EXPERIMENTAL STUDIES IN INSECT PARASITISM

IV. THE EFFECT OF SUPERPARASITISM ON POPULATIONS OF *TRICHOGRAMMA EVANESCENS*

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(With One Text-figure)

INTRODUCTION

It was shown in the second paper of this series (Salt, 1934 *b*) that the chalcid parasitoid *Trichogramma evanescens* is able to distinguish healthy hosts from those already parasitised, and that it tends to avoid ovipositing in the latter. It was further demonstrated that when all the hosts available have been already attacked, the parasite is able, at least for a time, to retain its eggs rather than deposit them in parasitised hosts.

In that paper attention was largely confined to a demonstration of the discriminative ability and of the restraint of the parasite from the point of view of behaviour. The present paper traces the effect of these two abilities on the reproduction of the parasite; considers them, that is, from the point of view of parasite populations.

The material and methods used in these studies have been fully described elsewhere (Salt, 1934 *a*), and only a brief outline need be given here. The adult *T. evanescens*, a minute hymenopteron, lays its own eggs inside the eggs of other insects, especially moths. From the parasite egg hatches a larva which feeds on the contents of the host egg and, when full-fed, pupates in the now empty egg-shell of its host. Ten days (at 25° C.) after the parasitic attack, the parasite progeny is fully developed, bites its way through the shell of its host, and emerges as an adult insect. It is to be noticed that the developing parasite is confined to the host in which it was placed by the ovipositor of its parent. Should food run short, the larva is unable to leave that host to find more.

The eggs of some moths are large enough to provide nourishment for several parasites; but those of *Sitotroga cerealella*, the only host used in the present study, can support only one, rarely two. Most *Sitotroga* eggs containing two eggs of *Trichogramma*, therefore, and all containing three or more, are said to be superparasitised.

When a host is superparasitised some or all of the parasite progeny are insufficiently nourished, are unable to complete their development, and die. It has been shown before (Salt, 1934 *b*, p. 472), that when two, three, or perhaps even four *Trichogramma* eggs are laid in one egg of *Sitotroga*, the competition that ensues among the parasite progeny for possession of the host leads to the victory and ultimate emergence of one of them. It will be shown below, however, that when a host is heavily superparasitised (as many as 19 *Trichogramma* eggs have been found in 1 egg of *Sitotroga*) the too fierce competition of the parasite progeny for food may lead to the death of them all, so that neither host nor parasite emerges in the next generation. It is with the occurrence and the effect of superparasitism of this sort that the present paper deals.

THE EXERCISE AND FAILURE OF RESTRAINT

As far as is yet known, the discriminative ability of *Trichogramma* is perfect—the insect appears always to be able to distinguish parasitised from unparasitised hosts. Its restraint, however, is not perfect, and when the number of hosts is limited the parasite sometimes lays more than one egg in a single host. The occurrence of superparasitism, then, is chiefly due to the failure of restraint.

In order to understand the occurrence of superparasitism, therefore, and its effect upon the populations of both the parasite and its host, it is first necessary to consider the conditions under which restraint is exercised and those under which it fails. How far females of *Trichogramma* can restrain themselves from committing superparasitism, when the number of hosts available is small, is well shown by the following series of experiments.

Groups of 1, 2, 3, ..., 10 *Sitotroga* eggs were fastened on graph paper, 1/10 in. apart, in such a manner that each group could be covered separately by a small glass container, $\frac{3}{8}$ in. across and $\frac{1}{4}$ in. deep. A female *Trichogramma*, 2–4 hours old, was placed on each group, and the dish was put in the incubator at 25° C. for 8 hours. The parasites were then removed and the hosts were examined microscopically for parasite eggs. Control females were placed in standard dishes of 100 hosts for the same period and their progeny allowed to develop. The experiment was repeated 10 times.

Since these experiments were intended to deal with cases of enforced superparasitism, those in which the parasite laid fewer eggs than the number of hosts available were considered incomplete. The results of ten completed experiments are given in Table I.

The 10 control females placed in standard dishes parasitised a total of 225 hosts. It must be supposed, therefore, that on the average each of the females used in the experiment likewise had 22·5 eggs to deposit. But none of them laid nearly so many. Eight of them, indeed, having only one host available laid only 1 egg each, less than 5 per cent. of their supply; 6 of those confined with only 2 hosts laid only 2 eggs each; and so on. The restraint exercised by these isolated females in 8 hours, then, was very considerable.

Table I. *Result of exposing* 1, 2, 3, ..., 10 *eggs of* Sitotroga *to* 1 *female* Trichogramma *for* 8 *hours* (10 *experiments at each number*)

No. of hosts exposed	No. of hosts containing...eggs					Total no. of hosts	Total no. of parasite eggs	% of hosts super-parasi-tised	Average no. of eggs per host	Average no. of eggs laid per female
	0	1	2	3	4					
1	—	8	—	1	1	10	15	20	1·5	1·5
2	1	13	4	1	1	20	28	30	1·4	2·8
3	—	26	3	1	—	30	35	13	1·2	3·5
4	—	27	7	6	—	40	59	33	1·5	5·9
5	—	38	3	3	6	50	77	24	1·5	7·7
6	1	39	12	3	5	60	92	33	1·5	9·2
7	—	41	20	7	2	70	110	41	1·6	11·0
8	1	56	19	4	—	80	106	29	1·3	10·6
9	1	71	14	4	—	90	111	20	1·2	11·1
10	—	69	25	5	1	100	138	31	1·4	13·8

Further than this, the experiment shows that the ability to refrain from oviposition is not an absolute ability, merely enabling the parasite to limit itself to a certain number of ovipositions in a certain time; but a relative ability, enabling the parasite to adjust its oviposition to the number of hosts available. The proportion of hosts superparasitised did not increase as the number available decreased, but remained fairly constant between 20 and 33 per cent. The number of parasite eggs placed in each host did not increase as the number of hosts decreased, but varied slightly about an average of 1·4. There appear to be two possible explanations of these figures: either that the restraint is inversely proportional to the oviposition stimulus received from a varying number of hosts; or that the parasite considers about 27 per cent. of *Sitotroga* eggs large enough to receive two of its own eggs. This is a matter of behaviour, and will receive attention in a later paper. The explanation does not matter here, where we are concerned merely with the fact.

From this series of experiments, then, it may be concluded: (1) that *Trichogramma* females in the presence of a limited number of hosts are able to restrain themselves to the deposition of as few as 5 per cent. of their available eggs for a period of at least 8 hours; (2) that the degree of restraint is not fixed but is proportional to the scarcity of hosts.

The restraint demonstrated in the foregoing experiments was maintained through a period of only 8 hours. It might be supposed that after a longer time the restraint might break down and the available hosts be much more heavily superparasitised. To investigate this possibility groups of 5 and of 10 *Sitotroga* eggs were placed on graph paper as in the preceding experiment, and each exposed to a parasite for 24 hours. Control groups were exposed for only 8 hours. The hosts were then microscopically examined for parasite eggs. Control females were placed in standard dishes for 8 and 24 hours and their progeny allowed to develop. One experiment in which the parasite died before the expiration of the 24 hours was not counted. Five experiments were completed with the results shown in Table II.

Table II. *Result of exposing* 5 *and* 10 *eggs of* Sitotroga *to* 1 *female* Trichogramma *for* 8 *hours and for* 24 *hours* (*total of* 5 *experiments*)

No. of hosts exposed	Period of exposure	No. of hosts containing...eggs									Total no. of parasite eggs	% of hosts superparasitised	Av. no. of eggs per host	Av. no. of eggs laid per female
		0	1	2	3	4	5	6	7	8				
5	8 hours	—	17	8	—	—	—	—	—	—	33	32	1·3	6·6
	24 hours	—	9	11	1	1	—	1	—	2	60	64	2·4	12·0
10	8 hours	1	35	10	4	—	—	—	—	—	67	28	1·3	13·4
	24 hours	—	22	18	8	2	—	—	—	—	90	56	1·8	18·0

The control females in standard dishes laid an average of 24·2 eggs in 8 hours and 28·8 eggs in 24 hours.

The parasites confined for 24 hours had, on the average, 28·8 eggs to lay; but those confined for that period with 5 hosts restricted themselves to an average of 12 eggs, and those having 10 hosts available to 18 eggs. Restraint, then, was exercised over the period of 24 hours. But the increased period did lead the parasites to commit more superparasitism. Twice as many of the hosts were superparasitised in 24 hours as in 8 hours; and the intensity of the parasitism (the average number of parasite eggs laid in a host) rose from 1·3 to 2·4 eggs per host when 5 hosts were available and from 1·3 to 1·8 when 10 were present.

It may be concluded that, although *Trichogramma* does continue to exercise restraint for 24 hours, more superparasitism occurs in that period than in only 8 hours.

In the preceding experiments a single parasite was isolated with each group of hosts and left to attack them undisturbed. It would appear likely that if several parasites were placed with each group of hosts a greater amount of superparasitism might be produced. In the following experiments groups of 5 and 10 *Sitotroga* eggs were exposed to 5 fertilised female *Trichogramma* for 8 hours. Control groups (the same as in the preceding experiments, with which these were simultaneously performed) were exposed to only 1 parasite. The hosts were then microscopically examined for parasite eggs. The results of five such experiments are summarised in Table III.

Table III. *Result of exposing* 5 *and* 10 *eggs of* Sitotroga *to* 1 *female and to* 5 *females of* Trichogramma *for* 8 *hours* (*total of* 5 *experiments*)

No. of hosts exposed	No. of parasites	No. of hosts containing...eggs												Total no. of parasite eggs	% of hosts superparasitised	Av. no. of eggs per host	Av. no. of eggs laid per female
		0	1	2	3	4	5	6	7	8	9	10	11				
5	1	—	17	8	—	—	—	—	—	—	—	—	—	33	32	1·3	6·6
	5	—	6	6	2	3	2	2	1	1	2	—	—	91	76	3·6	3·6
10	1	1	35	10	4	—	—	—	—	—	—	—	—	67	28	1·3	13·4
	5	—	23	12	5	4	2	—	1	2	—	—	1	122	54	2·4	4·9

A great increase in the proportion of hosts superparasitised and in the intensity of parasitism is at once apparent. Both were more than doubled in the 5-host groups and nearly doubled in the 10-host groups. Nevertheless, great restraint was exercised, since an average of only 3·6 or 4·9 eggs was laid by each parasite although, judging from the control females in standard dishes, they had 24·2 to lay. It is of interest that the average number of eggs laid by each parasite was smaller when 5 were present than when the parasites were isolated (see below, p. 374). What is chiefly important at this point, however, is the fact that many of the hosts exposed to 5 parasites were excessively superparasitised, containing 8, 9, and as many as 11 parasite eggs.

This series of experiments, then, shows clearly that when several parasites instead of only one are confined with a small number of hosts for 8 hours, restraint is still exercised—indeed, individual restraint may be greater—but, nevertheless, superparasitism is greatly increased and some of the hosts are excessively superparasitised.

THE EFFECTS OF SUPERPARASITISM

In the experiments described above several eggs of *Trichogramma* were sometimes laid in a single egg of *Sitotroga*. What happens in such cases directly affects the number of parasites that emerge in the next generation, and so is of great importance to the whole problem of parasite populations. This experimental study must now be interrupted, therefore, by a descriptive interlude relating what does happen to superparasitised hosts.

If the *Sitotroga* egg is of ordinary size and only 2, 3, or perhaps 4 parasite eggs were laid in it, the parasite progeny compete for the host with the result that one wins sole possession, is able to complete its development, and emerges as an adult parasite. If the *Sitotroga* egg is very large there may be enough food for two parasites out of three or four competing, and such a host may produce two normal though rather small adults. It must be supposed, however, that the competition weakens even the victorious contestants, for sometimes the two that emerge from a superparasitised large host or the one that comes from a superparasitised small host are so small and weak that they remain "walkers", their wings, though present, never becoming expanded. Sometimes they are so very minute and so weak that they move about feebly for only a short time and then die. One of the first signs of superparasitism, as the density of the parasites is increased, is the appearance of these "walkers" in the cultures.

The same weakening of the contestants explains the occurrence in superparasitised cultures of hosts which blacken normally and give every sign of producing a parasite, but from which no *Trichogramma* emerges. In some cases such hosts are found to contain fully developed adult parasites which died without being able to emerge; in other cases they contain a parasite pupa which died before transforming to an adult.

Finally, excessively superparasitised hosts turn dark and shrivel without ever seeming likely to produce a parasite. Their appearance is quite different from that of dead unparasitised hosts. These latter retain their cream or pink colour; those which shrivel as a result of superparasitism turn brown or blackish and in the majority of cases can be distinguished with certainty from ordinary dead hosts. This effect is produced by the death of all the parasite progeny in the larval stage. In very heavily superparasitised hosts, so much nourishment is used by the several competitors before any one of them obtains full possession that there is not enough food left for the victor, and it dies beside the others before completing its larval development. Hosts of this category are described in the following pages as "black shrivelled".

These, then, are the visible indications of superparasitism: appearance of "walkers"; black eggs giving no emergents; and black shrivelling of the hosts. It is impossible, of course, to link each of these conditions to a definite degree of superparasitism, so much depends upon the size of the host and accidents of the competition between the parasites; but in general they probably occur in the above order as the degree of superparasitism increases.

THE EFFECTS OF DENSITY ON POPULATIONS OF *TRICHOGRAMMA*

Foregoing experiments have shown that an increased density of parasites causes a failure of restraint and therefore an increased amount of superparasitism. The observable effects of that superparasitism have been described in the preceding section. With these data in hand it is possible to attack directly one of the principal questions of the population problem—to determine the effect of increasing densities of parasites on the population both of their host and of their own species.

In the following experiments 0, 1, 5, 10, 25 and 50 fertilised female parasites respectively were placed for 8 hours at 25° C. in standard dishes, each containing 100 *Sitotroga* eggs fastened to 1/10 in. apart in 1 sq. in. of the surface. Since the number of hosts emerging and the sex of the parasite progeny were to be noted, particular care was taken to obtain standard animals. The hosts were in every case *Sitotroga* eggs 0–24 hours old. The parasites, from the pure *Sitotroga*-strain, were fertilised females 2–4 hours old at the beginning of the experiment. The results were noted on the 6th and 9th days and finally recorded on the 14th day, these being the best times to count the parasitised hosts, the hosts that escaped, and the number and sex of the parasite progeny, respectively.

Table IV. *Summary of experiments to show the effect of increasing density of parasites upon the population of the host and of the parasite*

Density of parasites per 100 hosts	Hosts escaped and gave larvae	Hosts died and gave neither larvae nor parasites	Hosts parasitised and gave parasite progeny	No. of parasite progeny	Sex ratio of parasite progeny (males in 100)
0	93·6	6·4	0	—	—
1	71·5	6·9	21·6	21·6	22·4
5	6·9	8·9	84·2	84·4	25·5
10	1·7	15·9	82·4	83·3	32·3
25	0·3	29·5	70·2	75·5	45·3
50	0·1	73·7	26·2	29·8	56·2

Each density of parasites was tested ten times so that the whole series of experiments involved 60 dishes. The results, which are detailed in Table V so that the data can be critically examined, agree very closely; and amply justify a discussion based on the averages. These are brought together for ready comparison in Table IV.

The number of hosts that escaped parasitisation and emerged as larvae steadily decreased as the density of parasites increased. This was to be expected. Indeed, the principal interest lies in the opposite point of view—the failure of the parasite to annihilate its host completely and regularly even at very high densities. Ten parasites capable of distributing 217 eggs and able to avoid superparasitism might

Table V. *Detail of experiments to show the effect of increasing density of parasites upon the population of the host and of the parasite*

Exp.	Larvae emerged	Hosts shrivelled	Hosts turned black	Black eggs not emerged	Black eggs gave parasites	No. of parasites emerged	Sex of parasite progeny		
							♂	♀	?
				No parasites					
1	88	12	0						
2	89	11	0						
3	91	9	0						
4	91	9	0						
5	92	8	0						
6	95	5	0						
7	95	5	0						
8	97	3	0						
9	98	2	0						
10	100	0	0						
Total	936	64	0						
				1 parasite					
1	73	9	18	0	18	18	5	13	—
2	68	14	18	0	18	18	5	13	—
3	78	2	20	0	20	20	4	16	—
4	79	1	20	0	20	20	4	16	—
5	71	9	20	0	20	20	4	16	—
6	73	6	21	0	21	21	4	15	2
7	72	6	22	0	22	22	4	18	—
8	68	9	23	1	22	22	5	17	—
9	65	9	26	0	26	26	7	19	—
10	68	3	29	0	29	29	6	23	—
Total	715	68	217	1	216	216	48	166	2
				5 parasites					
1	4	17	79	2	77	78	17	61	—
2	11	9	80	0	80	80	14	66	—
3	15	4	81	0	81	81	30	51	—
4	7	11	82	2	80	80	28	52	—
5	8	9	83	1	82	82	16	66	—
6	4	9	87	1	86	86	30	56	—
7	5	8	87	1	86	87	23	64	—
8	6	4	90	3	87	87	20	67	—
9	7	1	92	1	91	91	20	71	—
10	2	5	93	1	92	92	17	75	—
Total	69	77	854	12	842	844	215	629	—

Table V (*cont.*)

Exp.	Larvae emerged	Hosts shrivelled	Hosts turned black	Black eggs not emerged	Black eggs gave parasites	No. of parasites emerged	Sex of parasite progeny		
							♂	♀	?
				10 parasites					
1	0	25	75	2	73	75	23	52	—
2	4	16	80	3	77	77	24	53	—
3	7	11	82	3	79	79	23	56	—
4	0	15	85	1	84	86	28	58	—
5	0	14	86	3	83	83	31	52	—
6	3	11	86	3	83	83	25	58	—
7	1	12	87	5	82	84	31	53	—
8	1	11	88	2	86	87	22	65	—
9	1	11	88	2	86	87	30	57	—
10	0	8	92	1	91	92	32	59	1
Total	17	134	849	25	824	833	269	563	1
				25 parasites					
1	0	37	63	14	49	51	21	30	—
2	0	34	66	4	62	68	36	32	—
3	0	33	67	8	59	64	35	29	—
4	0	24	76	8	68	78	40	38	—
5	0	21	79	5	74	77	28	49	—
6	0	20	80	5	75	77	32	45	—
7	1	18	81	4	77	79	32	47	—
8	0	19	81	1	80	89	44	45	—
9	2	16	82	6	76	81	36	45	—
10	0	14	86	4	82	91	38	53	—
Total	3	236	761	59	702	755	342	413	—
				50 parasites					
1	0	86	14	6	8	10	8	2	—
2	0	81	19	6	13	14	2	12	—
3	0	71	29	6	23	26	14	12	—
4	0	70	30	5	25	31	17	14	—
5	1	67	32	5	27	31	20	11	—
6	0	66	34	7	27	30	14	16	—
7	0	65	35	10	25	29	18	11	—
8	0	61	39	4	35	39	22	17	—
9	0	60	40	3	37	40	16	18	6
10	0	55	45	3	42	48	33	15	—
Total	1	682	317	55	262	298	164	128	6

be expected to parasitise all of 100 hosts; but in more than half the experiments at this density a few hosts were allowed to escape. At a density of 25 parasites, and even at the excessive concentration of 50 parasites, one or two hosts survived. True, this did not happen in several, but only in one or two of the experiments. Nevertheless, it appears that even with a sense enabling them to avoid superparasitism, even operating in a very restricted space with all the hosts freely exposed to them, even at a very high concentration of their numbers, the parasites cannot be depended upon always to destroy all of the available hosts.

At the higher densities of parasites, the number of hosts that shrivelled without producing either host larvae or parasite progeny increased. A certain proportion (6·4 per cent.) of hosts shrivelled even in the absence of parasites. This proportion was slightly raised, perhaps not significantly, at concentrations of 1 and 5 parasites; but at the higher concentrations of 10, 25 and 50 parasites it increased greatly and progressively. The increase was accompanied by the appearance of "black shrivelling" described above. At a concentration of 10 parasites there was 6·1 per cent. of this "black shrivelling" as well as 7·3 per cent. of apparently normal shrivelling; at 25 parasites there was more; and at 50 parasites most of the hosts came into this category. A great increase in the number of hosts that produce neither host larvae nor parasite progeny, then, is one of the important results of superparasitism resulting from too high a density of parasites.

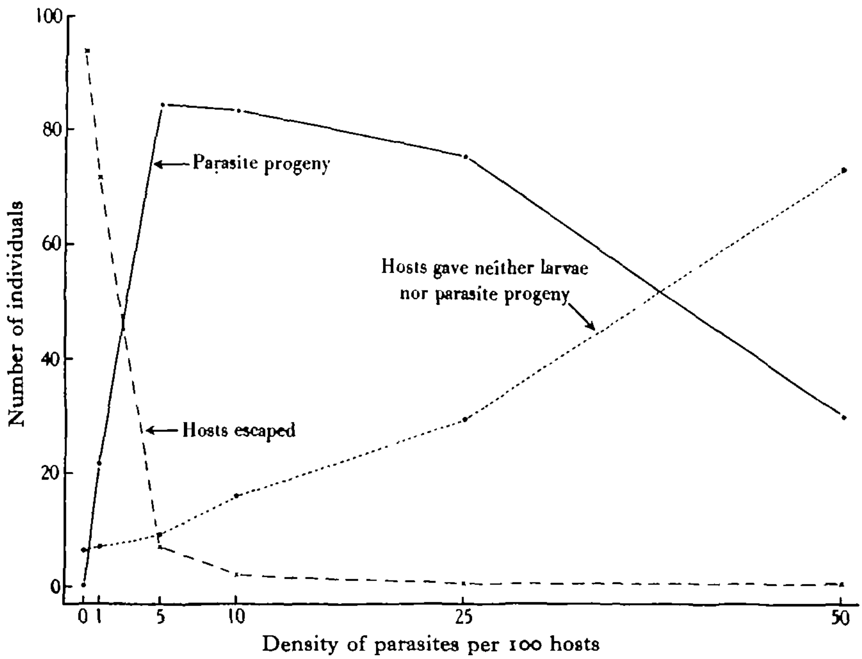

Fig. 1. Graph showing the effect of increasing density of parasites upon the population of the host and of the parasite (data of Table IV).

As a result of the effect of superparasitism pointed out in the preceding paragraph, the number of parasites that emerge in the next generation does not increase steadily as the density is increased; but reaches a maximum and then falls (Fig. 1). The maximum number of emergents in these experiments, 84·4 from 100 hosts, was obtained at that concentration of parasites (5) which was potentially capable of attacking a number of hosts (108) nearest to the number actually available. This follows logically from the parasites' ability to distinguish and avoid already parasitised hosts. Fewer parasites could not exploit all the hosts; more would be forced to commit superparasitism and so to destroy their own progeny. The falling off in the number of progeny is slow at first; slight when the number of parasites is twice too many, and not great when it is five times too many. This is probably an expression of the restraint of the parasites. But finally, at a concentration of ten times as many parasites as necessary, superparasitisation becomes rife even if each parasite restrains itself to 1/10 of its capacity, and serious superparasitism and loss results.

These three points—the steady decrease in the number of hosts surviving, and yet the occasional escape of some; the progressive increase in the number of hosts that produce neither larvae nor parasites; and the fact that the number of parasite progeny quickly reaches a maximum and then falls off as the density of parasites is increased—are the most important results of this experiment. But there are some minor results of considerable interest still to be pointed out.

Considering first the reproductive rate of the individual parasites, the average number of progeny per female can be obtained from Table IV by dividing the total number of progeny (fifth column) by the original number of parasites (first column). It was 21·6 at a density of 1 parasite per 100 hosts, but only 16·9 at 5, 8·3 at 10, 3·2 at 25, and 0·6 at 50. The average number of progeny per female, then, declined steadily as the density of parasites increased.

The occurrence of "walkers" (individuals that emerge, but are stunted and fail to develop their wings properly) was mentioned above as being a sign of superparasitism. In these experiments none appeared at densities of 1 or 5 parasite per 100 hosts; but there were, on the average, 1·5 per dish at a density of 10, 5·0 at 25, and 3·9 at 50. The proportion of walkers among the emergents, therefore, was 0 at concentrations of 1 and 5, 1·8 per cent. at 10, 6·6 per cent. at 25, and 13·1 per cent. at 50 parasites per 100 hosts. There is, then, a steady increase in the proportion of walkers among the progeny as the density of parasites is increased.

The number of hosts that produced two parasites increased as the density of parasites increased. The difference between the fourth and fifth columns of Table IV shows that at a concentration of 1 parasite 0 host, of 5 parasites 0·2 host, of 10 parasites 0·9 host, of 25 parasites 5·3 hosts, and of 50 parasites 3·6 hosts per dish produced 2 parasites. When these figures are calculated as proportions of the hosts that produced parasites at all, we have 0, 0·2, 1·1, 7·5 and 13·7 per cent. of the hosts that produced parasites at concentrations of 1, 5, 10, 25 and 50 parasites respectively, producing 2. These figures are similar to those given in the preceding paragraph for the number of walkers, and suggest that here, as is usual, chiefly walkers emerged from the hosts that produced two parasites.

Finally, a very interesting effect of superparasitism on the sex ratio of the progeny is shown by this series of experiments. The sex ratio of the progeny at a density of 1 female per 100 hosts was 22·4 males in 100 emergents. This figure is quite normal, being within 1 per cent. of the average sex ratio of the strain, known from very numerous experiments not yet published. As shown in Table IV, the proportion of males rose steadily as the density of parasites increased, becoming 25·5 per cent. at 5, 32·3 per cent. at 10, 45·3 per cent. at 25, and 56·2 per cent. at 50 parasites per 100 hosts.

From this series of experiments, then, it may be concluded that, as the density of parasites attacking a fixed number of hosts in a limited space is increased, (1) the number of hosts that escape steadily decreases; (2) the number of hosts that die without yielding either hosts or parasites steadily increases; (3) the total number of parasite progeny reaches a maximum and then decreases; (4) the number of progeny of the individual parasites steadily decreases; (5) an increasing proportion of the emergents are imperfectly developed; (6) an increasing proportion of the emergents are males. It is also to be noted that (7) even at very high densities of parasites, some hosts occasionally escape.

DISCUSSION

The discriminative ability and the restraint of *Trichogramma evanescens*, demonstrated in an earlier paper of this series, are again clearly exhibited in the present study. In all the experiments described in the second section above, it is plain that the parasites did not distribute their eggs at random, but had regard to the selection of hosts that had not previously been parasitised. The same experiments show the restraint of individual parasites during 8 and 24 hours, and of several parasites together during 8 hours, to be very considerable. Of the existence of these two faculties, then, and of their importance in the reproduction of the parasite, there can be no doubt. Nevertheless, in spite of these two safeguards, superparasitisation occurs. The principal contribution of this study is its analysis of the effect on populations of the parasite when superparasitism does occur.

The most important effect is the absolute reduction of the parasite population. Five females, capable of depositing 108 eggs, succeeded in rearing 84·4 progeny when 100 hosts were available to them; but 50 females, capable of distributing 1080 eggs, reared only 29·8 progeny on the same number of hosts. Moreover, the alteration of the sex ratio to an increasing proportion of males, most of which were unnecessary for the fertilisation of so few females, makes an even greater difference in the reproductive value of the parasite progeny. The number of emergents fell from a maximum of 84·4 to only 29·8; but the number of female emergents fell even more steeply from 62·9 to only 12·8. Further than this, owing to the appearance of walkers and perfectly developed but small individuals, the average size and vigour and probably, therefore, the fecundity of the emergents was reduced. The 62·9 female progeny produced at the maximum were all full-sized individuals, probably capable of normal reproduction. Of the 12·8 females produced at the highest density, 0·4 were walkers, incapable of reproduction at all, 0·3 others were recorded as "tiny", and still others were small. Owing to superparasitism, then, the number of parasite progeny effective in reproduction was reduced in these experiments from 63 to something less than 12.

That the parasites should waste a large part of their reproductive ability when hosts are too few and they lack an opportunity to deposit all their eggs, might go without saying. This would be only a relative loss, if the available hosts were so exploited as to yield the maximum number of parasite progeny. But the actual loss is greater than this. When the density of parasites is very high, owing to the failure of their restraint and the consequent superparasitism, that is, through the activities of the parasites themselves, an environment capable of yielding a certain number of parasite progeny is so exploited that it produces fewer. This absolute loss is the most important effect of superparasitism on the parasite population.

The steady decline in the average number of progeny produced per female as the density is increased (p. 372 above), is clearly similar to the density effect obtained by Pearl and Parker (1922) with populations of *Drosophila*, Park (1932) with *Tribolium*, and Maclagan (1932) with *Calandra*. The present result extends the demonstration of this effect to a parasitic organism. In all these cases, the final effect is the resultant of at least two factors: the effect of adult density on the fecundity of the ovipositing females; and the effect of larval density on the survival of the progeny. In *Drosophila*, Pearl (1932) has analysed the former factor; but the latter does not seem to have received separate investigation. In *Trichogramma*, reduction of fecundity at a higher density of parasites is indicated on p. 367 and in Table III; and mortality due to larval competition is illustrated throughout the preceding discussion.

The alteration of the sex ratio of the progeny as the density of parasites increased calls for further mention. *Trichogramma* is, of course, capable of arrhenotokous parthenogenesis; but care was taken to use fertilized females in these experiments, and both the normal sex ratio of the progeny of the isolated females, and the gradually increasing proportion of male progeny commencing from that perfectly normal figure, preclude any likely explanation based on the exercise of parthenogenesis. The effect, therefore, is probably due to the survival of the males when larvae of the two sexes are in competition. In the terms of H. S. Smith (1929) the males appear to be "intrinsically superior".

No claim is made, of course, that these results apply to any organism other than *Trichogramma*; but there is no reason to suppose that *Trichogramma* is extraordinary in these matters, and it is possible that similar results might be obtained in other cases. To this extent the group of numerically important and quantitatively unpredictable results exhibited in these experiments should give pause to those who still think to solve the problems of parasite and host relations on paper by mathematical speculation.

SUMMARY

Trichogramma evanescens is able to distinguish healthy from parasitised hosts, and when few hosts are available can restrain itself for 8 hours to the deposition of 5 per cent. of its available eggs.

As far as is yet known, the discriminative ability is perfect; but the restraint is limited and, in a longer period of time or when several parasites are together, it breaks down and superparasitism occurs.

When the superparasitism is slight and only two or three eggs are laid in a host, the competition between the parasite progeny leads to the victory and emergence of one; but when it is severe either a dwarfed or imperfectly developed individual or none at all emerges.

As the density of parasites in a fixed population of hosts is increased, more and more superparasitism occurs, and the following effects on the populations are observed:

(1) The number of hosts that escape steadily decreases; but even at high densities of parasites some hosts occasionally escape.

(2) The number of hosts that die without yielding either hosts or parasites steadily increases.

(3) The number of parasite progeny reaches a maximum and then decreases.

(4) The number of progeny of the individual parasites steadily decreases.

(5) An increasing proportion of the emergents are imperfectly developed.

(6) An increasing proportion of the emergents are males.

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