

Long-term egg retention and parasitization in *Trichogramma principum* (Hym., Trichogrammatidae)

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Abstract: Laboratory experiments with *Trichogramma principum* Sug. et Sor. females that were offered *Sitotroga cerealella* Oliv. eggs demonstrated that less than half of the ovipositing females started oviposition during the first 2 days of the experiment, whereas the rest of the ovipositing females showed a delay in parasitization ranging from 2 to 10 days after contact with the host. Almost 10% of the wasps refused to parasitize the grain moth eggs over 12 days. The delay in parasitization may be as long as 6–8 days without any significant decrease in the number of mature ovarian eggs, in the number of eggs laid during the first 48 h of oviposition, and in the total lifetime fecundity. This egg retention is responsible for the fact that in spite of a relatively short mean duration of the oviposition period in each individual female (approximately 4 days), host parasitization by a group of simultaneously emerged wasps was almost uniformly distributed over 8–10 days. When induced, the parasitization state (i.e. the tendency to parasitize sequentially offered portions of host eggs) was stable both in the presence of a host and under host deprivation extended up to 8 days. These data provide further evidence for our hypotheses that the stability of the parasitization state in *Trichogramma* is based on endocrine mechanisms.

1 Introduction

The oviposition behaviour of insect parasitoids is commonly considered as a sequence of stimulus–response reactions (VINSON, 1985; VAN ALPHEN and VET, 1986). Each host species is characterized by the combination of positive and negative stimuli received by the parasitoid from the host. However, lesser positive stimuli may cause a response if motivation to oviposit is high, whereas reduced motivation could raise the threshold of acceptance. Numerous investigations have revealed an apparent genetic variability in parasitization behaviour in various parasitoids including *Trichogramma* (VINSON, 1985; SMITH and HUBBES, 1986; VAN BERGEIJK et al., 1989; WAJNBERG et al., 1989; WAJNBERG, 1993; BRUINS et al., 1994; SMITH, 1996; BJORKSTEN and HOFFMANN, 1998a). The non-heritable modifications of parasitization behaviour are also important (BARTON BROWNE, 1993). For instance, a higher egg-load (higher number of mature eggs in the gonads) usually results in higher motivation to oviposit, i.e. in higher intensity and/or in broader selectivity of parasitism (DE JONG and PAK, 1984; PAK et al., 1985; COLLINS and DIXON, 1986; MANGEL, 1989; TRUDEAU and GORDON, 1989; VÖLKL and MACKAUER, 1990; ROSENHEIM and ROSEN, 1991; MINKENBERG et al., 1992; BJORKSTEN and HOFFMANN, 1998a). Learning may change the acceptance of a particular host (KLOMP et al., 1980; GROSS et al., 1981; VINSON, 1985; VAN ALPHEN and VET, 1986; GODFRAY and WAAGE, 1988; KAISER et al., 1989a,b; VET and GROENEWOLD, 1991; BJORKSTEN and HOFFMANN, 1995; KERGUÉLEN and CARDÉ, 1996; BJORKSTEN and

HOFFMANN, 1998a,b). In some insects, an advanced age causes females to lower the threshold of acceptance (COURTNEY, 1989).

The present paper concerns individual non-heritable variation in the parasitization behaviour in *Trichogramma*, an egg parasitoid that is not only widely used for inundative biocontrol, but also represents a convenient object for laboratory investigations on insect physiology and behaviour. It has repeatedly been reported that some host species were readily accepted for oviposition by certain *Trichogramma* females, whereas the other females of the same strain delayed parasitization or even permanently refused to parasitize the same host (SOROKINA, 1978; ZASLAVSKIY and MAY FU KVI, 1982; SMITH and HUBBES, 1986; HOHMANN et al., 1988; FLEURY and BOULÉTREAU, 1993; PAVLIK, 1993; SCOTT et al., 1997; BJORKSTEN and HOFFMANN, 1998a,b).

For some years, our specific approach has been to study the reaction of *Trichogramma* females to a poor quality host (near the lower threshold of acceptance). This method reveals minute behavioural variations, because all reactions are usually more variable in the neighbourhood of a threshold. We studied the parasitization of eggs of the grain moth, *Sitotroga cerealella* Oliv. by various *Trichogramma* species. At present, the same host–parasitoid combination has been advantageously used, for example by BJORKSTEN and HOFFMANN (1998a,b). We have shown that females that refused to parasitize *Sitotroga* eggs carried a high number of mature ovarian eggs, but the usual sequence of behavioural reactions resulting in parasitization was interrupted at the stage of arrestment and host

recognition, suggesting that refusal to oviposit may be considered as egg retention. The mean number of eggs laid during the first 48 h of oviposition was the same when the parasitization was delayed until the third day of life of the female. As for *Trichogramma* females that accepted *S. cerealella* eggs, they appeared to maintain a relatively stable 'parasitization state' when sequentially offered two different portions of the host eggs during 4 days (2 days per portion). This stability suggested that egg retention when a suitable host is available might be considered not as a simple behavioural reaction, but rather as a sort of diapause-like state in which it is not oogenesis, but oviposition that is subject to hormonal regulation (REZNIK and UMAROVA, 1990, 1991; REZNIK et al., 1997, 1998). However, this conclusion was derived from relatively short-run (4 days) experiments and so a longer study (comparable to the average lifetime of *Trichogramma* females) was required.

The aims of the present study were: (i) to estimate the stability of the parasitization state in *Trichogramma* females kept over a long period of time with and without host eggs; and (ii) to investigate the influence of the long-term 'voluntary' egg retention on the number of mature ovarian eggs and on further fecundity.

In spite of their poor quality, *S. cerealella* eggs are still used for mass rearing of *Trichogramma* wasps in the republics of the former Soviet Union and in certain other countries (LAING and EDEN, 1990; SMITH, 1996). Therefore, the problem of 'refusing females' is also of practical importance.

2 Materials and methods

2.1 Insects and general methods

In all experiments, we used a laboratory strain of *Trichogramma principium* Sug. et Sor., which was collected in Chimkent district (Kazakhstan) from Noctuidae eggs and cultivated for more than 50 generations on the eggs of the grain moth, *S. cerealella*. All studies were conducted at 20°C under a light regime of 17 h light : 7 h dark. Young (less than 1-day-old) *T. principium* females were placed individually into small (40 mm × 5 mm) test tubes. Honey (50% aqueous solution) was streaked on the glass to feed the wasps. When required according to the design of the experiment, *S. cerealella* eggs were presented as a paper strip with 50–60 eggs pasted to it using non-toxic water-soluble glue. *Sitotroga cerealella* eggs are rather small. When they are offered in excess, *Trichogramma* oviposition usually results in the laying of a single egg per host. Therefore after completion of *Trichogramma* larvae development, the number of darkened eggs of the grain moth was taken to be the approximate number of *Trichogramma* eggs laid.

2.2 Experimental design

2.2.1 First experiment

Four replicates of the first experiment were conducted. At the beginning of each replicate, 180–200 *Trichogramma* females were offered young (1-day-old) host eggs and during

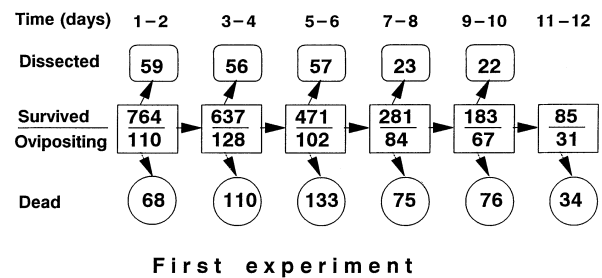


Fig. 1. The design of the first experiment. Number of surviving (among those ovipositing), dissected, and dead *T. principium* females is indicated for each period of the experiment

the next 12 days the host eggs were taken out of the test tubes every other day and a new supply of fresh host eggs was presented to each surviving female, i.e. six equal portions of the grain moth eggs were sequentially exposed and wasps were allowed to parasitize each portion during 2 days. The fecundity during each exposure was recorded for each female separately. At the end of each exposure, a proportion of the females (approximately 10% of surviving wasps) was dissected to determine the number of mature ovarian eggs. In addition 70 wasps (in each replicate, 15–20 females) were dissected shortly after their emergence (neither host nor honey were provided for these females). When estimating the percentage of ovipositing females and their fecundity, dissected females and also females occasionally lost or damaged during the experiment were excluded from consideration. Preliminary treatment of the results have showed that the differences between replicates were insignificant, and hence the data were summarized. Figure 1 shows the design of the first experiment and the number of surviving (among them ovipositing), dissected and dead females.

2.2.2 Second experiment

The second experiment included two 48 h periods of contact with host eggs with an interval of host deprivation inserted between the first and second exposure. During host deprivation, females were offered honey solution. In different variants of the second experiment, the host-deprivation interval lasted 0 (control), 2, 4, 6 or 8 days. To estimate the stability of the parasitization state, we used a special index $SP = [C/(C + F)] \times 100\%$, where C is the number of females that oviposited during both the first and second host exposure, and F is the number of females that oviposited only during the first host exposure. In total, more than 1000 wasps were studied in five replicates of this experiment, and the results were summarized. Females that died during the experiment, were excluded from consideration (the exact number of females used in each variant is shown in fig. 8).

2.3 Statistical analysis

The usual descriptive statistics (mean and SEM) was used for fecundity and number of ovarian eggs, and the Tukey HSD test with Tukey–Kramer adjustment was used to evaluate differences among the means. For the index of stability of parasitization state (SP), 95% approximate confidence intervals were calculated and Pearson χ^2 test was used to evaluate differences. All statistical procedures were calculated using SYSTAT (WILKINSON, 1990).

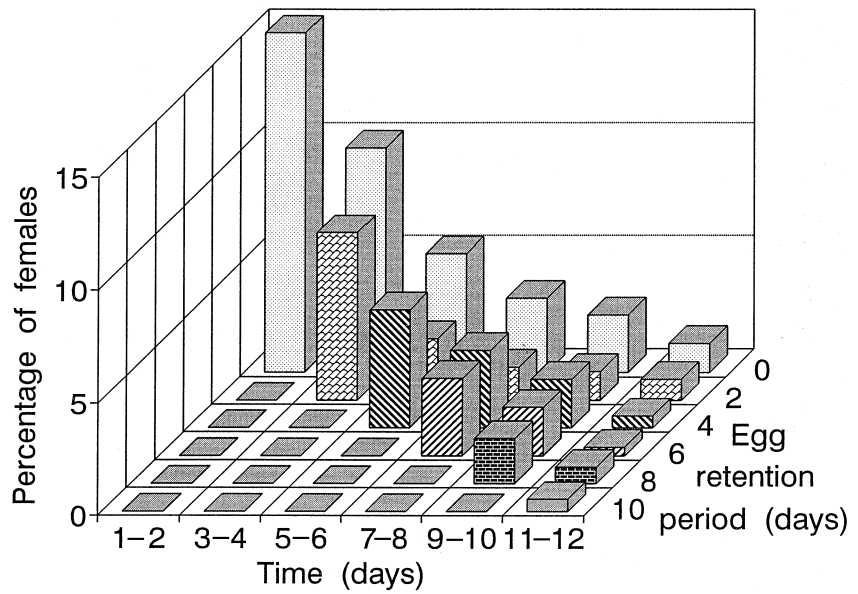


Fig. 2. The relationship between percentage of ovipositing *T. principium* females and time from the beginning of the experiment (total $n = 550$, the females were divided into six groups according to the duration of the egg retention period)

3 Results

3.1 First experiment

The first experiment showed that a lot of *T. principium* females refused to parasitize *S. cerealella* eggs over a long period of time or up to death. In particular, 54 females (almost 10% of non-dissected wasps) refused to parasitize grain moth eggs over 10–12 days (fig. 1). From fig. 2, where all ovipositing females are divided into six groups according to the duration of the egg retention period (i.e. delay in oviposition) it can be seen that 15% of wasps started oviposition during the first 2 days of the experiment. The rest of the ovipositing females showed a delay in parasitization, and some females never oviposited until 10 days of contact with the host.

On average, the oviposition period lasted approximately 4 days; however, the 10% of females that started oviposition during the first 2 days of the experiment continued oviposition over 12 days (fig. 3). The number of ovipositing females in each group gradually decreased almost independently of the duration of the delay period (fig. 2). Practically all of parasitizing females died shortly after the termination of the oviposition, and only 2% of them survived more than 2 days after the last parasitization.

The mean total lifetime fecundity of ovipositing females was 39.3 ± 1.7 eggs (fig. 4). It is noteworthy that the total lifetime fecundity was practically independent of the day when oviposition started (fig. 5, the Tukey test does not reveal any significant difference).

The mean number of eggs laid during the first 48 h of the oviposition was also independent of the day of the experiment when oviposition started (the difference is not significant by Tukey HSD test), whereas during the following days of oviposition the mean daily fecundity decreased gradually (fig. 6).

Dissection (fig. 7) showed that the mean number of mature ovarian eggs in refusing females slightly ($P = 0.045$, Tukey test) increased during first 2 days of egg retention and then did not vary significantly over the 8 days of life of the females, although after

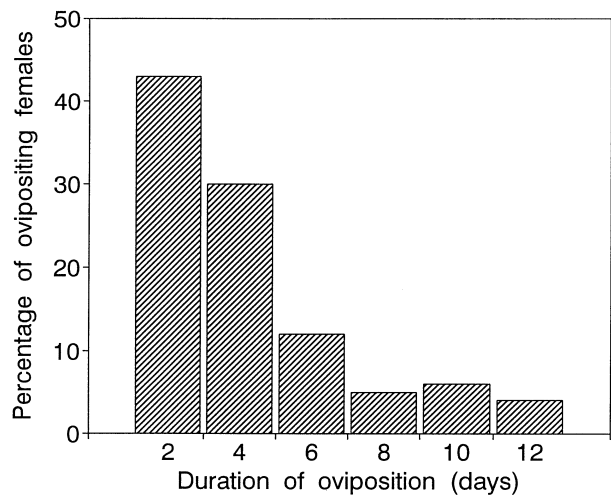


Fig. 3. Frequency distribution of *T. principium* females with different duration of oviposition period ($n = 189$)

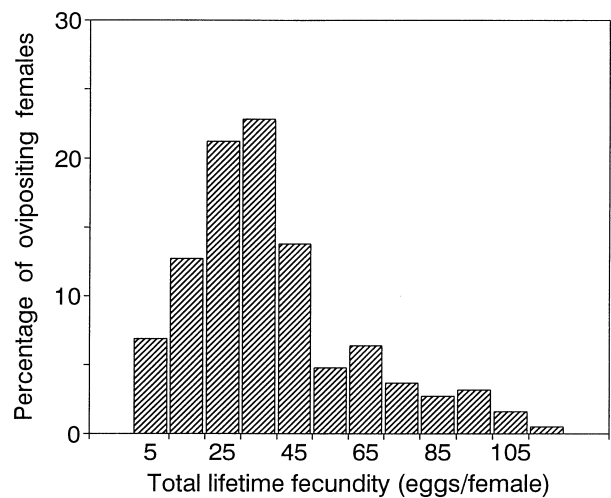


Fig. 4. Frequency distribution of *T. principium* females with different total lifetime fecundity ($n = 189$)

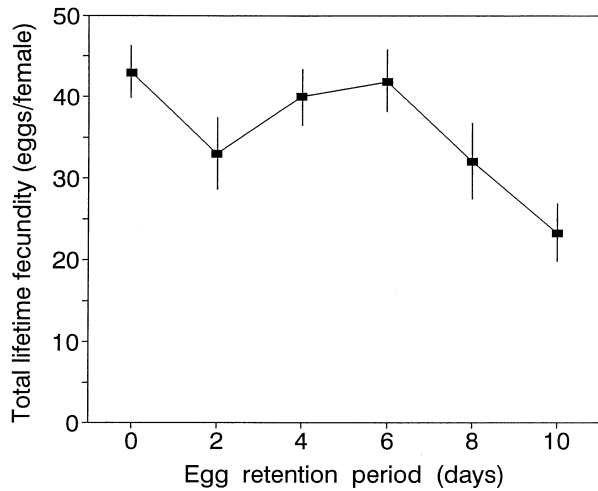


Fig. 5. The relationship between total lifetime fecundity of *T. principium* females and duration of the egg retention period (means \pm SEM are shown)

10 days of egg retention it was significantly ($P < 0.01$, Tukey test) lower than after 2–6 days. The mean number of eggs in the ovaria of ovipositing females was low over the whole course of the experiment. Females that had just started oviposition, had an intermediate number of ovarian eggs.

3.2 Second experiment

The second experiment (fig. 8) showed that most of females that parasitized at the first host exposure continued oviposition at the second host exposure. The duration of the host deprivation period did not influence the index of stability of parasitization state ($n = 426$, $\chi^2 = 3.95$, d.f. = 4, $P = 0.41$).

4 Discussion

In the first experiment (fig. 2), many of females that refused to oviposit during the first exposure started

oviposition 2–10 days later, as would be expected on the basis of our earlier published assumptions that their 'refusal' is a 'delay' in oviposition, namely an egg retention (REZNIK et al., 1997, 1998). Obviously, the process of egg retention might manifest itself as a delay of oviposition (when it is relatively brief) or as a refusal to oviposit (when it is longer than the experiment duration or even as long as the life of the wasp).

When induced, the 'parasitization state' was found to be much more stable than might be assumed, based on our previous short-term studies. In the first experiment, at 12 days of permanent contact with the host, egg retention only occurred in 2% of ovipositing females after a certain period of parasitization, whereas 98% of parasitizing females continued oviposition up to their death. Even after 8 days of host deprivation (the second experiment) the stability of the parasitization state was approximately 90%.

It is well known that oviposition experience may cause only gradual quantitative changes in a parasitoid behaviour, for example, a modification in the preference pattern or an increase in the host acceptance (KLOMP et al., 1980; GROSS et al., 1981; VINSON, 1985; EISENSTEIN and REEP, 1985; VAN ALPHEN et al., 1986; GODFRAY and WAAGE, 1988; VET and GROENEWOLD, 1991; PAPAJ and LEWIS, 1992; BJORKSTEN and HOFFMANN, 1995; KERGUÉLEN and CARDÉ, 1996; BJORKSTEN and HOFFMANN, 1998a,b). To our knowledge, a qualitative, highly persistent and practically irreversible imprinting comparable to the switch from egg retention to parasitization state described in this paper has never been reported in parasitoids.

However, the nervous system is only a part of the mechanism which controls the oviposition behaviour in insects. It is known that the responsiveness of insects to specific stimuli is modulated by endogenous factors (BARTON BROWNE, 1993). The egg-laying is subject to two forms of control, the nervous and the neuroendocrine. The endocrine control of oviposition has been confirmed by experiments conducted with different insect species (RAABE, 1986). Experiments described in the present paper provide additional convincing

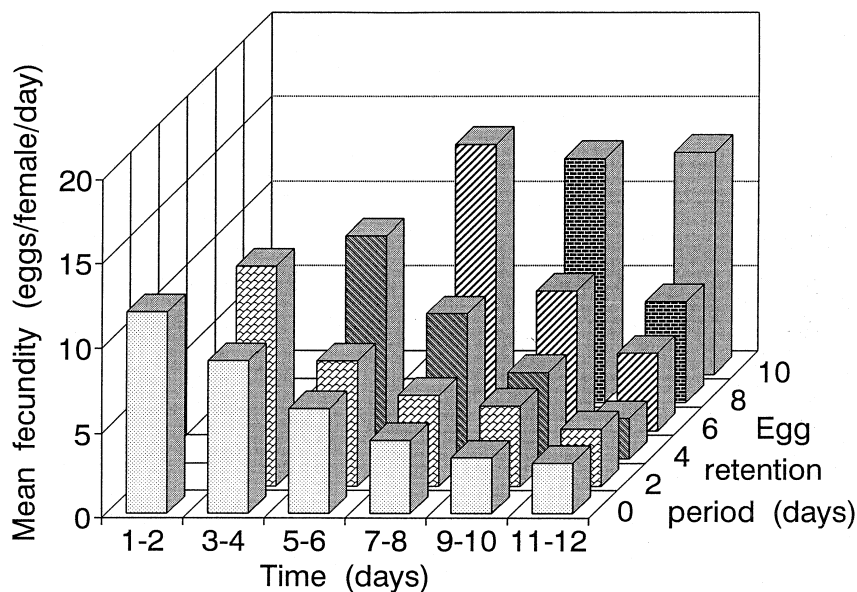


Fig. 6. The relationship between mean fecundity (eggs/day) of ovipositing *T. principium* females and time from the beginning of the experiment (total $n = 189$, the females are divided into six groups according to the duration of the egg retention period)

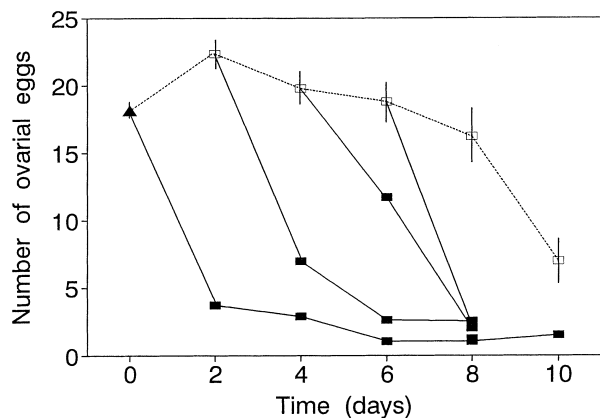


Fig. 7. The relationship between mean number of mature ovarial eggs in emerging (▲), refusing (□) and ovipositing (■) *T. principium* females and time from the beginning of the experiment (for clarity of presentation, SEM are not shown for ovipositing females). Solid lines indicate data related to females that started oviposition during the first host exposure, and after 2, 4, or 6 days of egg retention

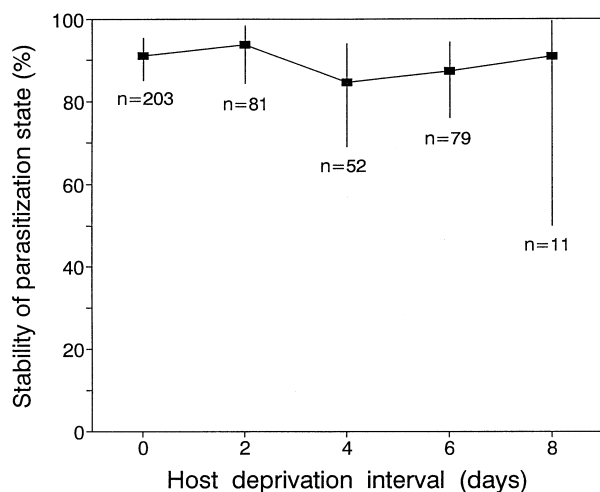


Fig. 8. The relationship between the index of stability of parasitization state (SP) in *T. principium* females and time of host deprivation (see Section 2.2.2. for the further explanations)

evidence of our previously published (REZNIK et al., 1997) hypotheses that the stability of the parasitization state in *Trichogramma* is based on neuroendocrine mechanisms. The precise mechanisms involved have still to be elucidated.

Refusal of and/or delay in oviposition has been recorded in different *Trichogramma* species (see Introduction). Delays in parasitization of less preferred hosts were observed in other parasitoids; for example, in two Chalcidae species (TEPEDINO, 1988). It is known that on emergence *Trichogramma* females have less drive to oviposit and a higher tendency to disperse than older females (KAISER et al., 1989a; SMITH, 1996; LUKIANCHUK and SMITH, 1997), which is a particular case of the 'reproduction – flight syndrome' (DINGLE, 1985).

Our data suggest that egg retention means that despite the relatively short mean duration of the oviposition period in each individual female (fig. 3), host parasitization by a group of simultaneously emerged wasps was almost uniformly distributed over 1 week (fig. 1). New females started oviposition as females that had oviposited from the beginning of the experiment died (fig. 2). Figures 5 and 6 show another important fact, namely that this long-term egg retention does not cause any significant reduction in fecundity. This dispersed-in-time oviposition obviously decreases the negative effect of unpredictable environmental changes and increases the chance that more suitable host species will be encountered. Generally speaking, the delayed oviposition can be considered as a particular case of the trade-off between current and future reproduction under egg-limited search (see ROSENHEIM, 1996 for discussion and further references).

The dynamics of the daily number of eggs laid by ovipositing *Trichogramma* females in our experiments (fig. 6) agree with other earlier publications: *Trichogramma minutum* and *Trichogramma chilonis* females had the highest rate of reproduction on the first day of oviposition when host eggs were unlimited (BAI and SMITH, 1993; MIURA and KOBAYASHI, 1995; WANG and SMITH, 1996), in *Trichogramma brassicae* and *Trichogramma nubilale*, some 50% of the eggs were laid during the first day of parasitization (FLEURY and BOULÉTREAU, 1993; OLSON and ANDOW, 1998). On average, *Trichogramma* females produced approximately 70% of their lifetime fecundity during the first 24 h of oviposition (CARRIÈRE and BOIVIN, 1997).

As has been mentioned in an earlier publication (REZNIK et al., 1997, 1998), the presence of a relatively high number of mature eggs in females that refused to oviposit (fig. 7) means that they have only stopped oviposition and not oogenesis. During the first 2 days of egg retention, the egg load increases owing to oogenesis, whereas after 8 days intensive oosorption occurred (fig. 7). The approximate equalities of the mean number of eggs laid during the first 48 h of oviposition (fig. 6) and of total lifetime fecundity (fig. 5) in females that started oviposition shortly after their emergence and in females that refused to parasitize over 6–8 days also suggest that the differences among these groups are only in the oviposition behaviour (not in the intensity of oogenesis).

It is concluded that even in long-term experiments the stability of the parasitization state (a tendency to continue parasitization when sequentially offered different portions of the host eggs) in *T. principium* was very high both in females kept with and without host eggs. In the latter case, the stability of the parasitization state was practically independent of the duration of the host deprivation period in the range up to 6–8 days. These results provide further support for the assumption that the parasitization state is based on endocrine mechanisms. 'Voluntary' delayed oviposition, namely egg retention manifested by *Trichogramma* females in the presence of a suitable, but not preferred, host does not cause intensive oosorption and/or consequent reduction of parasitization ability, at least

in the range up to 6–8 days of delay. This egg retention means that in spite of a relatively short mean duration of the oviposition period in each individual female (approximately 4 days), host parasitization by a group of simultaneously emerged wasps was almost uniformly distributed over 8–10 days.

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