ISSN 0013–8738, Entomological Review, 2009, Vol. 89, No. 1, pp. 5–15. © Pleiades Publishing, Inc., 2009.
Original Russian Text © S.Ya. Reznik, N.D. Voinovich, S.G. Karpova, 2009, published in Entomologicheskoe Obozrenie, 2009, Vol. 88, No. 1, pp. 16–28.

Daily Rhythms in Parasitization of the Angoumois Grain Moth *Sitotroga cerealella* Oliv. (Lepidoptera, Gelechiidae) Eggs by the Egg Parasitoid *Trichogramma principium* Sug. et Sor. (Hymenoptera, Trichogrammatidae) Females

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Received March 6, 2007

Abstract—Laboratory experiments conducted at L : D = 16 : 8 have shown that the observed temporal pattern of parasitization of the Angoumois grain moth, *Sitotroga cerealella* eggs by *Trichogramma principium* females represents a resultant of arrhythmic age-related trends and circadian rhythms. Most of females delayed parasitization. The daily number of females starting to parasitize was maximal on the first day of contact with the host and then gradually declined. Practically all of the females started parasitization during the photophase. Moreover, when the first contact with the host fell on the scotophase, the total cumulative percentage of females that started parasitization during four days of the experiment significantly decreased. Oviposition activities of parasitizing females also occurred mainly during photophase. However, under constant light, these circadian rhythms were damped out after one cycle. In addition, anticipatory period of darkness during photophase directly inhibited parasitization. This suggests that the observed rhythms can be easily modified by the direct environmental influence. Under natural conditions, such a flexible oviposition rhythm may be of advantage for these parasitoids enabling them to use any opportunity for reproduction. In biocontrol practice, the lability of parasitization rhythms may enable *Trichogramma* females to adapt immediately to any new light–dark regimes, although darkness may have negative effects on their efficiency.

DOI: 10.1134/S0013873809010023

INTRODUCTION

Temporal changes which may be revealed in all the types of insect activities, represent a summation of trends (connected with development, maturation, etc.) and cycles (primarily, circadian rhythms). Discovering of circadian components of temporal patterns of various activities is very important, particularly, for development of methods for predicting and controlling insect behavior.

Numerous species of the genus *Trichogramma* are excellent model insects for studying daily rhythms. Moreover, investigation of behavior and, particularly, oviposition behavior of these parasitoids has a great practical significance, because *Trichogramma* species are widely employed for biological control of lepidopteran pests of agriculture and forestry (Smith, 1996). Daily rhythms of parasitization activity should be kept in view in planning and execution of *Trichogramma* mass rearing and releases, particularly when the parasitoids are to be used under artificial lighting (in greenhouses) or in darkness (in grain storages, etc.).

We investigated daily rhythms of parasitization of hosts by females of *Trichogramma principium* Sug. et Sor. (Hymenoptera, Trichogrammatidae). A peculiarity of the studied strain of this species is a delay in parasitization of eggs of the Angoumois grain moth, *Sitotroga cerealella* Oliv. (Lepidoptera, Gelechiidae) ranging up to 10–12 days. The individuals which delay parasitization have a high number of mature ovarial eggs ready to be laid. Once a female began to parasitize it usually continued to do so even when less preferred hosts were offered or environmental conditions were changed. Thus, the switch from egg retention to oviposition is practically irreversible, resembling reactivation after the reproductive diapause (Reznik et al., 1997, 2001b, 2003).

Hence, the temporal pattern of host parasitization by *T. principium* females is a resultant of two different processes. The first process is the onset of parasitization, which is practically “once-in-a-life” event, therefore its dynamics could be observed only in a group of insects. The second process is the dynamics of oviposition activity of a female which has already started parasitization. This process could be observed in each individual female.

Delayed parasitization was recorded in different *Trichogramma* species (Degtyarev et al., 1988; Fleury and Bouletreau, 1993; Reznik, 1995; Monje et al., 1999) and in other egg parasitoids (Ruberson et al., 1988). However, in none of these studies the daily rhythm of probability of parasitization of the first host was investigated, although certain results (Reznik et al., 2001a) suggested that this process could be also governed by circadian rhythms. It is known that in many insect species studied various once-in-a-life events, such as larval hatching or adult emergence occur at a particular time of the day (Chernyshev, 1996; Saunders, 2002). Particularly, in *T. principium* a distinct circadian rhythm of adult emergence was recorded (Zaslavski et al., 1999; Karpova and Reznik, 2002; Karpova, 2006).

As for the cycles of oviposition intensity in parasitizing females, under natural conditions parasitization mostly occurs during daytime. In the laboratory, circadian rhythms of oviposition were also recorded in several *Trichogramma* species (Buleza, 1985; Aphonina et al., 1986; Tavares and Voegele, 1991; Pompanon et al., 1993, 1999).

The aim of the present study was a detailed analysis of the temporal dynamics of oviposition (parasitization of hosts) and, particularly, separation of trends and cycles. To investigate the possible role of circadian rhythms, we studied the dynamics of parasitization intensity under photoperiod, under constant light, and under a shifted photoperiod with light turned off earlier.

MATERIALS AND METHODS

All the experiments were conducted with a laboratory strain of *T. principium* which originated from females reared from Noctuidae eggs collected in Chimkent province (Kazakhstan) and then cultivated for more than 100 generations on the eggs of the Angoumois grain moth under constant laboratory conditions. All the individuals used in our experiments developed at 20°C under a photoperiod of L : D = 16 : 8. Emerging *T. principium* adults were given an opportunity to mate during 6 h in a large (100 × 30 mm) test tube with several hundred individuals. Then females were placed individually into small (40 × 5 mm) test tubes and randomly distributed over different treatments of the experiment. A drop of honey (50% aqueous solution) was smeared on the glass to as food for females. Standard portions of host eggs (50–60 *S. cerealella* eggs pasted to a paper strip with non-toxic water soluble glue) were sequentially presented to each female for 8 h long periods (host exposures) according to the design of the experiment. When *S. cerealella* eggs are offered in excess, *T. principium* females usually lay a single egg in each host egg. Therefore, after completion of the parasitoid larvae development, a number of parasitized (darkened) host eggs was taken for the approximate number of *Trichogramma* eggs laid. The number of eggs laid during each exposure was recorded for each female separately.

T. principium females usually delay the onset of parasitization. Thus, the exposure during which the first host was parasitized was recorded also for each female and when estimating the mean fecundity, only females that had already started parasitization were taken into account. By this method, in each replicate of each treatment of each experiment, the following set of data was obtained: (1) the cumulative percentage of females which parasitized at least one host during the experiment; (2) the percentage of females which started parasitization during each exposure of the experiment; (3) the mean fecundity of parasitizing females during each exposure of the experiment.

Three experiments were conducted.

The first experiment included 3 treatments (Fig. 1). In treatment *A*, the host eggs were first exposed at the beginning of the photophase (at the moment of light-on), and then during 4 days every 8 h (i.e., in the middle of the photophase, at the end of the photophase, and so on) the paper strip with host eggs was replaced with a new one presented to each female. Thus, 12 equal portions of host eggs were sequentially exposed to each female during 8 h each. In treatments *B* and *C*, females were first offered host eggs in the middle of the photophase (8 h after the light-on) and at the end of the photophase (16 h after the light-on), respectively, and then paper strips with host eggs were replaced in the same way, as in treatment *A*.

The second experiment also included 3 treatments differing in the time of the first contact with the host. But since this first contact, all females were kept under continuous light. Twelve equal portions of the grain moth eggs were sequentially offered to each female in

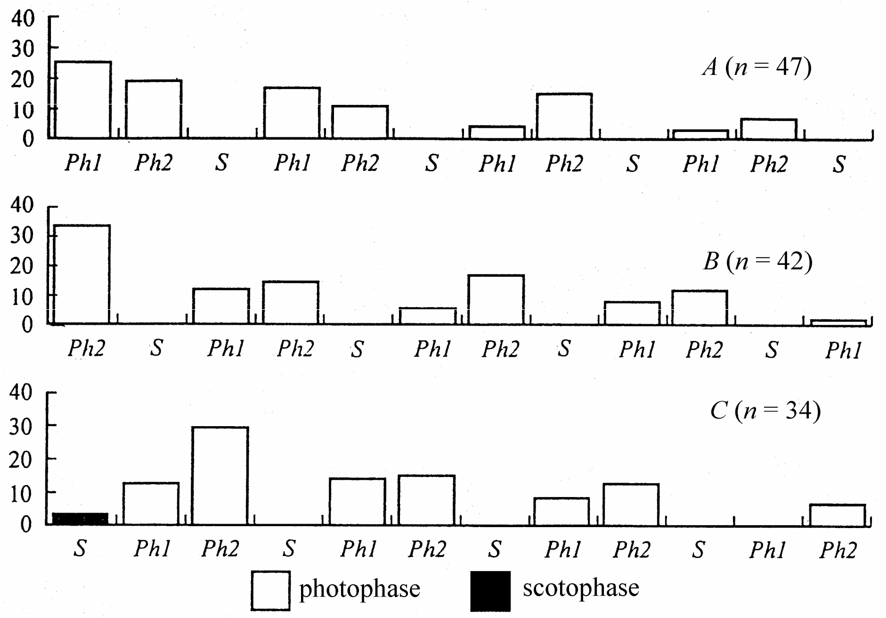

Fig. 1. Daily rhythm of onset of parasitization of the grain moth eggs by *Trichogramma principium* females under photoperiodic conditions. Abscissa: phases of the photoperiod: *Ph1*, first half of photophase; *Ph2*, second half of photophase; *S*, scotophase; ordinate: percentage of females that started parasitization during given phase of the photoperiod. *A*, *B*, *C*, Treatments of first experiment differed in the time of the first contact with the host. Percentages for the totals of all replicates are shown; *n*, sample size (total number of parasitizing females in a treatment of the experiment).

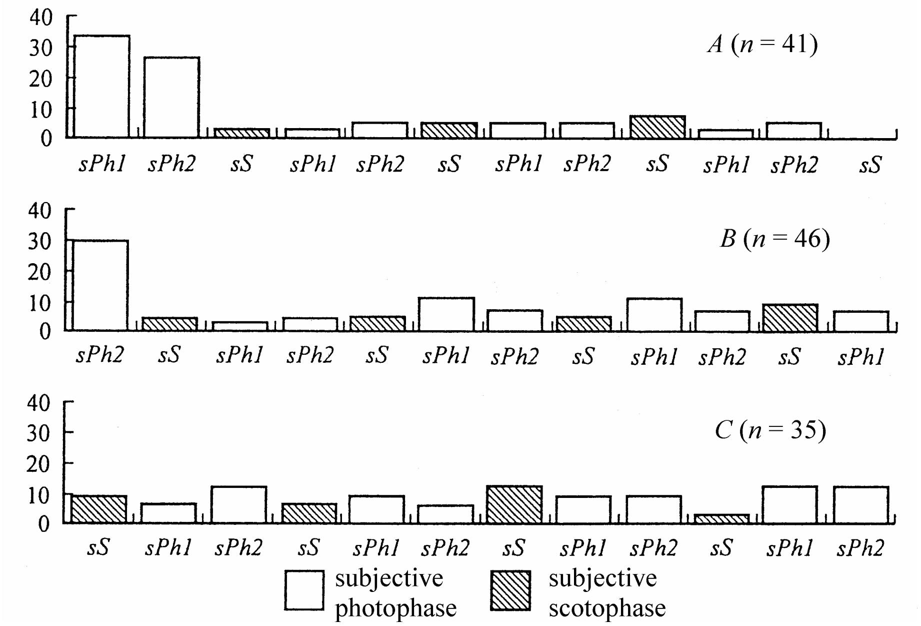

Fig. 2. Daily rhythm of onset of parasitization of the grain moth eggs by *Trichogramma principium* females transferred from photoperiodic conditions to constant light since the first contact with the host. Abscissa: subjective time of females, synchronized with the photoperiodic conditions during their development: *sPh1*, first half of subjective photophase; *sPh2*, second half of subjective photophase; *sS*, subjective scotophase. *A*, *B*, *C*, treatments of the second experiment differed in the time of the first contact with the host. Other designations are as in Fig. 1.

the same way as in the first treatment, but the time of the beginning and the end of each exposure were determined according to the "subjective time" of females, synchronized with the photoperiodic conditions during their development (Fig. 2).

Six replicates of the first and the second experiments were conducted with successive generations of the laboratory line. Each replicate included 96 *T. principium* females (16 per each of 3 treatments of 2 experiments).

The third experiment was conducted according to the same design as the first experiment, but in the middle of the 2nd photophase the light was prematurely switched off and the next (i.e., 4th, 5th, or 6th, depending on the treatment) portion of host eggs was offered for parasitization in darkness. Then the experiment was terminated. Ten replicates of this experiment were conducted, each including 60 females (20 per treatment).

Percentages of parasitizing females which started parasitization during each exposure were compared with the Kruskal-Wallis non-parametric test and the Spearman rank correlation coefficient, medians and quartiles being used as descriptive statistics (each replicate was considered as an experimental unit). In figures, percentages calculated for the pooled totals of all the replicates are given.

The cumulative percentage of parasitizing females markedly varied even in sequential generations of the laboratory strain, as was earlier recorded in *Trichogramma* by different authors (Reznik et al., 1996; Hoffmann et al., 2001). Hence, to compare different experiments and different treatments of the same experiment, cumulative percentages of parasitizing females were separately ranked for each replicate (each generation of the laboratory line) and these ranks were used for ANOVA test. Medians and quartiles calculated for untransformed pooled data were used as descriptive statistics.

Fecundity (number of eggs laid by a parasitizing female during a given exposure) also was not normally distributed. Thus, before statistical treatment, the data on fecundity were also replaced by ranks and then were analyzed with ANOVA and the Tukey test. Medians and quartiles of fecundity are shown in the figures. Preliminary treatment of the results did not reveal significant differences in the mean fecundity between the replicates of each treatment. Hence, before the final statistical analysis the data of all the replicates were pooled. All statistical procedures were calculated with SYSTAT 10.2.

RESULTS

The Onset of Parasitization

A clear change in rhythm was evident in all the treatments of the first experiment, (Fig. 1). Independently of circadian time of the first contact with the host, practically all females started parasitization during photophases and this tendency was significant ($p < 0.01$, the Kruskal-Wallis test) in all the treatments. The difference in percentages of females which started oviposition during the first and during the second half of the photophase was much less clear (Fig. 1). Pooling the data of all replicates of all treatments of this experiment (medians and quartiles are given) showed that 8% (2–15) and 14% (11–18) of ovipositing females started parasitization during the first and during the second half of each photophase, respectively. This difference was marginally significant ($p = 0.04$, the Kruskal-Wallis test).

In the second experiment (under permanent light), the onset of parasitization was generally arrhythmic (Fig. 2). Differences in the percentage of females that started parasitization during the first half of subjective photophase, during the second half of subjective photophase, and during subjective scotophase, were insignificant ($p > 0.2$) in all treatments. However, in spite of constant light, evident suppression of the onset of parasitization was observed during the first subjective scotophase in all the treatments of this experiment. Particularly, the first contact with the host occurring during subjective night (treatment 2*C*) stimulated oviposition only in 10% of females, whereas 35% and 30 % of females started parasitization when the first host exposure occurred during the first and the second half of subjective photophase (treatments 2*A* and 2*B*, respectively).

In the third experiment, when the light was switched off in the middle of the second photophase, this “premature night” completely blocked induction of parasitization. None of the tested females started to parasitize during the premature scotophase, although in the first experiment, which could be used as a control treatment of the third experiment, 10–15% of parasitizing females started parasitization during the second half of the second photophase. This difference between experiments was significant ($p < 0.05$) for each treatment. Note that the difference in cumulative percentage of females which started to parasitize before the middle of the second photophase between the corresponding treatments of the first and the third experiments (20–30% of all females, depending on the treatment) was insignificant ($p > 0.1$, Kruskal-Wallis test).

As seen from Figs. 1 and 2, in most of the treatments, the percentage of females which started to parasitize during a given day was maximal at the beginning of the experiment and then gradually declined.

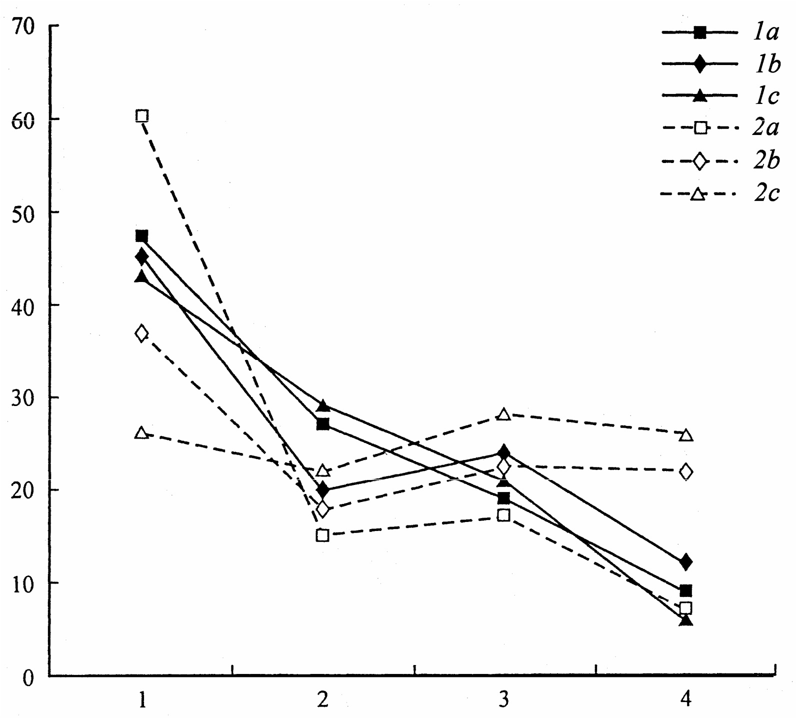

Fig. 3. Temporal pattern of onset of parasitization of the grain moth eggs by *Trichogramma principium* females. Abscissa: time (days from the first contact with the host); ordinate: percent of females that started parasitization during given day. Lines 1*a*–2*c* show results of corresponding treatments of the first and the second experiments (Figs. 1 and 2).

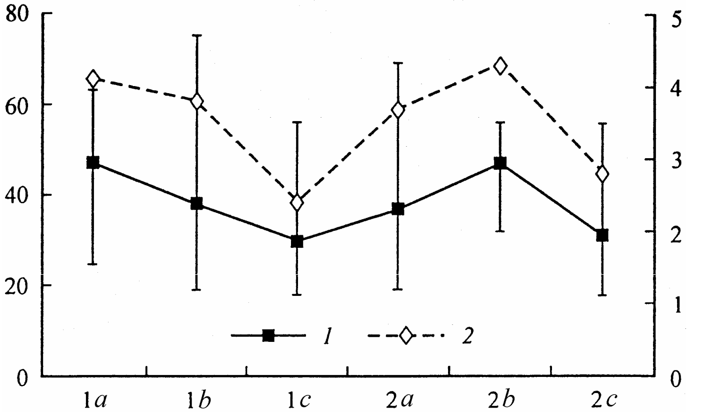

Fig. 4. Cumulative percentage of parasitizing *Trichogramma principium* females. Abscissa: treatments of the first and the second experiments (see Figs. 1 and 2); ordinates: *1* (left axis), untransformed percentages (medians and quartiles), *2* (right axis), ranked data (means).

In three treatments of the first treatment (Fig 3) patterns of this time-dependence practically coincided, the Spearman correlation coefficients were almost equal: $r = -0.46$, $r = -0.41$, and $r = -0.42$ in treatments 1*a*, 1*b*, and 1*c*, respectively ($n = 24$, $p < 0.05$ for all three treatments). In treatment 2*a* the correlation was also negative ($r = -0.40$, $n = 24$, $p < 0.05$). However, in treatments 2*b* and 2*c* the time-dependence was practically absent ($r = 0.07$ and $r = 0.06$, respectively).

The polled data on the final cumulative percentages of females that started parasitization during 12 exposures of all the treatments of the 1st and of the 2nd treatment were also analyzed. As noted above, percentages of parasitizing females were first separately ranked in each of 6 replicates and then treated with two-way ANOVA. Photoperiodic regimen (i.e., photoperiod vs. constant light) was the first factor, while the part of the circadian cycle, when the fist contact with the host occurred (i.e. treatments *A*, *B*, or *C*) was the second factor. The results were rather clear, despite extremely high variation (Fig. 4): the ranked cumulative percentage of parasitizing females was practically

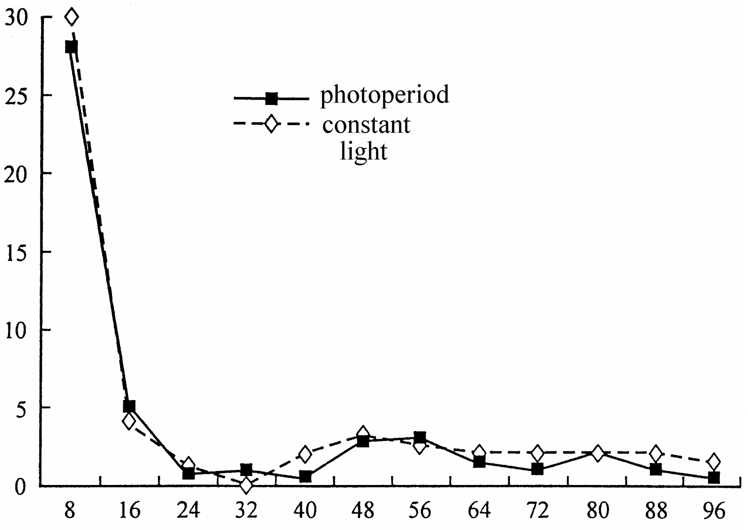

Fig. 5. Temporal pattern of fecundity (number of parasitized grain moth eggs) in *Trichogramma principium* females. Abscissa: time (hours from the first contact with the host); ordinate: average fecundity under photoperiod (first experiment) and under constant light (second experiment).

equal under the photoperiod and under the constant light conditions (p = 0.94), but markedly (p = 0.007) decreased when the first contact with the host occurred at scotophase (either real scotophase or subjective one). By pooled data of both experiments, 44% (25–66) and 34% (18–56) of *T. principium* females started parasitization of *S. cerealella* eggs during 4 days when their first contact with the host fell, respectively, on the first or the second half of a photophase and on a scotophase, no matter whether the scotophase was real or subjective (under constant light).

Fecundity of Parasitizing Females

Both during photoperiod (first experiment) and under constant light (second experiment) the average fecundity (the number of eggs laid by parasitizing females during a 8 h long exposure) was highest during the exposure, when oviposition started (Fig. 5). Then the average fecundity decreased steeply reaching its minimum at the 3rd–the 5th exposures (counting from the onset of parasitization) and then increased during the 6th–7th exposures. Spearman rank correlation coefficients for the interval between the 3rd and the 7th exposures was significantly positive both in the first and in the second experiments: r = 0.23 (n = 441, p < 0.001) and r = 0.40 (n = 352, p < 0.001), respectively. Then (between the 7th and the 12th exposures) fecundity decreased again: Spearman rank correlation coefficients were r = –0.24 (n = 328, p < 0.001) and r = –0.23 (n = 258, p < 0.001). However, both trends seem to be negligible, as compared to a sharp decrease in fecundity, occurred after the first two exposures (Fig. 5). According to the summation of two treatments, the average number of eggs laid by *T. principium* females during the 1st, the 2nd, and the following exposures (counting from the onset of parasitization) was 29 (19–35), 4 (0–10), and 2 (0–3) eggs per exposure, respectively. Hence, when analyzing the daily rhythm of oviposition, data on the first two exposures were left out. Thus, the analysis was started from the 2nd day of the experiment.

In the first experiment, oviposition exhibited a clear daily rhythm (Fig. 6). The two-way ANOVA test of ranked data revealed significant (p < 0.001) dependence of the number of laid eggs on the phase of the photoperiod, but not on the treatment of the first experiment (p = 0.89). The average fecundity of parasitizing females constituted 3 (1–6), 1 (0–3), and 0 (0–1) eggs during the first half of the photophase, the second half of the photophase, and the scotophase, respectively. The Tukey test of ranked data showed that differences between all the three phases of the photoperiod were significant (p < 0.001).

In the pooled data of the second experiment a significant (p < 0.01) dependence of fecundity on the subjective circadian time was also revealed, but the pattern of this dependence was quite different: 1.0 (0.0–3.0), 1.0 (0.0–2.5), and 3.0 (1.0–5.0) eggs / female / exposure during the first half of the photophase, the second half of the photophase, and the scotophase, respectively. Peaks of fecundity coincid-

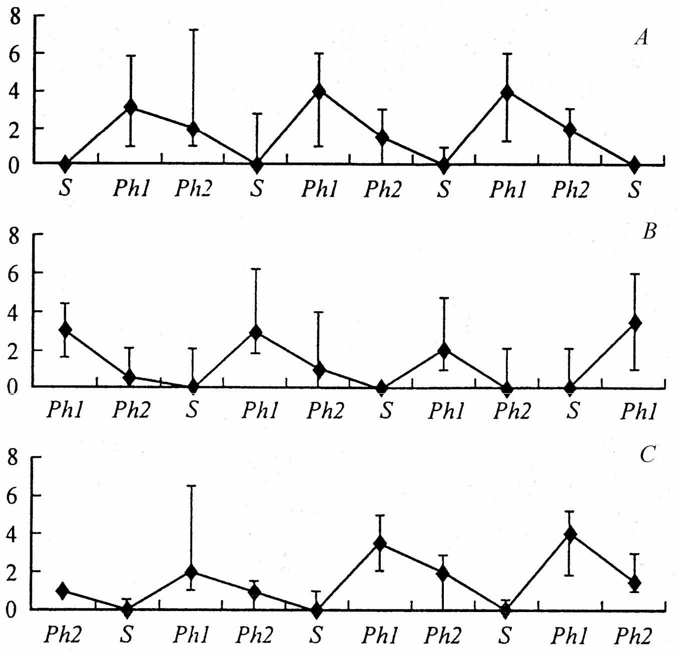

Fig. 6. Daily rhythm of fecundity in *Trichogramma principium* females under photoperiodic conditions. Ordinate: fecundity of parasitizing females (medians and quartiles). For other designations, see Fig. 1.

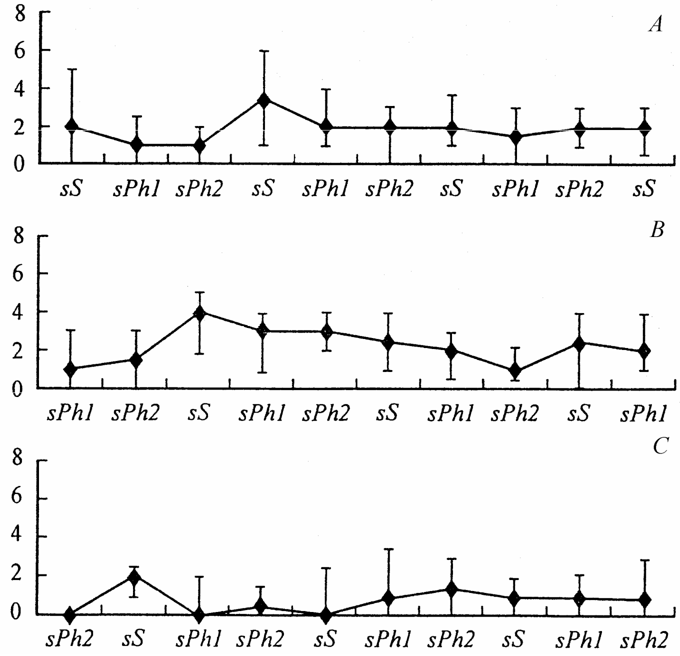

Fig. 7. Daily rhythm of fecundity in *Trichogramma principium* females under constant light. Ordinate: fecundity of parasitizing females (medians and quartiles). For other designations, see Fig. 2.

ing with the “subjective scotophases” are well seen in Fig. 7 (the left parts of graphs). However, as seen from the right parts of graphs, from the 3rd day under constant light, oviposition was practically independent of the subjective circadian time ($p = 0.64$).

In contrast to the first treatment, in the second experiment *T. principium* fecundity significantly ($p = 0.001$) depended on treatment. As also seen from Fig. 7, mean fecundity the 3rd and following exposures was approximately equal in females which first contacted the host during the first half and the second half of subjective photophase: 2.0 (0.0–3.0) and 2.0 (0.0–4.0), respectively. However, females which first contacted the host during the subjective scotophase, laid only 1.0 (0.0–2.0) eggs / female / exposure.

In the third experiment, premature scotophase caused a sharp decrease in parasitization intensity. In all the treatments, most of females laid no eggs during this exposure, which was significantly ($p < 0.05$) different from the data recorded during the second half of the second photophase in the first experiment (Fig. 6).

DISCUSSION

Host selection and parasitization behavior of insect parasitoids is a sequence of "stimulus - response" reactions (Vinson, 1998; Steidle and van Loon, 2002). If the threshold is low, a response could be caused by a relatively weak stimulus. It is known (Smith, 1996; Bjorksten and Hoffmann, 1998; Monje et al., 1999; Hoffmann et al., 2001) that although the grain moth is widely used for mass rearing of *Trichogramma* species, it is a poor quality factitious host (near the threshold of acceptance). Hence, the daily dynamics of the first parasitization of this host could be considered as a manifestation of underlying periodicity in activity, motivation to parasitize, sensitivity to host–related stimuli, or some other factors influencing the reaction threshold. The parasitization of the first host, in turn, sharply lowered the threshold of acceptance (at least for a given host species) ensuring continuation of parasitization (Reznik et al., 2001b, 2003).

The results of the present study show that *Trichogramma* start parasitization almost exclusively during the photophase (Fig. 1) and this rhythmicity is driven mainly by a direct inhibition of parasitization behavior during the scotophase (in the dark). The latter is particularly suggested by total inhibition of parasitization by an anticipatory dark period applied at the middle of the photophase. However, the results of the experiment conducted under constant light suggest that some endogenous circadian rhythms may also influence induction of parasitization. Particularly, in the second experiment, parasitization during the first subjective scotophase was inhibited despite constant light (Fig. 2). However, the subsequent parasitization dynamics was arrhythmic suggesting that the endogenous component of the observed rhythm was relatively weak and unstable.

In both experiments (Figs. 1 and 2) the probability of host acceptance was maximum during the first 8 h of contact with the host. Possibly, in certain emerging females the initial threshold level is low enough for acceptance of the grain moth eggs and these females started parasitization immediately after the first encounter with this host species. Note that the single case when female started parasitization in the dark phase was recorded during the first contact with the host (Fig. 1*C*).

The total cumulative percentage of parasitizing females in treatment 1*C* of the first experiment was significantly lower than that in treatments 1*A* and 1*B* (Fig. 4). Evidently, the first contact with the host falling on scotophase suppressed not only current but also further parasitization. The same conclusion is suggested by analysis of the results of the second experiment (Fig. 4). The mechanism of the influence of the circadian time of the first contact with the host not only on the current but also on the subsequent parasitization is not yet clear, although it may be supposed that it is partly based on learning. It is known that the host selection by *Trichogramma* females may be influenced by learning. Usually, prior oviposition induced an increased preference for the given host species (Kaiser et al., 1989; Reznik, 1993; Bjorksten and Hoffmann, 1995, 1998). This reaction is typical of other insect parasitoids and commonly considered as the result of conditioning (Alphen and Vet, 1986; Vet and Groenewold 1990; Reznik, 1993; Vinson, 1998). However, habituation (another type of learning, waning of a response to a stimulus upon its repeated presentation) on the contrary, may result in a decreased preference of a given host (Eisenstein and Reep, 1985; Reznik, 1993). Normally, the first contact with the host induced parasitization in certain *T. principium* females, thereby sharply increasing preference for the grain moth eggs and thus assuring further parasitization (Reznik et al., 2001b, 2003). When the first contact with the host fell on the scotophase, parasitization did not start and the conditioned reflex was not induced in the absence of reinforcement. Conceivably, in such a situation, habituation to host stimuli occurred, as it does not require reinforcement. Habituation, in turn, decreased the probability of host acceptance during the coming photophase. Thus, not only current, but also further parasitization could be suppressed.

The general dynamics of the daily number of eggs laid by parasitizing females of *T. principium* revealed in the present study (Fig. 5) are in agreement with previously published results (Reznik et al., 2001b). Females of other *Trichogramma* species also laid 40–60% of their total number of eggs during the first day of oviposition (Fleury and Bouletreau, 1993; Olson and Andow, 1998; Park et al., 1999; Zhang et al., 2001). In all the cited studies, fecundity was maximum on the first day of parasitization and then gradually decreased. The slight but significant dip immediately following the peak in both experiments (Fig. 5) was reported in only one of the above listed studies (Park et al., 1999), supposedly because of too large a time scale. However, similar results were recently obtained with another insect parasitoid (Abe and Tahara, 2003). This dip in fecundity could be possibly connected with the short period of time when all mature eggs stored in ovaries of emerging females were already laid, while new eggs were not mature yet.

As for the rhythm of *T. principium* females parasitization intensity recorded under photoperiodic conditions (Fig. 6), it is similar to that previously reported for other *Trichogramma* species (Afonina et al., 1986; Pompanon et al., 1993, 1999), although certain other species continued parasitization during the scotophase (Buleza, 1985; Tavares and Voegele, 1991). Under constant light, parasitization quickly became arrhythmic (Fig. 7), but one peak of oviposition was observed during the subjective scotophase on the second day. It is interesting that this spontaneous peak occurred at the same exposure in all the treatments of the second experiment. Hence, its position did not depend on the subjective time of the first contact with the host. It is of interest that it is delayed in comparison with the peak of fecundity recorded under photoperiodic conditions (comp. Figs. 6 and 7). Such spontaneous phase-shifted peaks of activity recorded after transfer to constant light conditions are common in insects and considered to be of endogenous origin (Saunders, 2002). This suggests that the endogenous circadian rhythms participated in the regulation of the daily cycles of *Trichogramma* oviposition. On the other hand, manifestation of these rhythms strongly depends on exogenous factors, as darkness seems to inhibit parasitization directly (exogenously).

The endogenous nature of circadian rhythms of oviposition was previously proved for numerous insect species (Chernyshev, 1996; Saunders, 2002). In one of the thoroughly studied model insects, *Drosophila melanogaster* Mg. (Diptera, Drosophilidae), both adult emergence, locomotion activity and oviposition exhibit robust circadian rhythms, which proved to be under rigid endogenous control (Sheeba et al., 2001b). In *Trichogramma*, on the contrary, both the rhythm of the onset of parasitization and further oviposition intensity are very unstable and could be easily modified by direct influence of the environment. A significant role of direct exogenous influence of light and temperature was also revealed in the regulation of daily rhythms of *Trichogramma* adult emergence (Zaslavski et al., 1999; Karpova and Reznik, 2002; Karpova, 2006). Possibly, under natural conditions, such flexible rhythms of behavior allow parasitoids to use any favorable conditions independently of the time of the day. This is particularly important for minute parasitoids with a short life span.

Other studied insect species differ in flexibility of oviposition rhythms. For instance, females of the orange wheat blossom midge, *Sitodiplosis mosellana* (Gehin) (Diptera, Cecidomyiidae) are capable of direct reaction to the environment: they mostly lay eggs during the evening crepuscular period, but cloudy conditions induced an earlier onset of oviposition (Pivnick and Labbe, 1993). In flesh flies (Diptera, Calliphoridae), circadian rhythm of oviposition is much more stable: eggs are laid only during the daytime and oviposition does not occur at night regardless of artificial or full moon light (Tessmer et al., 1995).

CONCLUSIONS

The observed dynamics of host parasitization intensity by *T. principium* females represents a mixture of arrhythmic age-related trends (increase in the cumulative percentage of parasitizing females and decrease in their average fecundity) and daily rhythms (both parasitization and its continuation occurred mainly during photophase).

Special experiments revealed an endogenous component of daily rhythms, but it is very weak: under constant light the rhythms damped out after one cycle, while darkness could directly inhibit parasitization. Evidently, exogenous factors are the main regulators of the studied rhythms.

Circadian time of the first contact with the host can influence further parasitization. The first contact with the host falling on the dark phase (in individuals kept at the photoperiod) or on the subjective circadian scotophase (in individuals transferred to the constant light conditions) caused a decrease in the final cumulative percentage of parasitizing females.

The lability of parasitization dynamics enables *Trichogramma* females to adapt immediately to any light–dark regimes, although darkness may have negative effects on their parasitization intensity.

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