Entomological Review, Vol. 81, No. 8, 2001, pp. 895–903. Translated from Entomologicheskoe Obozrenie, Vol. 80, No. 3, 2001, pp. 545–556.

Comparative Behavioral Analysis of Ovipositing Females and Females with Egg Retention in *Trichogramma principium* Sug. et Sor. (Hymenoptera, Trichogrammatidae)

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Received November 10, 2000

Abstract—Comparative behavioral analysis of *Trichogramma principium* Sug. et Sor. females parasitizing or refusing to parasitize eggs of the grain moth, *Sitotroga cerealella* Oliv., was conducted in laboratory conditions. As expected, the behavioral differences between parasitizing and refusing females are mostly manifested in the reaction to a host. The data obtained suggest that the arrestment reaction to the host sharply arises as a switch from egg retention to parasitization behavior, rather than develops gradually. Differences in the activity and vertical distribution are less pronounced when a host is present, and are insignificant under host deprivation. Analysis of daily behavioral rhythms demonstrates that experienced females start oviposition earlier than females that have not yet parasitized any host.

The oviposition-related behavior is the main component of activity of insect parasitoids, which determines the specifity of parasitization and, consequently, the role of this parasitoid species in the ecosystem and its economic importance. The search, selection, and parasitization of the host is traditionally regarded as a sequence of elements of the "stimulus-response" type (Viktorov, 1976; Vinson, 1985). Each parasitoid can be characterized by a set of required stimuli, and each potential host, by a combination of positive and negative stimuli received by the parasitoid. However, a lower positive stimulus can induce response in the case of high motivation, while a decrease in motivation leads to an increasing response threshold. The presence of mature eggs in a parasitoid female is regarded as necessary and sufficient motivation for a search, selection, and parasitization of a host, while the selectivity of parasitization is quite often considered to be a stable feature of the species, typical of all individuals of a certain species. However, the increasing number of authors tend to reject the "typological" approach in ethology, and the interest in individual behavior variability is growing (Mikheev, 1999). In particular, recent studies clearly demonstrated the intraspecific variability of behavior in search, selection and parasitization of a host in the majority of insect parasitoids studied (Alphen and Vet, 1986; Reznik, 1993; Roitberg, 1993). Various manifestations of the intraspecific variability of parasitization specificity have also been revealed in *Trichogramma* species, which are widely used as agents of biological control of various agricultural and forestry pests, being also the excellent laboratory objects (Wajnberg and Hassan, 1994; Smith, 1996). Numerous studies revealed the significant heritable variability of parasitization behavior between different species and, in some cases, strains of *Trichogramma*, and the role of nonheritable modifications was also very important (Reznik, 1995).

The present study is devoted to a manifestation of the individual nonheritable variability, repeatedly revealed in different *Trichogramma* species. In laboratory, many species of less preferred hosts are parasitized only by some, sometimes a few females, whereas other females of the same *Trichogramma* strain show a delay of oviposition for some days or even do not parasitize the hosts at all (Sorokina, 1978, 1983; Zaslavski and Mai Fu Kvi, 1982; Smith and Hubbes, 1986; Hohmann *et al.*, 1988; Fleury and Boulétreau, 1993; Pavlik, 1993; Losey and Calvin, 1995; Scott *et al.*, 1997; Glenn *et al.*, 1997; Song *et al.*, 1997; Bjorksten and Hoffmann, 1995, 1998a, 1998b; Basso *et al.*, 1998; Silva, 1999). It should be noted that refusal to parasitize has been almost disregarded previously. As a rule, the dependence of the percentage of parasitizing females on temperature, humidity, photoperiod, and other exogenous factors has been studied (Meier, 1941; Sorokina, 1978; Zaslavski and Mai Fu Kvi, 1982; Sorokina and Dvali, 1985; Kasinskaya, 1988; Pavlik, 1991). Some authors (Nagarkatti and Nagaraja,

1978) regarded all nonovipositing females as "sterile," although this was not confirmed by dissection. Furthermore, even in some relatively recent papers (e.g., Hegazi and Khafagi, 1998) such "nonovipositing females" were simply excluded from data processing.

During the last years, we studied parasitization of eggs of grain moth *Sitotroga cerealella* Oliv., a laboratory host less preferred (near the threshold of suitability and acceptability for parasitization) by females of different *Trichogramma* species. It was expected that this method would reveal fine changes in the behavior of *Trichogramma* females, because near-threshold area provides best conditions for studying the variability of any physiological or behavioral response. Our studies showed that the percentage of females refusing to parasitize depends not only on a host species and a stage of development of its embryo, but also on the number of host eggs and their spatial distribution (Reznik and Umarova, 1985, 1989; Voinovich *et al.*, 1999). The females refusing to parasitize have a great amount of mature eggs in their ovaries. The mean number of eggs produced during the first two days of parasitization is independent of whether parasitization is delayed by a few days, or begins soon after the contact with a host. Consequently, the refusal to parasitize is not associated with female sterility or low intensity of oogenesis, but should rather be regarded as a delay of oviposition, or "egg retention" (Reznik *et al.*, 1997).

Our previous observations (Reznik and Umarova, 1991) showed that females refusing to parasitize move actively and sometimes even come in contact with a host. However, the sequence of reactions, normally leading to parasitization, is interrupted at the stage of host detection and beginning of its examination. The present study is devoted to a more detailed comparative analysis of the behavior of parasitizing females of *Trichogramma* and the females in the "egg retention" state.

MATERIALS AND METHODS

The experiments were conducted using a laboratory strain of *Trichogramma principium* Sug. et Sor., reared on eggs of grain moth for many generations. *Trichogramma* developed under constant conditions (thermostated room) at 18h photophase and 20ºC. Observations of the *Trichogramma* behavior were conducted at 23–25ºC with only young (1–2-days old) females, which, however, had an opportunity to copulate before the experiment. At the beginning of each replicate, 40 females of *T. principium* were placed individually in Petri dishes 3.8 cm in diameter and about 1 cm high. When needed according to the experiment design, an artificial "clutch of host eggs," comprising 50–60 closely adjacent grain moth eggs, was placed at the bottom of the Petri dish. Each experiment continued for 2 days. In each replicate, the females were randomly distributed among 4 treatments. In the first treatment, host eggs were offered to each female in each of the 2 days of experiment; in the second, host eggs were offered to females only on the first day; in the third, only on the second day; and in the forth, the females were deprived of a host during the entire experiment. In each day of experiment, the female behavior was recorded for 10 hours from the instant of switching-on the light. Every 10 min, the position of each of 40 females in the Petri dishes was recorded (on the cover, on the side, on the bottom, on the clutch of host eggs). If a female was moving at the instant of observation, this was also recorded. Thus, 60 records were made during 10 hours for each female. After the 10 hours of the first day, all females were transferred to new Petri dishes, where they remained till the second day of experiment. During the rest of the "day" and the whole "night," the females were fed with honey, but no host eggs were offered. On the second day, immediately after switching-on the light, the females were again transferred to new Petri dishes, in some of which (according to the treatment) "clutches" of host eggs were placed. During the second day, the behavior was recorded in the same way as on the first day. At the end of development of *Trichogramma* larvae, the number of parasitized hosts for each female was determined by the number of darkened grain moth eggs. According to the preliminary processing of observation results and of counts of parasitized eggs, the following parameters were determined for each female of *T. principium* and for each of the 2 days: attraction by host eggs (percentage of observations of *Trichogramma* on host "clutches," including the cases of *Trichogramma* observed near a "clutch," examining or parasitizing one of the eggs); moving activity (percentage of observations of moving females; activity or passivity on the "clutches" was not recorded); vertical distribution (ratio between the number of observations of females on the cover and that on the bottom of Petri dishes; the time on "clutches" was not recorded); and the number of parasitized grain moth eggs .

The preliminary data treatment revealed significant differences between females from replicates in moving

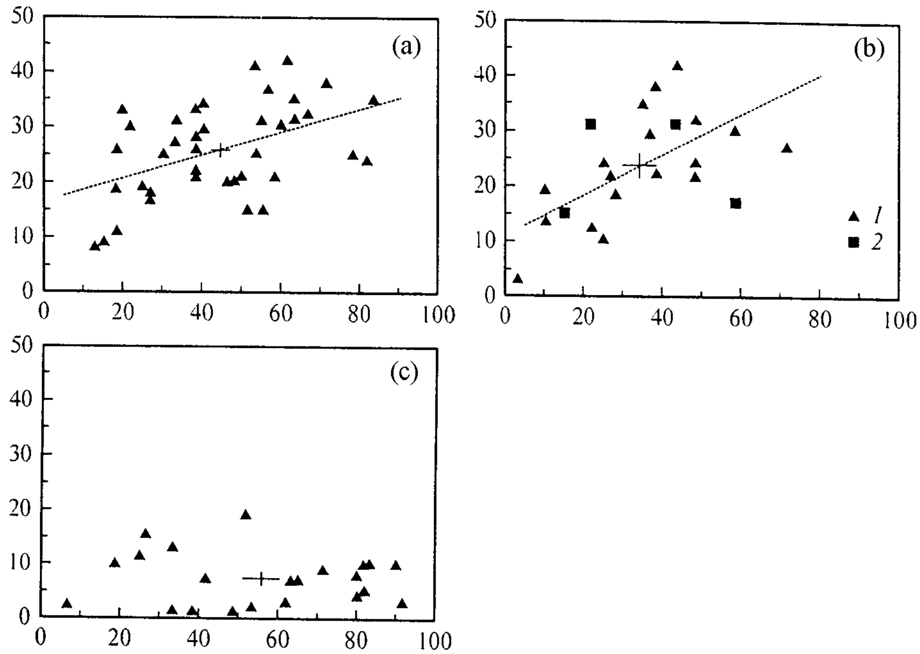

Fig. 1. Relation between the number of parasitized eggs and the time spent by females of *Trichogramma principium* in contact with a host. Abscissa, time spent on a "clutch" of grain moth eggs (%); ordinate, the number of parasitized eggs. Each symbol in the plot represents data for a single female, the cross indicates the mean and its standard error, dotted line shows regression. (a) The first day of experiment: females were offered host eggs and began to parasitize, regression $y = 0.21x + 16.4$, $r = 0.49$, $n = 39$, $p < 0.01$; (b) the second day of experiment: *1*, females were offered host eggs only on the second day and began to parasitize, regression $y = 0.37x + 10.9$, $r = 0.69$, $n = 18$, $p < 0.01$; *2*, females were offered host eggs on both the first and the second days of experiment, but began to parasitize only on the second day, $n = 4$ (the mean and regression for this treatment are not represented); (c) the second day of experiment, the females began to parasitize on the first day and continued on the second day, $n = 22$, $r = 0.003$, nonsignificant.

activity and vertical distribution. This is probably associated both with some exogenous factors and with endogenous processes, which occur in successive laboratory generations of *Trichogramma* strains and, as repeatedly noted previously (Zaslavski and Umarova, 1981; Chernyshev *et al.*, 1986, 1989; Salmanova *et al.*, 1992; Reznik *et al.*, 1996; Schmuck *et al.*, 1996), make study of this parasitoid difficult. Thus, the data on moving activity and vertical distribution were transformed for the subsequent analysis. During this transformation, the percentages were replaced with their square roots (for less dispersion) and then each value was replaced with its relative deviation from the mean value for a given experimental replicate (in order to exclude the influence of the replication factor). These transformed values are presented in Figs. 2 and 3; they were used for the comparison of means (Kruskal-Wallace test), correlation analysis (Spearman coefficient), and linear regression analysis. The mean percentage of time spent by parasitizing females on host egg "clutches" and the number of successfully parasitized host eggs were rather similar in experimental replicates, because of which it was possible to present original (untransformed) data in Figs. 1 and 4. The data were statistically processed using SYSTAT software.

RESULTS AND DISCUSSION

As expected, the most striking differences in behavior between "parasitizing" and "refusing" females were observed in their response to a host "clutch." The parasitizing females ($n = 39$) spent about 50% of the record time in contact with host eggs (scatter of data on individual females in different experimental treatments is shown in Fig. 1). By contrast, contact of refusing females ($n = 49$) with a host was recorded in 1–2 cases out of 100 (on the average, 1.6 ± 0.3% of the record time).

Further analysis of experimental data reveals a significant positive correlation between the time of contact of a parasitizing female with a host and the number of parasitized eggs. This correlation, however, is only observed on the first day of parasitization, regardless of whether this is the first or the second day of experiment (Fig. 1a, 1b). We also note that the

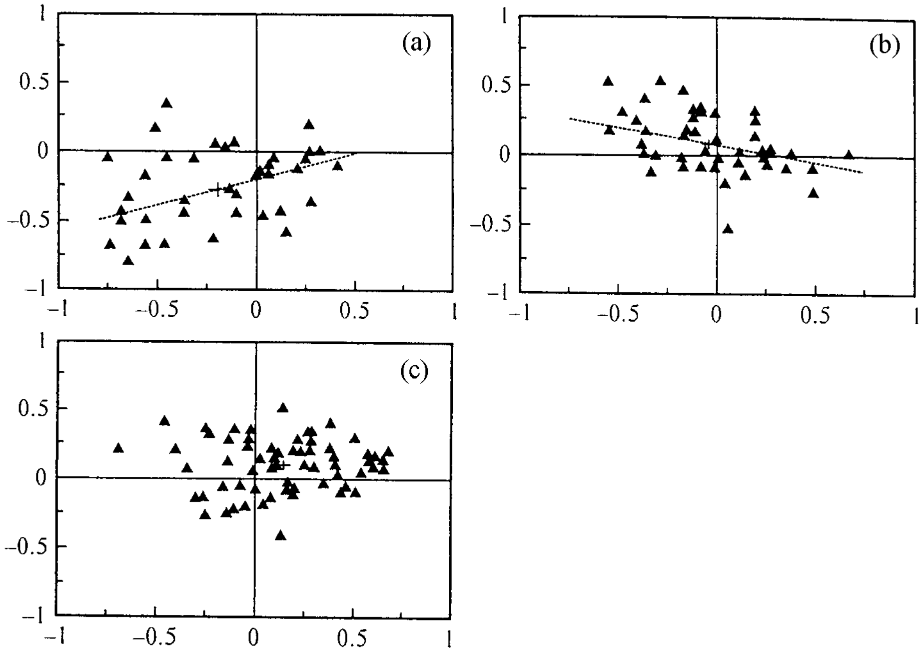

Fig. 2. Moving activity and vertical distribution of females of *Trichogramma principium* (first day of experiment). Abscissa, moving activity; ordinate, vertical distribution. Both parameters are represented as relative deviations from the experimental mean (see Materials and Methods). (a) Parasitizing females, regression $y = 0.36x – 0.20$, $r = 0.40$, $n = 39$, $p = 0.01$; (b) females refusing to parasitize, regression $y = –0.24x + 0.06$, $r = –0.39$, $n = 48$, $p < 0.01$; and (c) females deprived of the host during the first day of experiment ($n = 64$). Designations for original data, mean and regression as in Fig. 1.

mean data for females deprived of a host during the first day of experiment are practically the same as those for females which refuse to parasitize during the first day, but begin to parasitize on the second (Fig. 1b). As for the second day of parasitization (Fig. 1c), there is no correlation ($r = 0.003$) between the time of contact of parasitizing female with a host and the number of parasitized eggs (the mean time on the "clutch" is nearly the same as that on the first day). What is more, the number of parasitized eggs is approximately half that on the first day of parasitization.

It has also been repeatedly reported previously that the daily egg production decreases steeply with female age. Most of *Trichogramma* species, given an unlimited number of hosts, show the most intensive parasitization is observed at the beginning of oviposition. *Trichogramma* females produce, on the average, about 50% of the total number of eggs during the first day (Bai and Smith, 1993; Fleury and Boulétreau, 1993; Miura and Kobayashi, 1995; Wang and Smith, 1996; Carrière and Boivin, 1997; Olson and Andow, 1998).

In our opinion, far more interesting is the approximate equality of the average number of eggs produced during the first 10 hours of oviposition (1) by females that were offered a host soon after emergence and began ovipositing soon after encounter with the host, (2) by females that were offered a host on the second day of experiment, and (3) by females that were offered a host soon after emergence, but refused to parasitize during the first day of experiment (Fig. 1). Firstly, these data once again (but on a different time scale) confirm our previously reported opinion (Reznik *et al.*, 1998) that parasitizing females and females with delay of oviposition differ just in behavior, but not in oogenesis intensity. Secondly, it is evident that the result of oviposition delay, demonstrated by *Trichogramma* females in the presence of a suitable but less preferred host, is the same as that of host deprivation during the same period of time.

It is also of interest that a twofold decrease in oviposition intensity did not lead to any decrease in the time during which *Trichogramma* females contacted with the host eggs (Fig. 1c). It has been shown previously that the number of eggs that are mature for oviposition decreases soon after the beginning of parasitization, so that only few mature eggs are usually observed during dissection in the ovaries of ovipositing *Trichogramma* females (Pak *et al.*, 1985; Pavlik, 1993; Bai *et al.*, 1995; Reznik *et al.*, 1997). However, it is the number of mature eggs in ovaries (egg load) that is regarded by many authors as a measure of stimulus to

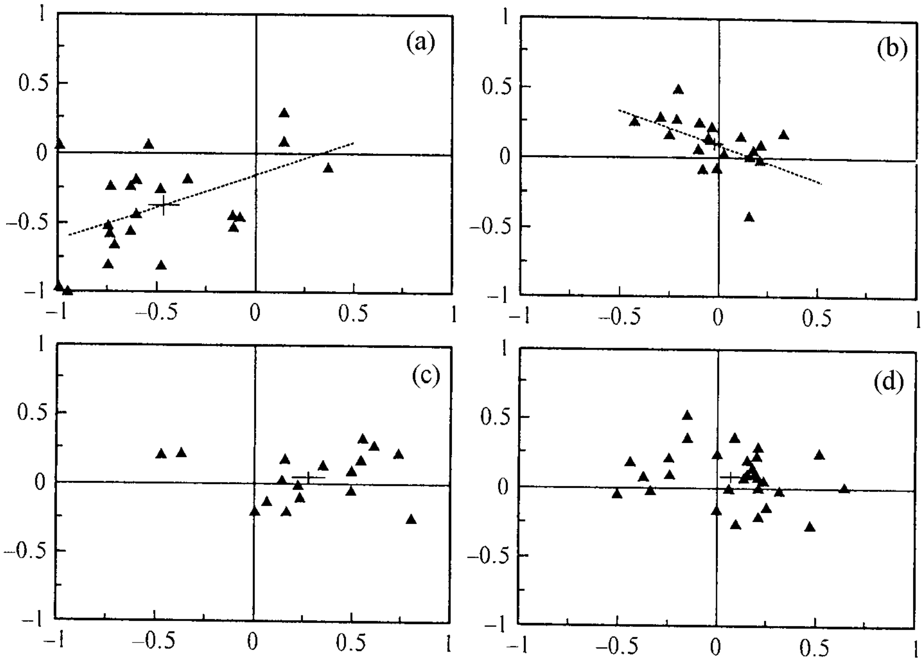

Fig. 3. Moving activity and vertical distribution of females of *Trichogramma principium* (second day of experiment). All designations as in Fig. 2. (a) Parasitizing females, regression $y = 0.46x - 0.16$, $r = 0.54$, $n = 23$, $p < 0.01$; (b) females refusing to parasitize, regression $y = -0.49x + 0.09$, $r = -0.55$, $n = 18$, $p < 0.05$; (c) females that parasitized during the first day and were deprived of a host during the second day of experiment ($n = 17$); (d) females refusing to parasitize on the first day and deprived of a host during the second day of experiment ($n = 29$).

a search for, and parasitization of a host, because the increase in the number of mature eggs usually enhances parasitization and often also decreases its selectivity (Pak *et al.*, 1985; Collins and Dixon, 1986; Mangel, 1989; Völkl and Mackauer, 1990; Rosenheim and Rosen, 1991; Minkenberg *et al.*, 1992; Barton Browne, 1993; Bjorksten and Hoffmann, 1998a). It should be noted that females refusing to parasitize on the first and the second days of the experiment contacted the host on the average for 1–2% of record time, which approximately corresponds to the ratio of the area of the artificial "clutch" to the total area of Petri dish. Similar observations have also been made by other authors (Hohmann *et al.*, 1988; Pavlik, 1993): females refusing to parasitize behave as if they "do not notice" a host, while the parasitizing females, as a rule, spend most of time on host eggs or nearby. These facts suggest that the absence or presence of response to host eggs is determined by a drastic "switch," or transition from the state of "refusal" to the state of "parasitization," rather than by gradual quantitative response (in which case it would be expected to depend on the number of mature eggs).

However, the differences between parasitizing females and females during "delay of oviposition," are not limited to the time of contact with a host. Comparing Figs. 2a and 2b, one can see that parasitizing females spend more time in the lower part of a Petri dish during the first day of experiment, while the refusing females spend more time in the upper part of the dish (differences in vertical distribution are significant: $p < 0.001$ according to the Kruskal-Wallace criterion). The moving activity of females of both types correlates significantly with their vertical distribution (Fig. 2), but this correlation is positive for parasitizing females and negative for females "refusing to parasitize." Analogous differences in the behavior of parasitizing females and females "refusing to parasitize" are also revealed during the second day of experiment (compare Fig. 3a and 3b). This suggests that parasitizing females tend to spend time in the lower part of a Petri dish, while those "refusing to parasitize" are inclined to spend time in its upper part, but these differences are eliminated in the case of high moving activity (because of the small size of a Petri dish).

Moreover, a significant difference ($p = 0.002$) in mean moving activity between females refusing to parasitize and those deprived of a host is revealed on the first day of experiment (compare Figs. 2b and 2c). In addition, in females deprived of the host, the correlation between moving activity and vertical distribu-

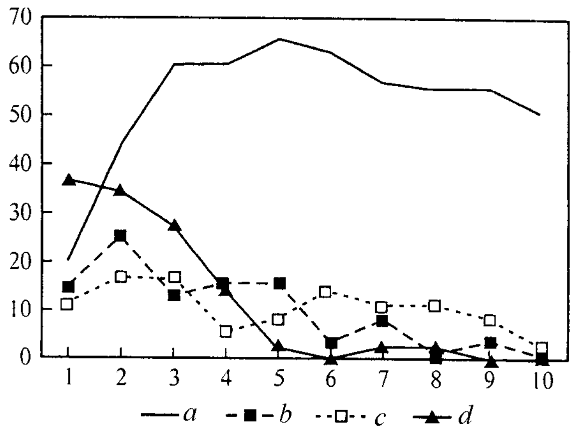

Fig. 4. Dynamics of parasitization intensity and frequency of "parasitization induction" in females of *Trichogramma principium* during the first 10 hours of photophase. Abscissa, time of experiment (mean data for each hour of observation); ordinate, frequency of different manifestations of females behavior. *a*, Intensity of parasitization (frequency of contacts with a host during the second day of experiment in females that begin to parasitize on the first day of experiment, $n = 24$); *b*, parasitization of the first host by females that were offered a host and began to parasitize on the first day of experiment (data for the first day, $n = 91$); *c*, parasitization of the first host by females that were offered a host and began to parasitize on the second day of experiment (data for the second day, $n = 18$); *d*, parasitization of the first host by females that were offered a host and began to parasitize on the first day of experiment (data for the second day, $n = 22$). Curves *c* and *d* were smoothed by the moving average method (lag = 2).

tion is virtually absent ($r = 0.07$). The differences between females deprived of a host and females refusing to parasitize indicate that females in the state of "oviposition delay," although refusing to parasitize the host, nevertheless respond in some way to its presence.

Interesting results were obtained by comparing 2 groups of females deprived of a host on the second day of experiment. Females of both groups were offered a host during the first day, but some females began to parasitize (Fig. 3c), while others delayed oviposition (Fig. 3d). It can be seen that the differences between these 2 groups virtually disappear on the second day: the difference between means is non-significant (the moving activity of parasitizing females is slightly higher than that of refusing ones). Although the correlation between the moving activity and the vertical distribution remains positive in parasitizing females ($r = 0.13$) and negative in refusing ones ($r = -0.22$), it is strongly reduced in the absence of host, being non-significant in both groups. These data confirm once more that parasitizing and "refusing" females differ in their response to a host, so that these differences are not revealed in the absence of host.

Particular attention should be given to the above-mentioned high variability of behavior of individual females of *T. principium* with respect to all of the parameters studied, especially the moving activity and vertical distribution (Figs. 2 and 3). A question naturally arises about the exogenous or endogenous nature of this variability. To answer this question, all the data obtained were subjected to special analysis to reveal a correlation between the behavior of the same female on the first and the second day of experiment. To eliminate the differences between experimental treatments and replicates, the analysis was conducted separately, for each treatment of each replicate and, naturally, separately for parasitizing and refusing females. In the overwhelming majority of cases, such a subdivision of data rendered the correlation coefficients non-significant because of the small size of a sample. Therefore, mean correlation coefficients were calculated for all samples ($n = 28$). They proved to be significantly different from zero, both for the moving activity ($r = 0.30 \pm 0.09$) and for the vertical distribution ($r = 0.28 \pm 0.09$). This suggests that the scatter of experimental data strongly depends on the endogenous (probably inherited) differences between individuals.

Regular observations conducted during the major part of the photophase allowed us to describe also the pattern of the diel rhythmicity of the processes studied. Changes in the response to a host are of most interest for the present study. It is evident (Fig. 4*a*) that the percentage of females contacting with a host during the recording increases sharply during the first hours after switching-on the light and then becomes stable, decreasing somewhat in the second half of the day (females refusing to parasitize were disregarded when determining the frequency of contacts with a host). These results approximately correspond to those published previously in the papers devoted to the diel rhythmicity of host search and parasitizing activity in different *Trichogramma* species (Afonina and Bil'dushkinova, 1983; Afonina *et al.*, 1984, 1986).

Another pattern is observed in the daily rhythmicity of the process of "induction of the state of parasitization," judged by the time when the first host is parasitized. It is evident that, in females provided with a host during the first day of experiment (Fig. 4*b*) and in those provided with a host only on the second day (Fig. 4*c*), the parasitization mostly begins in the first half of the photophase, after which the frequency of parasitization induction decreases, although many individuals begin to oviposit only 7–8 h after switching-on the light, when the total intensity of oviposition decreases. In the females for which the second day of experiment is also the second day of parasitization (those starting to parasitize on the first day and continuing on the second), the first host was usually parasitized less then 3–4 h after switching-on the light (Fig. 4*d*), i.e., much earlier than in females that encountered a host for the first time. Similar results were obtained by Timokhov and Kartsev (1998): *T. evanescens* females that parasitized two hosts one or several times switch from contact to parasitization more frequently than the females that had no previous contacts with a host.

Analysis of the diel rhythmicity of parasitization induction leads to some interesting conclusions. Firstly, the very existence of the states of "refusal to parasitize" and "parasitization" is confirmed; otherwise, one could hardly explain why females experienced in parasitization start to oviposit earlier than females of the same age having no previous contact with a host (Fig. 4*c* and 4*d*). However, as shown previously (Pak *et al.*, 1985; Pavlik, 1993; Bai *et al.*, 1995; Reznik *et al.*, 1997), the latter have more eggs mature for oviposition, i.e., apparently they have a higher stimulus to parasitize. Secondly, the difference between two processes: parasitization and induction of parasitization is evident. In females in "the state of parasitization," the dynamics of parasitization of the first host (Fig. 4*d*) approximately corresponds, as would be expected, to the first derivative of the general intensity of oviposition (Fig. 4*a*). By contrast, the process of induction of the "state of parasitization" (Fig. 4*b* and 4*c*) is weakly associated with the dynamics of the total intensity of oviposition. Thirdly, it is evident that whatever the mechanism of "counter" or "timer" inducing the parasitization may be, it works only in the presence of a potential host; otherwise, the females offered a host only on the second day (Fig. 4*c*) would begin parasitization much earlier than young females that were offered a host at the beginning of experiment (Fig. 4*b*).

As regards the states of "parasitization" and "refusal" (or more precisely "delay of oviposition"), whose external manifestations are the subject of this study, their nature remains obscure. Some experiments suggest that the onset of parasitization is not simply a change of female behavior, but switching to a different physiological state. This appears to be the ultimate reason for the "stability of parasitization": a female that has started to parasitize the more preferred host will continue parasitization when offered a less preferred host (Reznik *et al.*, 1997). Moreover, this "state of parasitization" proved to be stable even in a treatment in which 2 periods of contact with a host were separated by a 6–8-day interval. Such a stability of behavior is probably based not on learning (which is usually unstable and easily reversible), but on deeper endocrine mechanisms (Reznik *et al.*, 1998). In this case, the observed phenomenon can be compared with imaginal reproductive diapause (in contrast to which, oviposition, rather than oogenesis, is arrested). However, the induction of diapause and subsequent reactivation are usually not restricted to termination and resumption of reproduction, but are followed by profound changes in the whole organism; whereas the induction of the parasitization state affects a narrower sphere of behavioral responses, as shown, in particular, in the present paper. However, detailed comparison of physiological characteristics of "parasitizing" and "refusing" *Trichogramma* females invites a special study.

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