

Effect of Experience on Response of *Trichogramma buesi* Voeg. and *T. principium* Sug. et Sor. (Hymenoptera, Trichogrammatidae) Females to Different Ages of Host Eggs

S. Ya. Reznik and N. P. Vaghina

Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199034 Russia

Received may 12, 2005

Abstract—Laboratory experiments have demonstrated that patterns of distribution of *T. principium* and *T. buesi* females by the number of mature ovarial eggs is strongly dependent on the age of the host (*Sitotroga cerealella*) eggs offered for parasitization. The approximate percentage of parasitizing females estimated from these distributions was 1.5–2 times higher for females offered young host eggs than for those offered “old” eggs, that had developed for six days at a temperature of 20°C. In both species, females more often oviposited in old (non-preferred) eggs when they had previously experienced fresh (preferred) eggs. This result contradicts the widely accepted assumption that in insect parasitoids, experience of parasitizing a preferred host decreases the probability of parasitizing a non-preferred host. One might expect that under natural conditions, a rather long time interval also precedes parasitization of less preferred host eggs by *Trichogramma* females, and duration of this interval may be also dependent on availability of other host species.

DOI: 10.1134/S0013873807010010

The host age (more correctly, the stage of the host embryo development) is one of the most important factors determining the specificity of egg parasitoids of the genus *Trichogramma* Westw. Usually, the percentage of parasitizing females, the number of hosts parasitized, the proportion of larvae completed their development, and the fecundity of emerging adults decrease with the host embryo development, although more complicated pattern of dependence was also recorded (Kochetova, 1969; Reznik and Umarova, 1985; Pak, 1986; Schmidt, 1994; Reznik et al., 1997; Olson, 1998; Monje et al., 1999; Honda and Luck, 2000).

Earlier (Reznik et al., 1997) we have demonstrated that the prior experience of parasitizing of freshly laid eggs of the Angoumois grain moth, *Sitotroga cerealella* Oliv. (Lepidoptera, Gelechiidae) by *Trichogramma principium* Sug. et Sor. females increased the probability of parasitization of “old” (i.e., developed during six days at 20°C) eggs of the same host species. This effect had not previously been observed in any other *Trichogramma* species. Moreover, just the opposite dependence was revealed in most of the studied insect parasitoids: the prior experience of parasitizing of a “good” host decreased the probability of a “bad” host acceptance (Vinson, 1985; Reznik, 1993; Turlings et al., 1993).

In the above experiments, parasitization by individual females was directly recorded, which was an exact but very time-consuming method. The present work was conducted with two *Trichogramma* species: *T. principium* and *T. buesi* Voeg. by the method of mass parasitization. The first aim of this study was to compare results obtained with the same species (*T. principium*) using two different methods. The second aim was to conduct the experiments with the other *Trichogramma* species, to ensure that the earlier observed effect was not unique property of the studied species.

MATERIALS AND METHODS

The experiments were conducted with the laboratory strains of *T. principium* and *T. buesi*, originated from females reared from Noctuidae eggs collected, correspondingly, in Chimkent Province (Kazakhstan) and in Saratov Province (Russia) and then reared during 15–20 years on the grain moth eggs. The insects were identified by Dr. E.S. Sugonyaev (Zoological Institute) and Dr. A.P. Sorokina (Institute of Plant Protection, St. Petersburg, Russia). Voucher specimens are stored in the insect collection of the Zoological Institute.

The mass parasitization method which was used in the present study was based on the fact that parasitiz-

ing females usually had in their oviducts much less eggs than those refusing to parasitize (Chumakova, 1968; Pak et al., 1985; Pavlik, 1993; Volkoff and Daumal, 1994; Bai et al., 1995; Reznik et al., 1998, 2001). This method, although it is not perfectly precise, was repeatedly used both for *Trichogramma* (Honda and Luck, 2000; Mansfield and Mills, 2002), and for other insect species (e.g., Veenstra and Byrne, 1998). Our previous studies have demonstrated the mean number of mature ovarian eggs in females parasitizing "old" eggs of the grain moth (9–10 eggs/female, depending on the treatment) was somewhat higher than that in females parasitizing young eggs (3–4 eggs/female), but still much lower than that in females refusing to parasitize (about 20–27 eggs/female). Based on the other research carried out with *T. principium* (Reznik et al., 1998) the threshold could be roughly estimated as 15 eggs/female. In the present study, this boundary is evident when the wasps refusing to parasitize constituted about half of the sample and the distribution became bimodal (Figs. 2 and 3, treatments O, O→O, O→→O).

The laboratory lines were reared and all experiments were conducted under constant conditions (20°C, L : D = 18 : 6). In each experiment, a standard sample of several hundred individuals emerged during the given day were placed in a glass test tube (3 cm in diameter, 10 cm in length). Honey (50% aqueous solution) was streaked on the glass to feed adults. The grain moth eggs glued to paper cards were offered to females according to the design of the experiment, the parasitoid : host ratio was about 1 : 20. In our experiments, we used "young" (stored at 20°C for no more than 1–2 days) and "old" (developing during 5–6 days at the same temperature) grain moth eggs.

If several portions of host eggs were sequentially provided, they were replaced simultaneously in all treatments of the experiment. At the end of each experimental period, a random sample of females was selected. These females were dissected, the number of mature eggs in their ovaries was counted, and the approximate percentage of parasitizing females in a sample was estimated from the frequency distribution of females by the number of mature eggs. Particular experimental designs and sample sizes are given below.

The experimental results are presented as frequency distributions of females over classes with a different number of mature ovarian eggs (Figs. 1–3). As the distribution patterns were not normal, the data were averaged with medians and quartiles and the signifi-

cance of differences was estimated by the Kolmogorov-Smirnov test. As mentioned above, the total proportion of individuals of the first 3 classes (less than 15 eggs/female) was taken for the approximate percentage of parasitizing females. All calculations were made using SYSTAT 10.2.

RESULTS AND DISCUSSION

The First Experiment

In the first experiment, females have no possibility to parasitize, as they were provided with carbohydrate food, but not with host eggs. On the 1st, the 3rd, the 4th, and the 5th day of the experiment (*T. buesi*) and on the 1st, the 3rd, and the 7th day of the experiment (*T. principium*) part of the females were dissected. On the 1st day of the experiment (Figs. 1A, 1D) emerging *T. principium* and *T. buesi* females had in their ovaries, correspondingly, 23 (19–28) and 24 (18–29) mature eggs (hereafter medians and quartiles are given). Similar results were obtained by various authors for different *Trichogramma* species: ca 15 mature ovarian eggs at emergence in *T. cacoeciae* Marchal, ca 20 eggs in *T. maidis* Pint. et Voeg., 30–40 eggs in *T. brassicae* Voeg. and in *T. evenescens* Westw. (Chumakova, 1968; Pak et al., 1985; Volkoff and Daumal, 1994). Note that in both species emerging females which had less than 10 eggs ready to be laid constituted no more than 5% of the sample. Thus, practically all the females were ready to parasitize several hours after emergence, as had been earlier demonstrated for many other *Trichogramma* species (e.g., Telenga and Shchepetilnikova, 1949; Sorokina, 1983; Rusnak, 1988; Takada et al., 2000). On the 3rd day of the experiment (Figs. 1B, 1E) the number of mature eggs in females which had no possibility to parasitize significantly ($p < 0.001$, Kolmogorov-Smirnov test) increased up to 34 (29–39) and 34 (28–39) in *T. principium* and in *T. buesi*, correspondingly, and then became stable (Figs. 1C, 1F–1G). An increase in the number of mature eggs was earlier shown for *T. platneri* Nagarcatti females deprived of the host during two days (Hohmann et al., 1988).

As seen from Figs. 1B, 1C, and 1E–1G, in spite of the increase in the average values, in certain females prevented from parasitization, the number of mature eggs is less than 15, although these females constituted not more than 5–7% of the sample. It is known (Raabe, 1986) that the presence of mature, but not yet laid eggs may inhibit vitellogenesis. Several authors (Flanders, 1942; Pak et al., 1985; Jervis and Kidd,

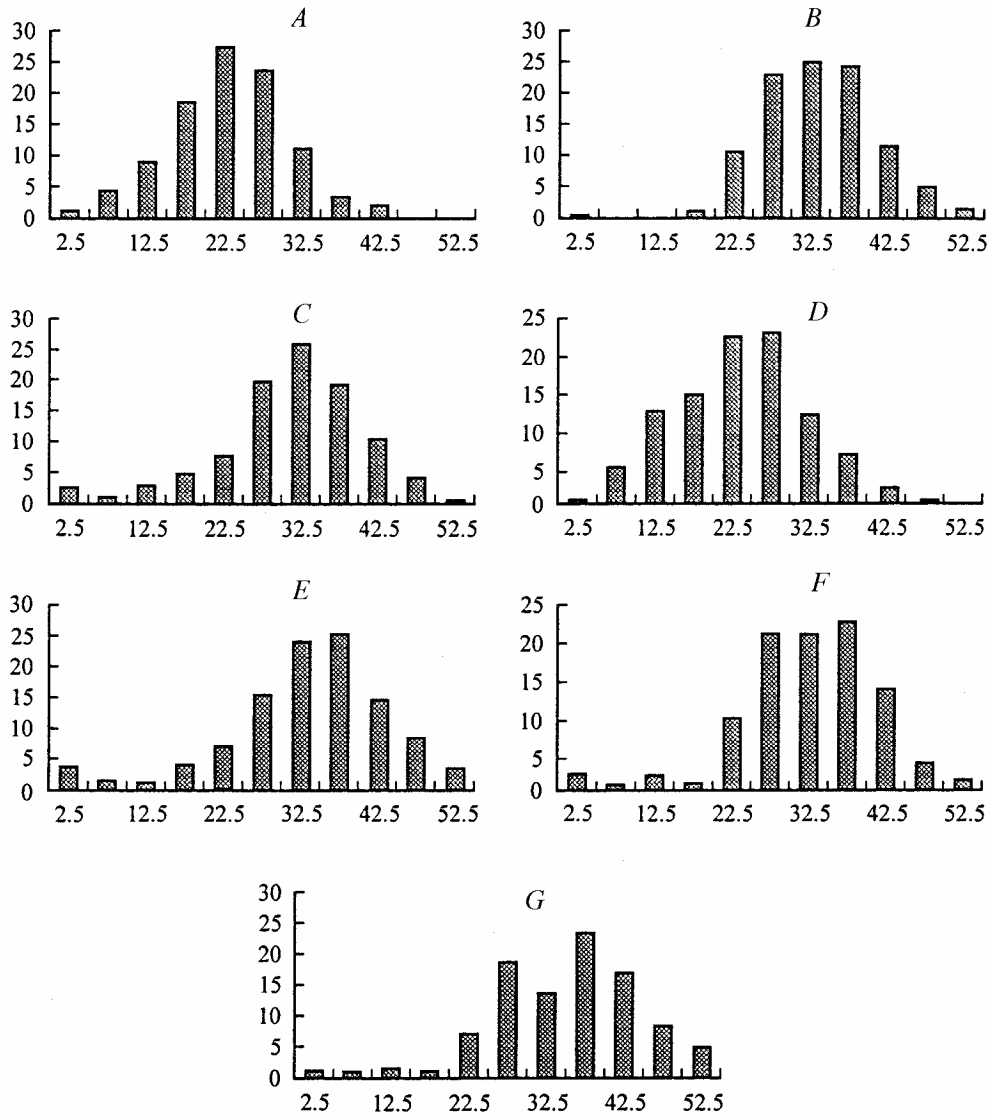


Fig 1. Distribution of *Trichogramma* females deprived of hosts by the number of the mature ovarian eggs. Abscissa: number of eggs (means for classes); ordinate: percentage of females. Age of females (in parenthesis, sample size is given): *Trichogramma principium*: (A) emerging ($n = 539$), (B) 3 days ($n = 317$), (C) 7 days ($n = 206$); *T. buesi*: (D) emerging ($n = 307$), (E) 3 days ($n = 278$), (F) 4 days ($n = 269$), (G) 5 days ($n = 245$).

1986; Fleury and Bouletreau 1993; Wang and Messing, 2003) suggested that in non-parasitizing females, the number of mature ovarian eggs is determined by the balance of two concurrent processes, i.e., oogenesis and oosorption. Thus, it is conceivable that the number of mature ovarian eggs gradually increases in females with predominating oogenesis and decreases in females with predominating oosorption.

The Second Experiment

Trichogramma principium. In the second experiment, females were provided with “young” and/or “old” grain moth according to a definite pattern. In

treatments “Y” and “O” (Fig. 2) *T. principium* females were offered, correspondingly, young or old host eggs during 48 h and then (on the 3rd day of the experiment) all females were dissected and the mature ovarian eggs were counted. In treatments “Y→A” and “O→A” the periods of contact with the host were the same, but the females were dissected on the 5th day of the experiment (during the 3rd and the 4th days the host eggs were absent). In treatments “Y→Y,” “Y→O,” “O→O,” and “O→Y” females were sequentially offered two portions of young or old host eggs in four possible combinations. Each portion was offered during 48 h and then (on the 5th day of the experi-

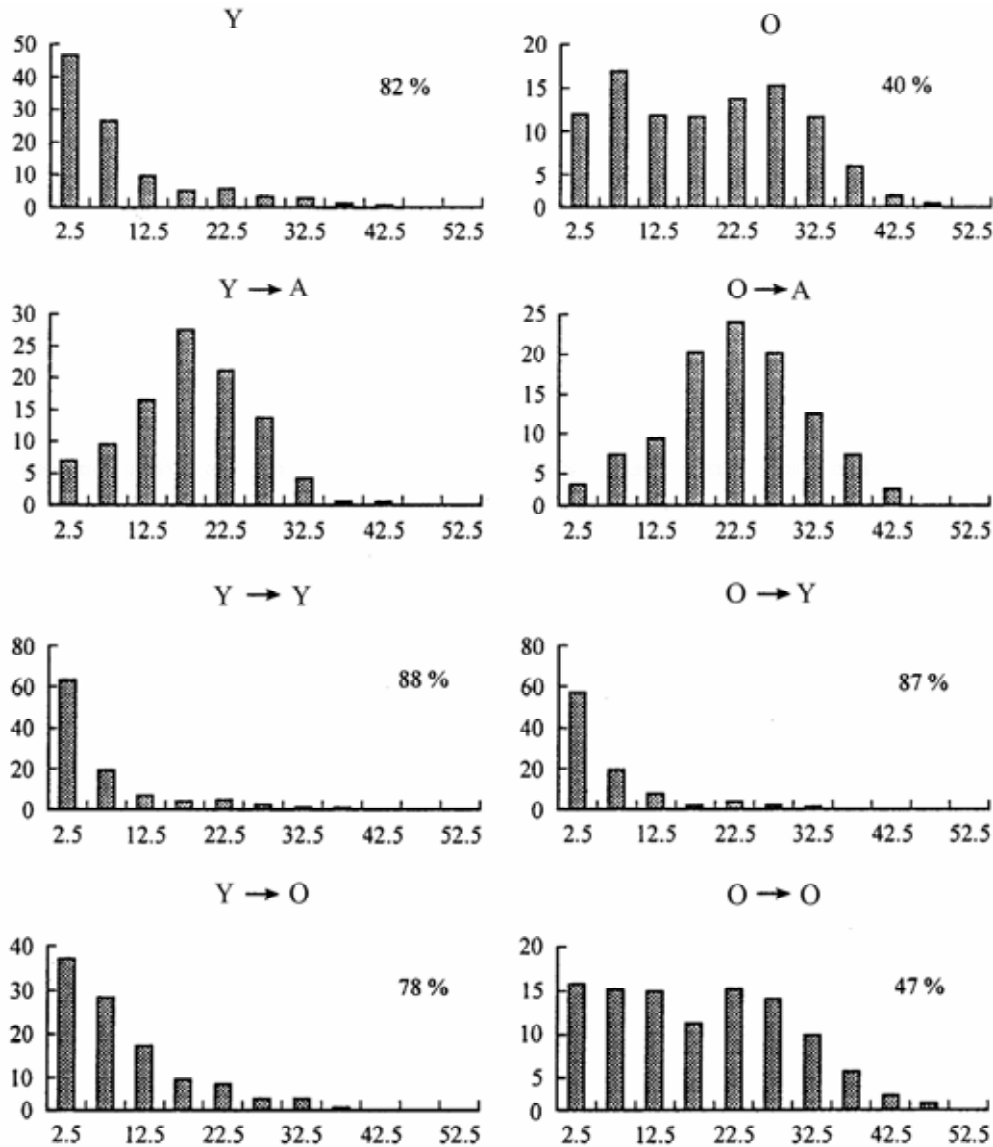


Fig 2. Distribution of *Trichogramma principium* females offered young (fresh) or old (developed during 6 days at 20°C) eggs of the grain moth by the number of parasitizing females at dissection is indicated. For other designations, see Fig. 1. Treatments (in parenthesis, sample size is given): **Y**, young eggs offered for two days, dissection on the 3rd day ($n = 783$); **O**, old eggs offered for two days, dissection on the 3rd day ($n = 602$); **Y → A**, young eggs offered for two days followed by host deprivation during two days, dissection on the 5th day ($n = 200$); **O → A**, old eggs offered for two days followed by host deprivation during two days, dissection on the 5th day ($n = 154$); **Y → Y**, young eggs offered for two days followed by a new portion of young eggs for the next two days, dissection on the 5th day ($n = 416$); **O → Y**, old eggs offered for two days followed by a portion of young eggs for the next two days, dissection on the 5th day ($n = 351$); **Y → O**, young eggs offered for two days followed by a portion of old eggs for the next two days, dissection on the 5th day ($n = 436$); **O → O**, old eggs offered for two days followed by a new portion of old eggs for the next two days, dissection on the 5th day ($n = 340$); **Y →→ Y**, young eggs offered for two days followed by a 2-days-long interval of host deprivation and by a new portion of young eggs for the next two days, dissection on the 7th day ($n = 332$); **O →→ Y**, old eggs offered for two days followed by a 2-days-long interval of host deprivation and by a portion of young eggs for the next two days, dissection on the 7th day ($n = 268$); **Y →→ O**, young eggs offered for two days followed by a 2-days-long interval of host deprivation and by a portion of old eggs for the next two days, dissection on the 7th day ($n = 203$); **O →→ O**, old eggs offered for two days followed by a 2-days-long interval of host deprivation and by a new portion of old eggs for the next two days, dissection on the 7th day ($n = 159$).

ment) the wasps were dissected. Treatments “**Y →→ Y**,” “**Y →→ O**,” “**O →→ O**” and “**O →→ Y**” were conducted with the same design, but a two day

long interval of host deprivation was inserted between two exposures of host eggs (during host deprivation, females were offered honey solution, but no hosts

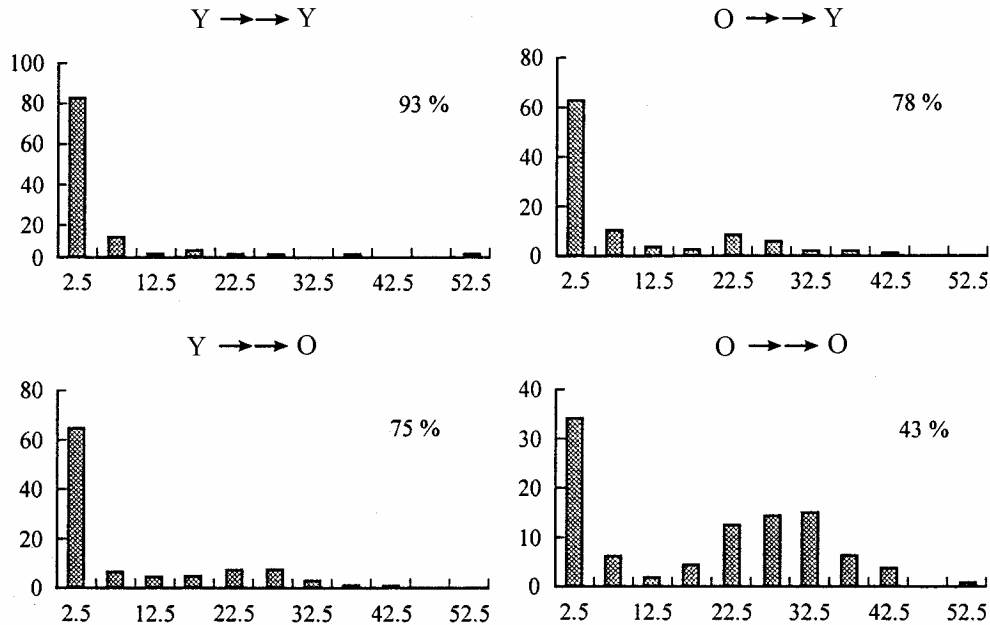


Fig. 2. (Contd.)

were provided) and females were dissected on the 7th day of the experiment.

As seen from Fig. 2 (treatments “Y” and “O”), even on the 3rd day of the experiment, the distribution *T. principium* females by the number of mature eggs significantly ($p < 0.001$) depended on the age of the offered host eggs. As could be expected, the approximate percentage of parasitizing individuals estimated from these distributions with the young hosts was twice as high as that with the old hosts. However, after two days of oogenesis in the absence of the host the difference between distributions partly leveled, although it was still significant ($p < 0.01$), medians and quartiles being 19 (13–23) and 23 (18–29) in treatments “Y→A” and “O→A,” correspondingly.

When two portions of host eggs were sequentially offered, the reaction markedly depended on their order. Particularly, treatments “Y→Y” and “O→Y” were practically indistinguishable, but in treatments “Y→O” and “O→O” the results significantly depended not only on the age of the second portion of host eggs (which was offered just before the dissection), but also on the age of the first portion of the host eggs. When one portion of the old hosts was provided (treatment “O”) the number of mature eggs was 19 (9–29), and after the second portion (treatment “O→O”) the results were practically the same. But if fresh, host eggs were provided after the much more preferred six-days-old eggs (treatment “O→Y”), the number of eggs ready to be laid drastically ($p < 0.001$) decreased to

4 (2–8.5) suggesting a rather high proportion of parasitizing females. The most interesting were the results of treatment “Y→O,” confirming a high stability of the “parasitization state” when the older hosts were offered after the younger hosts, the average number of mature ovarian eggs significantly ($p < 0.01$) increased from 6 (2–11) to 8 (4–13), but the difference between treatments “Y→O” and “O→O,” was also significant ($p < 0.001$) and much more pronounced: 8 (4–13) and 18 (9–27), correspondingly (Fig. 2). These data clearly supported the earlier conclusion made from experiments with individual females (Reznik et al., 1997): the parasitization of the fresh eggs markedly increased the willingness to parasitize the less preferred old eggs of the grain moth.

This tendency was also revealed in the next experiment, conducted by the same design but with a two-day-long interval of host deprivation, when females were fed, but the hosts were not provided. Dissections (Fig. 2, treatments “Y→→O” and “O→→O”) suggested that in this case, 6 days old eggs of the grain moth were much more voluntary parasitized if they had been preceded by other (young) eggs. The approximate proportions of parasitizing females constituted ca 75% and 40%, and the numbers of eggs ready to be laid, 4 (2–15) and 21 (3–31) in the two treatments, correspondingly.

Noteworthy also are the typical differences between the results of the present study and the data earlier

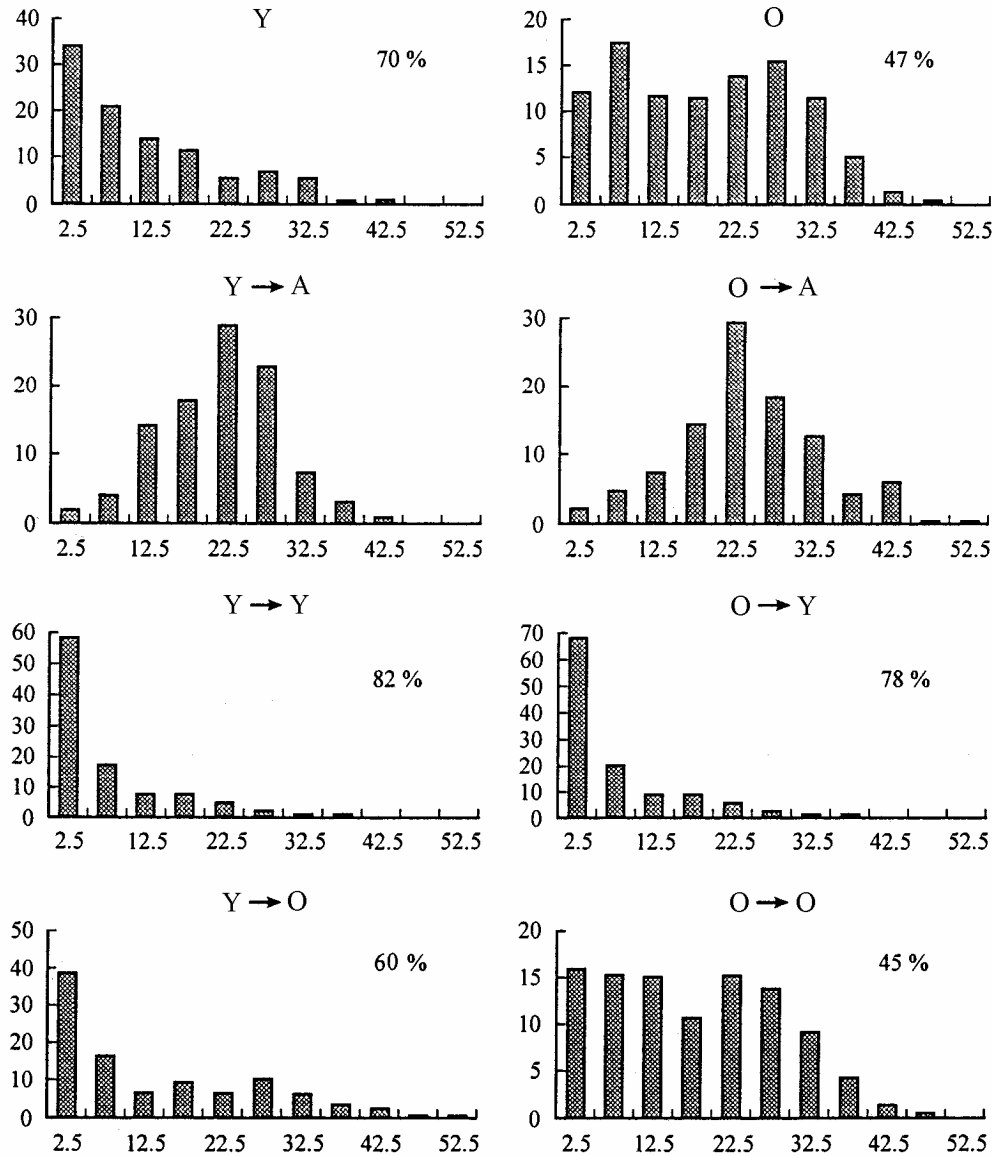


Fig. 3. Distribution of *Trichogramma buesi* females offered young (fresh) or old (developed during 5 days at 20°C) eggs of the grain moth by the number of the mature ovarian eggs. For the designations, see Fig. 2. Treatments (in parenthesis, sample size is given): **Y**, young eggs offered for two days, dissection on the 3rd day ($n = 404$); **O**, old eggs offered for two days, dissection on the 3rd day ($n = 377$); **Y→A**, young eggs offered for two days followed by host deprivation during two days, dissection on the 5th day ($n = 233$); **O→A**, old eggs offered for two days followed by host deprivation during two days, dissection on the 5th day ($n = 230$); **Y→Y**, young eggs offered for two days followed by a new portion of young eggs for the next two days, dissection on the 5th day ($n = 316$); **O→Y**, old eggs offered for two days followed by a portion of young eggs for the next two days, dissection on the 5th day ($n = 257$); **Y→O**, young eggs offered for two days followed by a portion of old eggs for the next two days, dissection on the 5th day ($n = 311$); **O→O**, old eggs offered for two days followed by a new portion of old eggs for the next two days, dissection on the 5th day ($n = 275$); **Y→→Y**, young eggs offered for one day followed by a 1-day-long interval of host deprivation and by a new portion of young eggs for the next day, dissection on the 4th day ($n = 446$); **O→→Y**, old eggs offered for one day followed by a 1-day-long interval of host deprivation and by a portion of young eggs for the next day, dissection on the 4th day ($n = 324$); **Y→→O**, young eggs offered for one day followed by a 1-day-long interval of host deprivation and by a portion of old eggs for the next day, dissection on the 4th day ($n = 333$); **O→→O**, old eggs offered for one day followed by a 1-day-long interval of host deprivation and by a new portion of old eggs for the next day, dissection on the 4th day ($n = 383$).

obtained for *T. principium* females by means of the method of individual parasitization. Under mass parasitization, parasitizing females constituted more than 80% and about 40% when they were offered fresh and

six day old eggs, correspondingly (Fig. 2). Under individual parasitization, these indexes were ca 40% and ca 20%, respectively (Reznik et al., 1997). These differences could be due to the fact that the higher num-

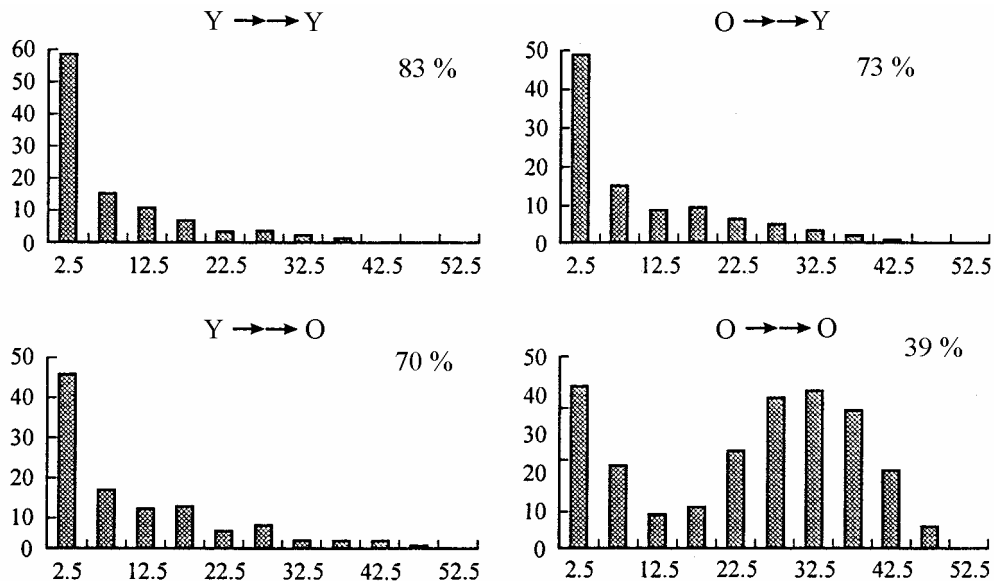


Fig. 3. (Contd.)

ber of hosts (several thousand under mass parasitization vs. several tens under individual parasitization) provided a much stronger stimulus for parasitization, although the mean number of hosts per female under mass parasitization was not higher than that under individual parasitization.

***Trichogramma buesi*.** Experiments conducted according to the same design with *T. buesi* gave practically the same results (Fig. 3). The percentage of parasitizing wasps was also dependent on the host age: the difference between treatments “Y” and “O” was significant ($p < 0.001$, Kolmogorov-Smirnov test): the number of ovarial eggs ready to be laid was 9 (4–18) and 16 (7–26), correspondingly. However, when the parasitization was prevented during two days this difference was almost leveled off: 22 (17–27) and 24 (20–30) in treatments “Y→A” and “C→A,” correspondingly. When young eggs were offered after old eggs, females voluntarily started parasitization. The difference between treatments “Y→Y” and “O→Y” was not significant ($p = 0.66$), the number of eggs ready to be laid being 4 (1–10) and 4 (2–12), correspondingly. Similarly to *T. principium*, parasitization induced by more preferred hosts was continued even when less preferred hosts were provided: the difference between treatments “O→O” and “Y→O” was significant ($p = 0.001$), the number of eggs ready to be laid being 17 (6–26) and 9 (3–24), correspondingly. On the other hand, treatment “Y→O” was significantly ($p < 0.001$) different from treatment “Y→Y,” suggesting that certain females terminated parasitiza-

tion or at least decreased its intensity. When a one-day-long interval of host deprivation was inserted between two host exposures, the same differences were revealed (Fig. 3, treatments “Y→→Y,” “O→→Y,” “Y→→O,” and “O→→O”).

We conclude that both *T. principium* and *T. buesi* females which started to parasitize fresh eggs of the grain moth, continued the parasitization even if the second portion consisted of old (usually rejected) eggs. This “stability of parasitization” was still high even when one- or two-day-long interval of host deprivation was inserted between the two host exposures. Thus, in two *Trichogramma* species previous experience of parasitization of the more preferred hosts increased the probability of parasitization of less preferred hosts. In all insect parasitoids studied earlier, as far as we know, either previous parasitization experience did not influence the probability of parasitization of other hosts, or the contact with the more preferred host caused an increase in the number of females refusing to parasitize the less preferred host (Vinson, 1985; Kaiser et al., 1989; Turlings et al., 1993; Reznik, 1993). The latter was clearly demonstrated, e.g., for learned discrimination of overparasitized hosts (Klomp et al. 1980; Alphen and Dijken, 1988).

In certain insects, the so called “cross induction” was revealed, when an experience of a stimulus changed the reaction to another stimulus (Jaenike, 1983; Papaj et al., 1989; Barron and Corbet, 2000). However, in this case the contact with a “good” host

decreased the probability of a “bad” host acceptance (Papaj and Prokopy, 1989; Courtney et al., 1989; Reznik, 1993), i.e., the reaction was the opposite of that revealed in the present study. Yet, priming (a special form of learning) may induce a positive reaction to an unsuitable substrate after contact with a suitable substrate. For example, certain Lepidoptera females tended to lay eggs on unsuitable host plants after the contact with a suitable host plant (Traynier, 1979; Thibout et al., 1985).

However, the results of our long-term experimental studies (Reznik et al., 1998, 2001) suggest that induction of parasitization is based not only on learning but also on neuroendocrine mechanism. Generally, instant release of a hormone caused by host- or food-related stimuli can also induce sharp stable changes in behavior, similar to those caused by sensitization, by priming, or by conditional response (Barton Browne, 1993). For example *Nicrophorus orbicollis* Say (Silphidae) females show a twofold increase in the level of the juvenile hormone 10 min after locating an animal carcass, which, in turn, causes not only sharp increase in oogenesis intensity, but also corresponding behavioral changes (Trumbo et al., 1995; Trumbo, 1997).

Whatever the mechanism, it may function not only in the laboratory but also under the natural conditions, where it may well be that a parasitoid female could sequentially locate different host species or different stages of the host development. In this case, although emerging *Trichogramma* females have a significant number of eggs ready to be laid, a rather long period of time can precede the onset of parasitization of a less preferred host, and the duration of this period may depend on the presence of other host species.

CONCLUSIONS

(1) Experiments conducted with *T. principium* females by individual and by mass parasitization methods gave similar results. Thus, the applicability of mass parasitization method for studies on host selection by *Trichogramma* and, possibly, by other insect parasitoids was experimentally supported.

(2) When *T. principium* and *T. buesi* females were deprived of the host, the number of mature eggs slightly but significantly increased and then became stable.

(3) The pattern of the distribution of *T. principium* and *T. buesi* females by the number of eggs ready to be

laid strongly depended on the age of the offered grain moth eggs. When fresh eggs of the grain moth were offered, the approximate percentage of parasitizing individuals estimated from these distributions was twice or half as high as that with old eggs, developed during 5–6 days at 20°C.

(4) In both the studied species previous experience of parasitization of the fresh grain moth eggs markedly increased the tendency to parasitize the less preferred old eggs.

(5) It is possible that under natural conditions rather a long period of time can precede the onset of parasitization of a less preferred host by *Trichogramma* females, the duration of this period being dependent on the presence of eggs of other host species.

ACKNOWLEDGMENTS

This work was partly supported by the Programme of the Department of Biological Sciences of RAS “Fundamental Bases of Biological Resources Management.”

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