again the maximum fecundity has been observed in the IARI male × Ajmer female. The fecundity of the IARI strain is a little less than that of IARI male × Ajmer female. The IARI strain is followed by the Ajmer male × IARI female, and the Ajmer strain.

The fecundity is much less than that of *Nf*, *ANfm*, and *ANff* in the two strains and their crosses. The statistical significance is the same as in *Dfm*. There is no significant difference between the fecundity of *Dfm* and *Dff* in any strain or cross.

(As in *Dfm* the progeny of the first generation were not defective, and hence observations on the succeeding generations were not made.)

Longevity

A consolidated account of the data on the longevity of the three generations of the inbred forms and their crosses is given in Table 7.

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Table 7

Consolidated account of the longevity of three successive generations of the two strains and the crosses between them

Type of development	Strain or cross	First generation	Second generation	Third generation
Nf	IARI strain	11.85 ± 1.17	9.13 ± 1.09	7.75 ± 0.75
	IARI male × Ajmer female	18.50 ± 2.24	18.88 ± 0.40	17.63 ± 1.16
	Ajmer male × IARI female	10.38 ± 0.94	9.25 ± 1.25	11.25 ± 2.11
	Ajmer strain	3.00 ± 0.33	3.75 ± 0.16	5.38 ± 0.32
ANfm	IARI strain	2.75 ± 0.37	3.38 ± 0.32	3.38 ± 0.26
	IARI male × Ajmer female	5.88 ± 0.95	6.75 ± 0.59	6.25 ± 0.70
	Ajmer male × IARI female	5.66 ± 0.80	5.25 ± 1.03	4.63 ± 0.32
	Ajmer strain	3.00 ± 0.33	2.50 ± 0.19	2.25 ± 0.25
ANff	IARI strain	9.63 ± 1.38	10.50 ± 1.45	10.75 ± 0.56
	IARI male × Ajmer female	9.50 ± 1.28	11.38 ± 1.48	10.00 ± 0.46
	Ajmer male × IARI female	5.88 ± 0.97	5.38 ± 0.46	5.38 ± 0.65
	Ajmer strain	3.13 ± 0.29	3.63 ± 0.26	3.38 ± 0.26
Dfm	IARI strain	2.14 ± 0.22	No defective forms procured	
	IARI male × Ajmer female	2.13 ± 0.23		
	Ajmer male × IARI female	1.38 ± 0.18		
	Ajmer strain	1.13 ± 0.13		
Dff	IARI strain	2.00 ± 0.19	No defective forms procured	
	IARI male × Ajmer female	2.25 ± 0.25		
	Ajmer male × IARI female	1.63 ± 0.18		
	Ajmer strain	1.50 ± 0.19		

Normal parasites (*Nf*):

The IARI male × Ajmer female shows the maximum longevity. This is followed by the Ajmer male × IARI female, the IARI strain, and the Ajmer strain. In the IARI strain the difference between the longevity of the first and third generations is significant at 5% level, and in the Ajmer strain the difference in the third generation from the first as well as the second generation is significant at 1% level (Table 5). In both the crosses of the strains there is no significant difference in the mean longevity of the three generations.

Apparently normal female that develops with apparently normal male (*ANfm*):

The maximum longevity is obtained in the IARI male × Ajmer female, and it is about a third of *Nf*. The Ajmer male × IARI female comes next, its longevity being about half that of *Nf*. This is followed by the IARI strain. The Ajmer strain has the least longevity.

There is no significant variation in the longevity of the three generations within the same strain or cross.

In the IARI male × Ajmer female, and in the IARI strain the longevity is much less than that of *Nf*, and the difference is significant at 1% level.

In the Ajmer male × IARI female the decrease in longevity from the first generation of *Nf* is significant at 1% level; the decrease from the second generation is significant at 5% level with the first and second generations, and at 1%

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level with the third generation; the decrease from the third generation is also significant at 5% level with the first and second generations, and at 1% level with the third generation.

In the Ajmer strain the difference in the longevity from the first generation of *Nf* is not significant at all; the difference from the second generation of *Nf* is not significant with the first generation, but significant at 1% level with the second and third generations; the difference from the third generation of *Nf* is significant at 1% level for all the three generations.

Apparently normal females that develop together (*ANff*):

The longevity of the IARI male × Ajmer female and the IARI strain is more or less the same. The longevity of the Ajmer male × IARI female is much less, while that of the Ajmer strain is the least.

No significant variation is observed in the longevity of the three generations, either in the inbred forms or in the crosses.

In the IARI male × Ajmer female the reduction in longevity from that of *Nf* is significant at 1% level in all cases except one, viz., the difference in the second generation from the first generation of *Nf*, and here the significance is at 5% level only. The increase in longevity from the first generation of *ANfm* is significant at 5% level for the first generation, and at 1% level for the second and third generations; the increase from the second generation of *ANfm* is not significant in the first generation, but is significant at 5% level for the second generation, and at 1% level for the third generation; the increase from the third generation of *ANfm* is significant at 5% level for the first generation, and at 1% level for the second and third generations.

In the Ajmer male × IARI female the decrease in longevity from the first generation of *Nf* is significant at 1% level; the decrease in the first generation of *ANff* from the second generation of *Nf* is not significant, while the decrease from the second generation of *Nf* is significant at 5% level in the second and third generations; the decrease from the third generation of *Nf* is also significant at 5% level in all the three generations. There is no significant difference between the longevity of any generation of *ANff* and any generation of *ANfm*.

In the IARI strain there is a significant difference between the longevity of the third generation of *ANff* and the longevity of the third generation of *Nf*. Here the significance is at 1% level. However, there is a marked increase in longevity from that of *ANfm*, and the increase is significant at 1% level in all cases.

In the Ajmer strain the difference in the longevity from the first and second generations of *Nf* is not significant, while the difference from the third generation is significant at 1% level. The increase in longevity from the first generation of *ANfm* is not significant in any generation; the increase from the second generation of *ANfm* is not significant in the first generation, but is significant at 1% level in the second generation, and at 5% level in the third generation; the increase from the third generation of *ANfm* is significant at 5% level in the first generation, and at 1% level in the second and third generations.

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Defective female that develops with defective male (*Dfm*):
The longevity of the IARI strain and IARI male × Ajmer female is more or less the same, while that of Ajmer male × IARI female, and Ajmer strain is a little less.

The decrease in the longevity from any generation of *Nf*, *ANfm*, and *ANff* is significant at 1% level in the Ajmer strain and in the two crosses. In the IARI strain the difference from the first generation of *ANfm* is not significant, but the difference from any generation of the other types of development is significant at 1% level.

(As the progeny of the first generation were not defective, observations on the longevity of the succeeding generations were not made.)

Defective females that develop together (*Dff*):
The longevity of the IARI male × Ajmer female is a little more than that of the two strains and the other cross.

In the two crosses the reduction in longevity from any generation of the first three types of development is significant at 1% level. In the IARI strain too the reduction is significant at 1% level except in one case, viz., from the first generation of *ANfm* and here the difference is not significant. In the Ajmer strain also the difference is significant at 1% level, except from the third generation of *ANfm*, where the reduction is significant at 5% level.

There is no significant difference between the longevity of *Dfm* and *Dff* in any strain or cross.

(As in *Dfm* the progeny of the first generation were not defective, and therefore observations on the succeeding generations were not made.)

Size

It is seen from the data given in Table 8 that when two parasites develop in an egg a reduction in size occurs. It is also noted that when apparently normal parasites develop together, and if they belong to the opposite sexes, then the male is larger than the female. If the parasites that develop together are two females, then each is slightly larger than the female that develops along with a male. If the parasites that develop together are two males, then the size of each is less than that of the male that develops along with a female.

Table 8
Effect of superparasitism on the size of the parasites

Type of development	Average length in mm (of eight observations)	
	Male	Female
Normal	0.4112	0.4189
Apparently normal male and female	0.3594	0.3267
Two apparently normal females		0.3612
Two apparently normal males	0.3232	
Defective male and female	0.3310	0.3103
Two defective females		0.3465
Two defective males	0.3275	

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The same observations hold good in the case of defective forms also.

It is interesting to note that the average size of the defective males that develop together is slightly more than that of the apparently normal males that develop together.

Conclusions and Discussion

It is evident from the data obtained during the course of the present investigation on the two strains of *Trichogramma evanescens minutum* and their crosses that *Trichogramma* that develops singly in the egg of *Corcyra cephalonica* has the maximum fecundity and longevity. It is also larger than those that develop together in a host egg. This is because it gets sufficient nourishment for the successful completion of the life cycle and emergence as a normal adult. Therefore, its reproductive capacity, longevity, and size are not impaired. It is also observed that there is no marked difference in fecundity and longevity from generation to generation if the development continues to be normal.

However, when two parasites develop together in an egg of *Corcyra cephalonica*, superparasitism occurs. If the two parasites that develop together are apparently normal females, then the fecundity, longevity, and size are much less than those of the normal parasites. The reduction in fecundity and longevity is continued without any significant variation from generation to generation if the development continues to be similar.

A further reduction in fecundity, longevity, and size is observed if two apparently normal parasites belonging to the opposite sexes develop in the same egg. The reduction in fecundity and longevity is maintained in the succeeding generations that develop similarly.

NARAYANAN & CHACKO (1957) have observed that when superparasitism occurs in *Trichogramma*, the fecundity is reduced and is much less than that of normal forms. The present observations too corroborate this view. Reduced fecundity as a result of superparasitism has been observed by ULLYETT (1945) in *Microbracon hebetor* SAY. It has been reported by SIMMONDS (1943) that the reproductive capabilities of *Nemeritis canescens* GRAVENHORST might be impaired when superparasitism occurs. The author's (1963, 1964) observation that superparasitism lowers the fecundity of *Bracon gelechiae* ASHMEAD may also be pointed out in this connection. He has also reported that in *Bracon gelechiae* no significant variation in fecundity and longevity occurs in successive generations, both when the development is normal and when superparasitism occurs. A similar observation has been made during the present investigation.

When two larvae of *Trichogramma* develop in an egg of *Corcyra cephalonica*, the amount of food available in the egg is shared by them, with the result that neither gets sufficient nourishment for the successful completion of the life cycle into a normal adult. This, undoubtedly, affects the fecundity, longevity, and size. It has been pointed out by SALT (1936), and by NARAYANAN & CHACKO (1957) that when superparasitism occurs in *Trichogramma evanescens* WEST-

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WOOD, and *Trichogramma evanescens minutum* respectively, the competition between the developing parasites for the available amount of food in the host egg appears to be the factor that inhibits the normal development of the parasites. In his studies on *Bracon gelechiae*, the author (1963, 1964) has observed that when superparasitism occurs the competition among the developing parasites for the available food inhibits the development of the parasite into normal forms.

A very important and interesting observation made during the present investigation is that when superparasitism occurs, and if the two parasites that emerge belong to the opposite sexes, then the fecundity is less than that of either of the two females that develop together in an egg. In both the cases two parasites emerge from one host egg, and they should have opportunity for an equal sharing of the available food, and the development of the females should have been alike. However, the development of the male along with the female brings about a reduction in the fecundity of the latter, as compared to the fecundity of either of the two females that develop together. Here it must be mentioned that, as a general rule, the males are smaller than the females in the Hymenoptera, and this appears to be so, to some extent, in the case of normally developed *Trichogramma*, as will be seen from the measurements given in Table 8. It is, therefore, easy to consider that the normal food requirement of males is somewhat less than that of females. However, when superparasitism occurs in *Trichogramma* with the development of two parasites, the females that develop together are larger than the female that develops along with a male (Table 8), which is quite contrary to the expectations under the above postulate. The inference that can be drawn from the above finding is that the males have a quicker rate of food intake than the females. Therefore, when a male and a female develop together, the quicker food absorption coupled with the lesser food requirement enables the male to complete the minimum nutritional requirement to become an adult, thus leaving little food for the female. Such a female does not get even as much nourishment as either of the two females that develop together. Hence its fecundity is less than that of the latter. Its longevity and size are also similarly affected.

SALT (1936) has observed that when superparasitism occurs in *Trichogramma*, and when the number of parasites feeding on the same host increases, there is a preponderance of males. The author's (1963, 1964) work on *Bracon gelechiae* also shows that more males than females complete development and emerge as adults when superparasitism occurs. In view of the dietary habit and requirement of males this is just what can be expected. In severe cases of superparasitism the developing larvae of *Trichogramma* go on sharing the available food, but the males absorbing quicker are able to complete their minimum requirement to become adults, and thus they leave no food for the females which may succumb. Probably this accounts for the preponderance of males when superparasitism occurs in *Trichogramma*.

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Whenever superparasitism occurs with the production of defectively formed adults, there is a highly significant reduction in the fecundity and longevity. Probably more than two parasite larvae share the food in a host initially, with the result that none gets enough nourishment to become even an apparently normal adult. Therefore, the fecundity, and longevity are very adversely affected. The progeny of the defective parasites appear to be normal, if their development is without superparasitism; NARAYANAN & CHACKO (1957) have also observed this phenomenon. However, further work is necessary to ascertain whether such parasites are actually normal.

In general it may be remarked that the difference in the fecundity and longevity between the IARI and Ajmer strains appears to be due to the fact that the Ajmer strain was originally obtained from the eggs of *Chilo partellus,* whereas the IARI strain has been adapted for years to development in the eggs of *Corcyra cephalonica.* This is substantiated by the fact that in the succeeding generations of Ajmer strain the fecundity has increased, showing that from generation to generation the strain is getting more adapted to the new host (*Corcyra cephalonica*). This is also borne out by the trend in the increase in the longevity of the succeeding generations. This observation appears to corroborate MARCHAL's (1936) view that *Trichogramma* immediately on emergence from its host seems to have a very generalised conception of the host, and that the female's interest becomes restricted after she meets with a normal host similar to that from which it has emerged. However, this observation does not agree with that of HASE (1925) who has stated that when eight different host eggs are present simultaneously, no preference for any one is shown by *Trichogramma evanescens,* and that parasites bred from one species readily attack the eggs of all others.

It is noteworthy that when the cross is made between IARI male and Ajmer female, there is an increase in fecundity compared to that in which Ajmer male is crossed with IARI female. Bearing in mind that Ajmer strain has not become much adapted to the eggs of *Corcyra cephalonica* as the IARI strain, this may be interpreted as due to the male carrying the instinct towards the selection of the host rather than the female. It may be possible that if the original host of the Ajmer strain had been provided, the record of fecundity would have been the reverse, a fact which has to be borne out by further experimentation.

FISKE (1910) has shown that the combined reproductive capacity of two parasites that develop on a host large enough for one is much less than that of one developing under identical conditions. A similar observation has been made during the course of the present investigation. However, this does not hold good in the case of the Ajmer strain, probably because the later generations have become more adapted to the eggs of *Corcyra cephalonica.*

There is hardly any need to point out here that superparasitism is a very potent factor which determines the success or failure of the colonisation of *Trichogramma.* As has been mentioned earlier in this paper, a good deal of controversy exists as to the exact role that this parasite plays in the biological control of insect pests. It is clear from the data obtained during the present investi-

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gation that superparasitism brings about a marked reduction in the fecundity and longevity of *Trichogramma*. In the laboratory breeding of this parasite superparasitism invariably occurs, and when parasites emerging from superparasitised eggs are used for the control of insect pests, one cannot expect them to be of much value. Therefore, for the laboratory breeding of this parasite it is essential to develop a method whereby the incidence of superparasitism can be lessened, if not avoided altogether.

Results

1. The present work was undertaken to find out whether superparasitism affects the fecundity, longevity, and size of *Trichogramma evanescens minutum*.

2. *Trichogramma* that develop singly in the eggs of *Corcyra cephalonica* have the maximum fecundity, longevity, and size. There is no significant increase or decrease in the fecundity or longevity from generation to generation if the development continues to be normal.

3. When two parasites, either two females or a male and a female, develop in an egg of *Corcyra cephalonica*, superparasitism occurs adversely affecting the fecundity, longevity, and size. This reduction in fecundity and longevity is maintained without any significant variation in the succeeding generations, if the development continues to be similar.

4. The competition between the developing parasite larvae for the limited food appears to be the factor that inhibits the normal development.

5. If two parasites belonging to the opposite sexes emerge from an egg, then the fecundity longevity, and size of the female are less than those of either of the females that emerge from an egg.

6. The inference that is drawn is that the male has a quicker rate of absorption of nourishment in the larval stages, and this coupled with its lesser food requirement enables it to complete the development leaving little food for the female. Such a female does not get even as much nourishment as either of the two females that develop together. Hence the reduction in its fecundity, longevity, and size as compared to the latter.

7. In severe cases of superparasitism the quicker food absorption by the males results in the elimination of the females, thus accounting for the preponderance of males.

8. When defective forms are produced as a result of superparasitism, there is a highly significant reduction in fecundity and longevity.

9. It is suggested that the difference in fecundity between the IARI strain and the Ajmer strain is probably due to the fact that the latter which was obtained from the eggs of *Chilo partellus* has not become quite adapted to the eggs of *Corcyra cephalonica* which is the laboratory host.

10. There is an indication of increased fecundity and longevity in the succeeding generations of the Ajmer strain showing that the parasites are getting more adapted to the eggs of *Corcyra cephalonica*.

11. The experiments with the two strains and their crosses indicate that the instinct towards the selection of host is transmitted through the male parent.

12. The combined fecundity of two parasites that develop in an egg of *Corcyra cephalonica* is less than that of one developing in an egg.

13. It is suggested that a method should be developed whereby the incidence of superparasitism may be lessened or altogether avoided in the laboratory breeding of *Trichogramma*.

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Summary

When superparasitism occurs in *Trichogramma evanescens minutum* there is a reduction in fecundity, longevity, and size. If two parasites belonging to the opposite sexes emerge from a superparasitised egg of *Corcyra cephalonica*, then the fecundity, longevity, and size of the female are less than those of either of the females that emerge from an egg. It appears that the male has a quicker rate of absorption of nourishment in the larval stages, and this coupled with its lesser food requirements enables it to complete the development, leaving very little food for the female. In severe cases of superparasitism the quicker food absorption by the males results in the elimination of the females, thus accounting for the preponderance of males. When defective forms are produced as a result of superparasitism, there is a further reduction in fecundity and longevity.

Zusammenfassung

Wenn bei *Trichogramma evanescens minutum* Hyperparasitismus auftritt, gehen Fruchtbarkeit, Lebensdauer und Größe zurück. Wenn zwei Parasiten verschiedenen Geschlechts aus einem hyperparasitierten Ei von *Corcyra cephalonica* schlüpfen, sind Fruchtbarkeit, Lebensdauer und Größe des Weibchens geringer als die eines Weibchens, das mit einem anderen Weibchen aus einem Ei schlüpft. Anscheinend zeichnet sich das Männchen in den Larvenstadien durch eine schnellere Nahrungsaufnahme aus, die es ihm in Verbindung mit seinem geringeren Nahrungsbedarf ermöglicht, seine Entwicklung zu vollenden und dem Weibchen sehr wenig Nahrung zu lassen. In schweren Fällen von Hyperparasitismus führt die schnellere Nahrungsaufnahme der Männchen zur Beseitigung der Weibchen, was das Überwiegen der Männchen erklärt. Wenn infolge von Hyperparasitismus verkümmerte Formen entstehen, sind Fruchtbarkeit und Lebensdauer noch geringer.

Резюме

Если у *Trichogramma evanescens minutum* возникает гиперпаразитировка, то тогда уменьшается плодотворность, продолжительность жизни и величина. Если две паразиты разного пола из одного гиперпаразитированного яица *Corcyra cephalonica* вылупиваются, тогда плодотворность, продолжительность жизни и величина самки более маленьки чем у самки, которая вместе с другой самкой вылупивалась из одного яица. Очевидно выявляют самцы в личиночной фазе более быстрое питание, которое ими позволяет, вместе с более низким употреблением пищи, быстрее окончить развитие и для самки останется очень мало пищи. В серьёзных случаев гиперпаразитизма это приводит к удалению самок, это и объясняет тогда высокую долю самцов. Если впоследствии гиперпаразитизма возникают недоразвитые формы, тогда плодотворность и продолжительность жизни ещё ниже.

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