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Effect of photoperiod on parasitization by *Trichogramma principium* (Hymenoptera: Trichogrammatidae)

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Abstract. The effect of photoperiod on parasitization of the eggs of the Angoumois grain moth, *Sitotroga cerealella* (Olivier, 1789) by *Trichogramma principium* Sugonyaev & Sorokina, 1976 was investigated under several photoperiodic regimes of L : D = 3 : 21, 6 : 18, 9 : 15, 12 : 12, 15 : 9, 18 : 6 and 21 : 3. In all regimes, certain wasps delayed ovipositing in this non-preferred host. Potential fecundity of *T. principium* females (the number of mature ovarial eggs at emergence) and subsequent oogenesis (estimated by the number of mature ovarial eggs in non-ovipositing females) was independent of photoperiod. However, the percentage of females that oviposited was higher for females that developed and were kept under 6–12 h long photophase than for those that developed and were kept under ultra short (3L : 21D) and under long (18L : 6D and 21L : 3D) photophases. The average duration of the pre-oviposition (egg retention) period showed the opposite pattern to the photoperiodic response. A possible explanation of this reaction is that the delay in oviposition is adaptive if the probability of finding a better host is high. In autumn, when the last *Trichogramma* females are still active but their lepidopteran hosts are already much less abundant, then parasitization of any suitable host is the best strategy.

INTRODUCTION

It is well known that photoperiod may influence many aspects of insect life. Some of them are the components of the "diapause syndrome", while others are more or less independent of diapause (Danilevski, 1965; Zaslavski, 1988; Denlinger, 2002; Saunders, 2002; Danks, 2003). In particular, reproduction may be controlled by photoperiod both qualitatively (as a switch between reproduction and adult diapause) and quantitatively (as an influence on the duration of the pre-oviposition period, oviposition intensity, total lifetime fecundity, etc.). In earlier studies on insects, changes in observed oviposition were mediated by (or at least accompanied by) corresponding changes in oogenesis intensity. Although this correlation was not always clearly demonstrated, it was implied by the authors and, thus, the photoperiodic effects on the induction of the reproductive diapause, duration of the pre-oviposition period, fecundity, etc. were considered as qualitative or quantitative manifestations of the same causal relationships "photoperiod – oogenesis – oviposition" (Teraoka & Numata, 1995; Musolin & Saulich, 1999, 2000; Inoue, 2001; Tommasini & Van Lenteren, 2003; Fantinou et al., 2004, see Discussion for more references). However, oogenesis does not necessarily result in immediate oviposition. For a variety of reasons, females may retain mature eggs (e.g. Flanders, 1950; Spencer & Miller, 2002; Gillott, 2003; see Discussion for more references). Generally speaking, photoperiod may influence the behavioural components of oviposition. But, as far as we know, this hypothesis has never been verified. To do this, a suitable model is required, namely, an insect species inclined to retain mature eggs. It is well known that this feature is typical of insect parasitoids (Flanders, 1950) and particularly *Trichogramma* Westwood species (see Reznik et al., 1998, 2001, 2003 for the references).

The aim of the present study was to test the hypothesis that photoperiod may modify the reproductive behaviour of females not only through changes in oogenesis, but also through modification of the "behavioural component". For this purpose, we investigated the effect of photoperiod on various aspects of parasitization by *Trichogramma* females: their potential fecundity (as measured by the number of mature ovarial eggs at emergence), the duration of the pre-oviposition (egg retention) period, the percentage of females that oviposited, their survival, fecundity, and subsequent oogenesis (also estimated by the number of mature ovarial eggs). Numerous species of the genus *Trichogramma* are widely used for the biological control of various insect pests (Smith, 1996). Thus, the results of this study could also be of practical importance.

This study was conducted using an egg parasitoid *Trichogramma principium* Sugonyaev & Sorokina, 1976. Earlier (Reznik et al., 1998, 2001, 2003) we demonstrated that certain *T. principium* females successfully parasitized the eggs of the Angoumois grain moth, *Sitotroga cerealella* (Olivier, 1789), whereas other individuals delayed oviposition. The later females had a high number of mature ovarial eggs, suggesting that the delay in oviposition may be considered as egg retention. The reason for this delay is that *S. cerealella* is a poor quality (small) host (Smith, 1996). *T. principium* females prefer Noctuidae eggs, possibly because of their larger size. In natural conditions, *Trichogramma* females attack a wide variety of lepidopteran hosts using host size as the main cue for host acceptance (Schmidt, 1994). Similar results were obtained with other *Trichogramma* species offered non-preferred hosts. The percentage of parasitizing females and the number of parasitized hosts may depend not only on the host species, the stage of embryo development, the number of host eggs offered, etc. but also on temperature, humidity and other environmental factors (Orphanides & Gonzalez, 1970; Pak & Heiningen, 1985; Pavlik, 1992; Fleury & Boulétreau, 1993; Monje et al., 1999; Hoffmann et al., 2001; Reznik et al., 2001, 2003; Reznik & Vaghina, 2006a).

Photoperiod influence on the duration of egg retention was first demonstrated in *Trichogramma pretiosum* Riley, which shows a significant increase in the pre-oviposition period only under an ultra-short (0.5L : 23.5D) photophase (Orphanides & Gonzalez, 1970). Later, the effects of long (20L : 4D) and short (12L : 12D) photophases on parasitization of *S. cerealella* eggs by *T. evanescens* Westwood females were investigated by Zaslavski & Mai Phu Qui (1982). The percentage of ovipositing females was practically independent of photoperiod, although the mean fecundity was slightly higher under long day conditions. Similar results were later obtained for *T. dendrolimi* Matsumura (Park et al., 1999). However, the fecundity of *T. galloi* Zucchi is independent of day lengths ranging from 11 to 14 h (Cônsoli & Parra, 1994). *T. evanescens* adults kept in total darkness parasitized fewer hosts (Tunçbilek & Ayvaz, 2003), but fecundity in *T. minutum* Riley is not affected by developing in darkness (Corrigan et al., 1994). None of these earlier studies investigated the influence of day length over the entire photoperiodic scale on the parasitization of *Trichogramma* females, although this could be important for understanding of the physiology underlying this response (Zaslavski, 1988; Denlinger, 2002; Saunders, 2002).

It is known that the number of hosts parasitized by a female is affected by many interacting factors: host species, population density, egg load (number of mature ovarial eggs), etc. (Rosenheim & Rosen, 1991; Vinson, 1998; Janz, 2002; Fellowes et al., 2005). However, in only one of the previous studies (Zaslavski & Mai Phu Qui, 1982) were the photoperiodic responses of the different components of parasitization (the percentage of ovipositing females, their potential and realized fecundity) analyzed separately. Once *Trichogramma* females start to parasitize, they usually tend to continue until they die (Reznik et al., 2001, 2003). Hence, the average life span of females could also influence the total number of hosts parasitized.

MATERIAL AND METHODS

Insects and general methods

Experiments were conducted with a strain of *T. principium* collected in Chimkent province (Southern Kazakhstan) from eggs of Noctuidae and then cultivated on *S. cerealella* eggs for more than 100 generations under constant laboratory conditions (20°C, 18L : 6D). The species identity was checked by the author of the species, Dr. E.S. Sugonyaev (Zoological institute, St. Petersburg, Russia). All experiments were conducted at the same temperature (20°C), but under different photoperiods. To start the experiment, a paper card with several thousands of *S. cerealella* eggs glued on it was placed in a large test tube with ca 1000 *T. principium* adults and subjected to parasitization for 2–4 h. Then the card was cut into equal parts which were each put in a separate tube and placed in thermostatic chambers kept at different photoperiodic regimes. The first adults to emerge were killed just before the scotophase, ensuring that after the next light-on the tube will contain a significant number of practically even-aged wasps (*T. principium* adults never emerge when in dark). These adults were offered a mate for 4–6 h. Then an equal number of females from each photoperiodic regime were individually placed into small (8 × 45 mm) test tubes that contained honey (50% water solution) as a carbohydrate food source. A small paper card with 50–60 *S. cerealella* eggs was placed in each tube. After 48 h, each female was checked to determine whether it is still alive, the paper card with host eggs was taken from the tube and, if required according to the design of the experiment, was replaced with a new card.

When parasitoid larval development is complete, the parasitized grain moth eggs darken and could be counted and in this way the number of hosts parasitized during each exposure (period between host replacements) was determined. As *S. cerealella* eggs are rather small, they were offered in excess and *T. principium* females usually lay only one egg in each egg of the grain moth. Hence, the number of hosts parasitized was taken to be the number of eggs laid by *Trichogramma*. For each exposure of each replicate of each treatment in each experiment, the cumulative percentage of ovipositing females (i.e. those that laid at least one egg during the given or previous exposures) was calculated. The average oviposition period in *T. principium* is rather short (ca 4 days) and the wasps die shortly after the termination of oviposition (Reznik et al., 2001). Hence, to estimate the tendency to parasitize we used cumulative percentage, that at the 2nd and 3rd exposures was higher than the actual percentage of ovipositing females. For each ovipositing female, the number of eggs laid during each exposure and the duration of the pre-oviposition period (i.e. the period of time spent in a test tube with hosts before the first egg was laid) were determined. Time of laying of the first egg was taken to be the middle of the corresponding exposure period.

First experiment

The aim of the first experiment was to estimate the pattern of the photoperiodic response. In each replicate, *T. principium* females developed under photoperiods of L : D = 3 : 21, 6 : 18, 9 : 15, 12 : 12, 15 : 9, 18 : 6 or 21 : 3. Freshly emerged females were provided with host eggs for 48 h at the same conditions as they completed their development, i.e. at photoperiods of L : D = 3 : 21, 6 : 18, 9 : 15, 12 : 12, 15 : 9, 18 : 6 or 21 : 3, respectively. In total, 3000 females (350–560 per replicate) were tested under 7 photoperiods in 7 replicates of this experiment, using successive generations of the laboratory line.

Second experiment

The second experiment was aimed at more detailed analysis of the photoperiodic reaction. In this experiment, females that developed under four photoperiods (L : D = 3 : 21, 9 : 15, 15 : 9 or 21 : 3) were offered *S. cerealella* eggs under one of two photoperiodic regimes (3L : 21D or 15L : 9D). Thus, there were 8 treatments (combinations of 4 photoperiods during development and 2 during oviposition). This experiment included three exposures, i.e. each female was sequentially offered three standard portions of host eggs and each portion was exposed for 48 h. At the end of the third exposure, the percentage of wasps surviving was recorded and they were then dissected to determine the number of mature ovarial eggs. In addition, in each replicate of this experiment, 15–20 females that developed under each pho-

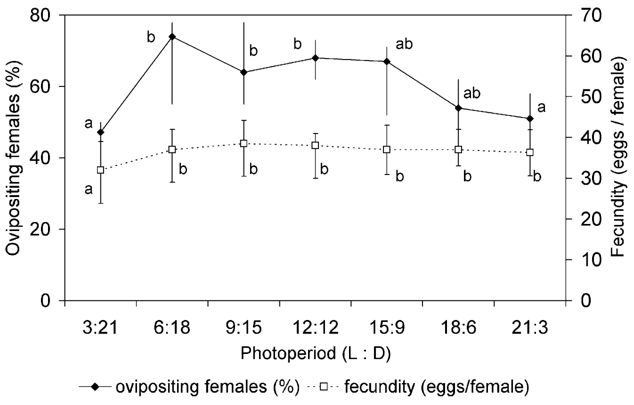

Fig. 1. The effect of photoperiod on the percentage of *T. principium* females that started to oviposit within 2 days of coming into contact with the host and on their fecundity. Percentages, n = 7; fecundity, n = 127–251. The symbols represent medians and the bars show the range between the first and the third quartile. Symbols with different letters are significantly different at $p < 0.05$ (Tukey test of the transformed data).

toperiod were dissected shortly after emergence (no host or honey were provided for these females). Nine replicates of the second experiment were conducted with successive generations of the laboratory line, each included 200 females (25 females per each of 8 treatments).

Statistical treatment

Preliminary statistical treatment of both experiments revealed significant difference among replicates for all the parameters studied. Similar high variability in successive generations of laboratory lines was recorded earlier in *Trichogramma* by different authors for various biological characteristics (Zaslavski & Mai Phu Qui, 1982; Zaslavski & Umarova, 1990; Reznik et al., 1996; Schmuck et al., 1996; Hoffmann et al., 2001; Reznik et al., 2002). Therefore, for the statistical treatment special transformations were used.

Non-parametric data (percentages of ovipositing females and survival) were separately determined for each replicate of each treatment. Medians and quartiles were used as descriptive statistics, each replicate being considered as an experimental unit. In addition, the percentages were ranked for each replicate separately and ranks were used to compare treatments by ANOVA.

Mean duration of the pre-oviposition period was also estimated for each replicate of each treatment of the 2nd experiment and then these means were tested using ANOVA and the Tukey HSD test and averaged once again to give the mean ± SE.

With fecundity, individual females were considered as experimental units. To approximate the general temporal pattern of fecundity, data of all replicates and treatments were pooled. To compare experimental treatments, absolute values were replaced by deviations from the means for pooled treatments of each replicate. Then, these deviations were analyzed with ANOVA and the Tukey HSD test. In the figures, untransformed pooled data of all replicates of each treatment (medians and quartiles) are given.

The distribution of the number of mature ovarial eggs in emerging females and in those that did not oviposit was close to normal. Thus, ANOVA was used for the statistical treatment but, because of the significant variation among replicates, medians and quartiles were used as descriptive statistics. Number of mature ovarial eggs in ovipositing females was not normally distributed (see Reznik et al., 1998, for distribution patterns). Therefore, medians, quartiles and the Kruskal-Wallis distribution-free test were used.

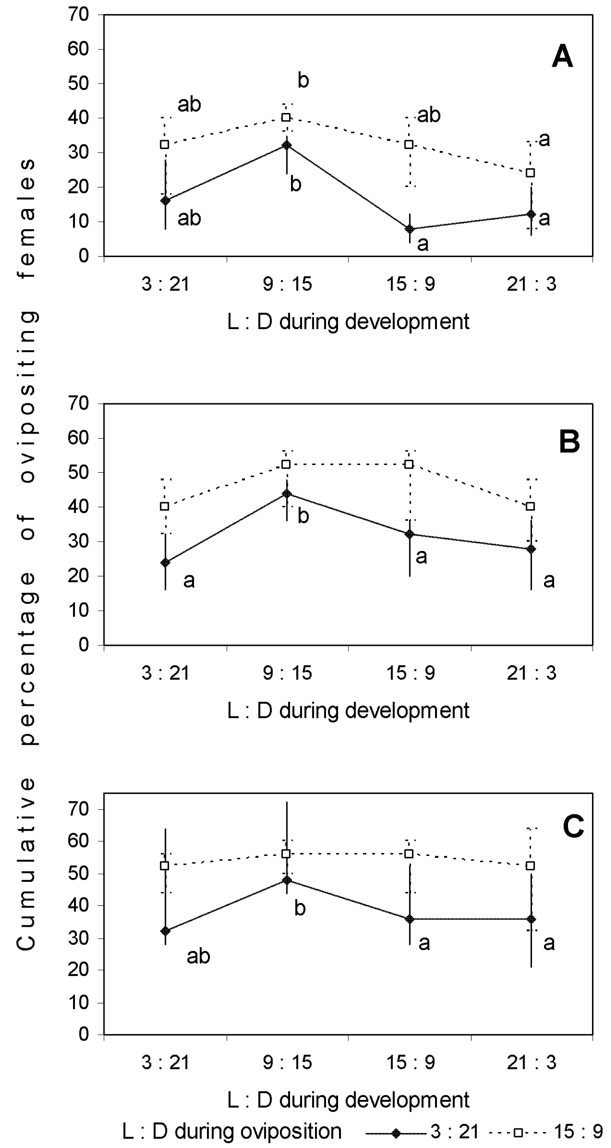

Fig. 2. The effect of photoperiod experienced during development and during contact with the host on the cumulative percentage of *T. principium* females that started to oviposit within 2 days (A), 4 days (B), and 6 days (C) of coming into contact with the host. The symbols represent medians and the bars the range between the first and third quartile, n = 9. Symbols with different letters are significantly different at $p < 0.05$ level (Tukey test of ranked data).

RESULTS

Percentage of ovipositing females

One-way ANOVA of the ranked data of the 1st experiment showed that the percentage of females that started to oviposit during the first 48 h of contact with the host was significantly ($F_{(6,49)} = 4.5$, $p = 0.001$) dependent on the photoperiodic conditions experienced during their development. Pairwise comparison using the Tukey test revealed significant ($p < 0.05$) differences only between the wasps that developed under a 6–12 h long photophase

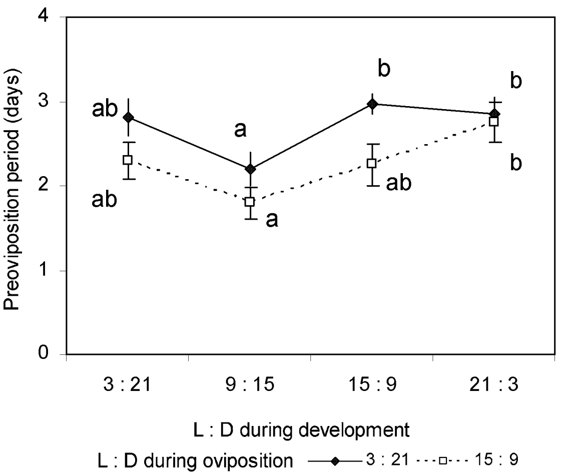

Fig. 3. The effect of photoperiod experienced during development and during contact with the host on the mean duration of the preoviposition period in *T. principium* females that started to oviposit within 6 days of coming into contact with the host. Means ± SE are given, n = 9. Symbols with different letters are significantly different at $p < 0.05$ level (Tukey test).

and those that developed under an ultra-short or ultra-long photophase (Fig. 1). However, the difference between pooled data for short (9–12 h) and long (18–21 h) days was highly significant ($F_{(1,26)} = 15.7$, $p = 0.001$).

Two-way ANOVA showed that the percentage of females that started to oviposit during the 1st exposure of the 2nd experiment significantly depended on the photoperiodic conditions they experienced during development ($F_{(3,64)} = 11.5$, $p < 0.001$) and as adults ($F_{(1,64)} = 27.1$, $p < 0.001$), with an insignificant interaction ($p = 0.21$). Independently of the photoperiod experienced as adults, the percentage ovipositing was greater for females that developed at 9L : 15D (Fig. 2a). This tendency was much more pronounced if the host eggs were offered under conditions of an ultra-short photophase, when the average percentage of ovipositing females (hereafter, medians and quartiles are given) was much lower: 16% (8–26%) and 32% (16–42%) at 3L : 21D and 15L : 9D, respectively. Similar results were recorded during the 2nd exposure (Fig. 2b): the cumulative percentage of females ovipositing significantly depended on the photoperiodic conditions they experienced during development ($F_{(3,64)} = 8.7$, $p < 0.001$) and as adults ($F_{(1,64)} = 19.8$, $p < 0.001$), with an insignificant interaction ($p = 0.49$). At the 3rd exposure, the effect of the two above mentioned photoperiods was also significant: $F_{(3,64)} = 3.6$, $p = 0.02$, and $F_{(1,64)} = 15.9$, $p < 0.001$, respectively, with a marginally non significant ($p = 0.09$) interaction (Fig. 2c). Analysis of the results obtained for adults exposed to the two photoperiods using the Tukey test showed that at the long photophase, the difference among females that developed under the different photoperiodic regimes gradually disappeared (Figs 2b and 2c).

Note that although the cumulative percentage of ovipositing females markedly increased with time (comp. Figs 2a and 2c), the difference between the data for two photoperiods acting on the adults remained stable. At the end of the experiment (Fig. 2c) the average cumulative percentage of ovipositing females was 38% (28–62%) and 52% (42–62%) under 3L : 21D and 15L : 9D, respectively.

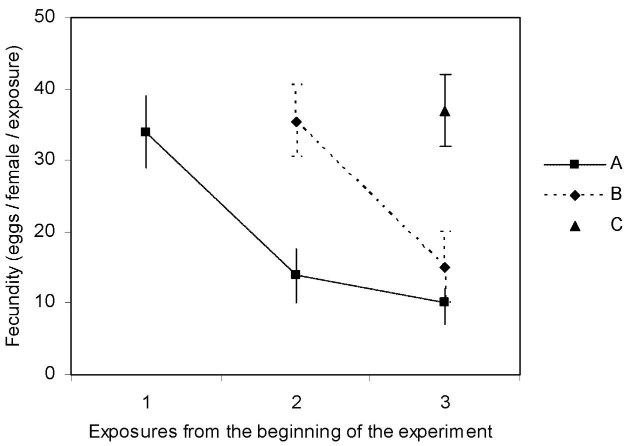

Fig. 4. Number of eggs laid by *T. principium* females during three successive 48 h long exposures (periods of contact with the host) of those that started to oviposit during the 1st (A, n = 285), 2nd (B, n = 193) and 3rd (C, n = 196) exposure from the beginning of the experiment. The symbols represent medians and the bars the range between the first and third quartile.

Pre-oviposition period

The duration of the pre-oviposition period significantly depended both on photoperiodic conditions experienced during development ($F_{(3,64)} = 4.4$, $p = 0.009$; two-way ANOVA) and those experienced as adults ($F_{(1,64)} = 7.3$, $p = 0.007$), with an insignificant ($F_{(3,64)} = 0.8$, $p = 0.51$) interaction between these factors. An ultra-short photophase acting on the adults increased the pre-oviposition period, while those that developed under a photoperiod of 9L : 15D had a shorter pre-oviposition period (Fig. 3).

Fecundity

In the first experiment, one-way ANOVA revealed significant ($F_{(6,1466)} = 5.1$, $p < 0.001$) dependence of *T. principium* fecundity on the photoperiodic conditions experienced during development and oviposition. However, pairwise comparison using the Tukey test revealed a slight but significant ($p < 0.05$) differences in fecundity only between the wasps that developed and oviposited under an ultra-short photophase and all other photoperiods (Fig. 1).

In the second experiment, the fecundity was highest for females that started oviposition during the first exposure and then oviposition decreased steeply (Fig. 4). In addition, the number of hosts parasitized during the exposure when they first oviposited was significantly ($F_{(2,869)} = 11.2$, $p < 0.001$) greater and increased with duration of the pre-oviposition period. Fecundity during the 2nd exposure (counting from the onset of oviposition) showed the same dependence ($F_{(1,542)} = 9.4$, $p = 0.002$). Hence, when analyzing the influence of photoperiod, data for different exposures (counting both from the beginning of the

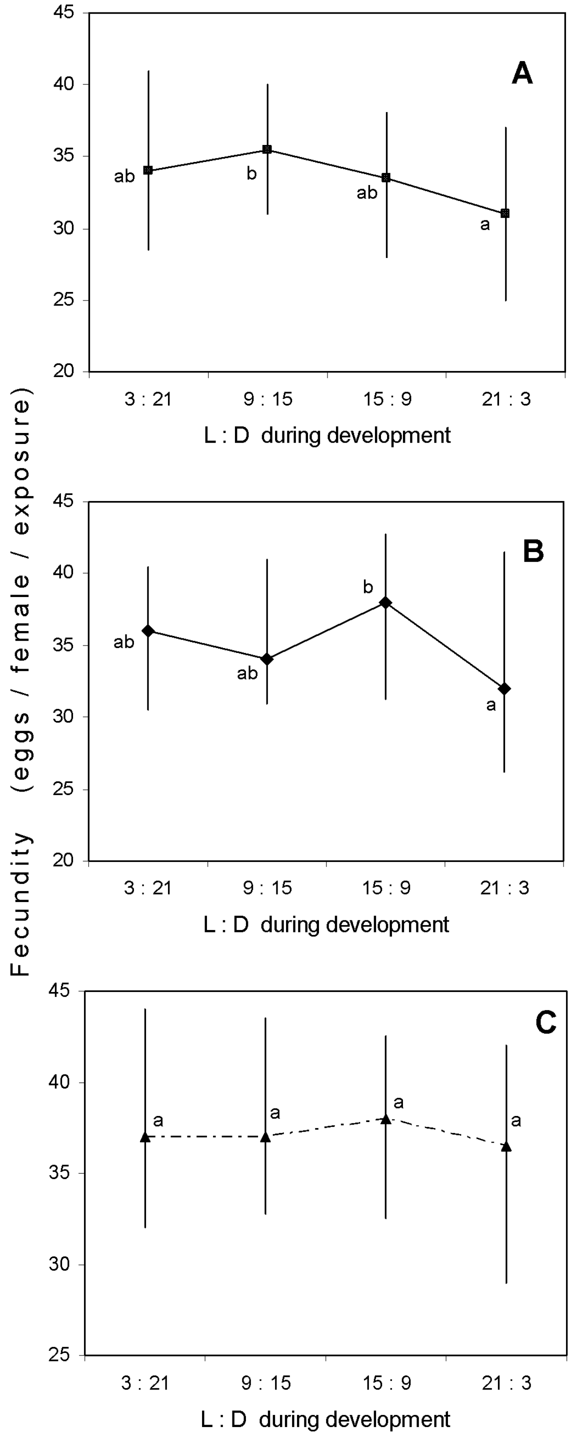

Fig. 5. The effect of photoperiod experienced during development on the number of eggs laid during exposure to hosts when oviposition was started by *T. principium* females ovipositing within 2 days (A), 4 days (B) and 6 days (C) of coming into contact with the host. The symbols represent medians and the bars the range between the first and third quartile, n = 40–150. Symbols with different letters are significantly different at $p < 0.05$ (Tukey test of transformed data).

experiment and from the onset of oviposition) were treated separately.

Two-way ANOVA showed that number of hosts parasitized by *T. principium*, which started to oviposit during the first exposure significantly ($F_{(3,422)} = 3.7$, $p = 0.01$) depended on the photoperiodic conditions they experienced during development, but not on that experienced during oviposition ($F_{(1,422)} = 0.03$, $p = 0.87$). The pooled data on oviposition by these females under two photoperiods are shown in Fig. 5a. In females that started to oviposit during the second exposure (Fig. 5b), fecundity during this exposure, was also dependent on the photoperiod experienced during development ($F_{(3,238)} = 2.8$, $p = 0.04$), but not during oviposition ($F_{(1,238)} = 0.02$, $p = 0.88$). In both cases (Fig. 5a and 5b) at an ultra-long photophase, the number of hosts parasitized was slightly lower, than that at a 9-h-long and 15-h-long photophase. However, females that delayed oviposition untill the 3rd exposure (Fig. 5c), had a fecundity during this exposure that was independent of both the photoperiod during development ($F_{(3,188)} = 0.02$, $p = 0.99$) and during oviposition ($F_{(1,188)} = 0.98$, $p = 0.32$).

The number of hosts parasitized during the 2nd exposure (counting from the onset of oviposition) was independent of the photoperiodic conditions experienced during development and during oviposition both for females that started to oviposit during the 1st exposure: $F_{(3,343)} = 0.96$, $p = 0.4$ and $F_{(1,343)} = 0.99$, $p = 0.32$, respectively, and in those that started during the 2nd exposure: $F_{(3,185)} = 1.5$, $p = 0.22$ and $F_{(1,185)} = 0.34$, $p = 0.56$, respectively. The number of hosts parasitized during the 3rd exposure from the onset of oviposition, which naturally was recorded only for females that started to oviposit during the 1st exposure, was also independent of the photoperiodic conditions they experienced during their development and oviposition: $F_{(3,277)} = 0.96$, $p = 0.42$ and $F_{(1,277)} = 3.1$, $p = 0.08$, respectively.

The number of mature ovarial eggs

The number of mature ovarial eggs in freshly emerged females was significantly ($F_{(8,837)} = 5.8$, $p < 0.001$; two-way ANOVA) different among generations (replicates), but was independent of the photoperiodic regimen under which the *Trichogramma* developed ($F_{(3,837)} = 0.6$, $p = 0.63$). Freshly emerged females that developed at photophases of 3, 9, 15 or 12 h, had (median and quartiles) 24 (18–30), 23 (18–28), 23 (18–29) and 24 (18–29) mature ovarial eggs, respectively. For pooled data for all photoperiods, the number of mature eggs in freshly emerged females was 24 (18–29) eggs/female (n = 873). In females that did not oviposit for six days, the average number of mature eggs increased up to 35 (29–40) eggs (n = 534), but was still independent of both photoperiod experienced during development ($F_{(3,526)} = 1.9$, $p = 0.13$), and when in contact with the host ($F_{(1,526)} = 1.8$, $p = 0.18$). Most ovipositing females lacked mature eggs: median and quartiles were 0 (0–2) eggs/female (n = 611). The Kruskal-Wallis test showed that for these females the number of mature ovarial eggs was also independent of the two above mentioned photoperiodic regimes ($p = 0.18$ and $p = 0.62$, respectively).

Survival

The percentage survival of females at the end of the 3rd exposure in the 2nd experiment (i.e. at an age of 6 days) significantly ($F_{(1, 64)} = 7.4$, $p = 0.008$; two-way ANOVA) depended on the photoperiodic conditions experienced during oviposition. Under an ultra-short photoperiod of 3L : 21D it was slightly higher than at 15L : 9D; medians and quartiles of pooled data of females that developed under all photoperiods were 74% (56–84) and 68% (50–76), respectively ($n = 36$). The dependence of survival on the photoperiodic conditions experienced during development was marginally insignificant: $F_{(3, 64)} = 2.4$, $p = 0.08$. Spearman correlation analysis of pooled data ($r = 0.14$, $n = 72$, $p > 0.05$) also showed that survival was independent of the photoperiod experienced during development.

DISCUSSION

The present study clearly revealed both "qualitative" and "quantitative" photoperiodic responses: both the cumulative percentage of ovipositing females and the duration of the pre-oviposition period depended on the photoperiod (Figs 1, 2 and 3). Note that the patterns of these responses were the inverse of one another (comp. Figs 2c and 3, 3L : 21D). This is not surprising, as we have earlier (Reznik et al., 2001, 2003) suggested that the process of egg retention might manifest itself either as a delay in oviposition or as refusal to oviposit (when it is longer than the duration of the experiment or even as long as the wasp's life).

As was noted in the Introduction, a significant increase in the pre-reproductive period was earlier demonstrated for *Trichogramma* under only an ultra-short (0.5L : 23.5D) photophase (Orphanides & Gonzalez, 1970). Other researchers who have studied the photoperiodic response in *Trichogramma* (Zaslavski & Mai Phu Qui, 1982; Cônsoli & Parra, 1994; Corrigan et al., 1994; Park et al., 1999; Tunçbilek & Ayvaz, 2003) either did not record egg retention or did not reveal any clear effect. However, certain of these results suggest that egg retention occurs and, moreover, it is dependent on photoperiod. For example (Park et al., 1999: Fig. 1), *O. dendrolimi* females that developed under 8L : 16D, during the first day of contact with the host laid much fewer eggs than those reared under a longer photophase, and during the following days, their daily fecundity was higher. This contradiction is easily explained by the increased pre-oviposition period of the short-day reared wasps. Similarly, *T. evanescens* adults kept in total darkness, during the 1st day parasitized fewer hosts, but during the 3rd day they parasitized more hosts than females kept in light-dark cycles (Tunçbilek & Ayvaz, 2003: Table 6). This tendency also suggests an increase in the pre-oviposition period, which in both of the above mentioned studies occurred under the shortest of the studied day lengths.

The opposite patterns in the effect of photoperiod on the percentage of ovipositing (non-diapausing) females and the pre-oviposition period was earlier recorded in many other insects (e.g. Ando, 1991; Ruberson et al., 1991; Canard et al., 1994; Kawano & Ando, 1997; Musolin & Saulich, 1999, 2000; Inoue, 2001; Tommasini & Van Lenteren, 2003; Fantinou et al., 2004). In these studies, delayed oviposition was considered to be a consequence of reproductive diapause (delayed oogenesis), although the adults were not dissected in some cases. In the present study, however, the number of mature ovarial eggs in freshly emerged females was independent of the photoperiodic conditions experienced during their development. The average number of mature eggs sharply decreased in ovipositing females and increased in those that did not oviposit. Both trends were earlier observed in *T. principium* and certain other insect parasitoids (see Reznik et al., 1998, 2001 for references). The present study is the first to demonstrate that the rate of these changes is independent of photoperiod.

Fecundity (number of hosts parasitized during 48 h) slightly depended on the photoperiodic conditions experienced during development, but this dependence was revealed only during the exposure when oviposition first occurred, and only after a short (less than 4 days) pre-oviposition period (Figs 1, 5a and 5b). In addition, the pattern of this dependence was opposite to that of the duration of the pre-oviposition period (comp. Fig. 3 with Figs 1 and 5a). As seen in Fig. 4 and demonstrated in numerous earlier studies, *Trichogramma* females laid about half of their eggs during the first day of oviposition (see Reznik et al., 2001 for references). Just after the onset of oviposition, females had a lot of mature ovarial eggs. During this period, they are time- rather than egg-limited. Hence, the earlier a female starts to oviposit, the more eggs she will lay during a given exposure. Thus, as both the initial egg load and the number of mature eggs in females delaying the onset of oviposition were practically independent of day length, it is conceivable that fecundity was (at least partly) indirectly influenced by changes in the duration of the pre-oviposition period. Note that in certain other studies (e.g. Atwal, 1955; Deseó & Sáringer, 1975; Weseloh, 1986; Umble & Fisher, 2002) photoperiod influenced fecundity and oogenesis intensity, but not the duration of the pre-oviposition period.

The expected life span of females was estimated using the percentage survival at the end of the 6th day. At 3L : 21D, females lived longer, but rarely oviposited. Earlier we demonstrated that the mean life span of ovipositing females was slightly shorter than that of females delaying oviposition, which could be considered as a trade-off between reproductive effort and longevity (see Reznik et al., 2003 for more discussion). Typical changes in behaviour are observed in senescent insects, in particular, a wider host choice was recorded (Fisher, 1959; Giebultowicz et al., 1990; Tallamy, 2000; Withers et al., 2000). However, the results of our recent study (Reznik & Vaghina, 2006b) suggest that egg retention influenced life span, rather than the reverse. Hence, the influence of photoperiodic conditions on *T. principium* female survival could be partly explained by an indirect action through egg retention.

Thus, we conclude that the photoperiodic conditions experienced by *T. principium* during development and oviposition have a direct influence on the willingness to oviposit in grain moth eggs, while the influence of photoperiod on fecundity and survival may be considered as (at least partly) indirect effects.

It is well known that intensity of various insect activities may depend on photoperiod (Danilevski, 1965; Zaslavski, 1988; Denlinger, 2002; Saunders, 2002), and our study represents one further example of such dependence. As for the pattern of the photoperiodic response revealed, a sharp decrease in the tendency to oviposit observed at ultra-short photophases (Figs 1 and 2) agrees well with the results of certain previous studies (Orphanides & Gonzalez, 1970; Tunçbilek & Ayvaz, 2003). Moreover, as most insect parasitoids show clear diurnal peaks in oviposition activity (Fellowes et al., 2005) and (as was shown by our unpublished observations) *T. principium* also lays most of its eggs during the photophase, it is not surprising that ultra-short photophases inhibit oviposition. Similar data were obtained, for example, with *Calliphora vicina* R.-D.: daily average flight activity of adults was the highest at 16L : 8D (Zotov et al., 1990). In the western flower thrips, *Frankliniella occidentalis* (Pergande) walking, feeding and oviposition activities increased with increasing photophase (Whittaker & Kirk, 2004).

As for the response to the photoperiod experienced during development, photophases of 9–12 h more often induced fast onset of oviposition, than long (18–21) photophases. Adaptive value of this reaction is not clear. In diapause regulation, this pattern of photoperiodic response is usually connected with aestivation or summer diapause (Danilevski, 1965; Tauber et al., 1986; Zaslavski, 1988; Denlinger, 2002; Saunders, 2002; Danks, 2003). But *T. principium* and many other Trichogrammatidae are typical "long-day species" with a facultative winter prepupal diapause (Zaslavski & Umarova, 1990; Boivin, 1994; Reznik et al., 2002; Reznik & Kats, 2004).

In natural conditions, delayed oviposition may result in temporal spread and spatial dispersal of parasitization by a group of females that emerge simultaneously, as the wasps that manifest egg retention show a significant increase in locomotory activity and dispersal rate when compared with females that oviposited (Pompanon et al., 1999; Reznik & Klyueva, 2006). Note that the refusal to oviposit in an available but not preferred host may be adaptive only if the probability of finding other (better) hosts is high. *T. principium* inhabits Central Asian deserts: Southern Kazakhstan, Uzbekistan and Turkmenistan (35–43°N). This species is well adapted to the hot and dry climate, being relatively resistant to low humidity and high temperatures (Sorokina, 1978). However, the geographical range of *T. principium* is characterized not only by hot summers, but also by very sunny and relatively mild autumns. In October and November, average temperatures varied between 12–16° and 6–12°C, respectively (Davitaya & Pastukh, 1960). As in the laboratory *T. principium* may oviposit at 15°C (Reznik & Vaghina, 2006b), these daily average temperatures allow parasitization of hosts at least during mid-day. In addition, *T. principium* showed a relatively weak tendency to diapause: at 13°C, less than 40% of prepupae diapaused and the threshold for the photoperiodic response lies between 12L : 12D and 15L: 9D (Reznik & Kats, 2004), while, e.g. in *T. embryophagum* Htg., inhabiting Central and Northern Europe, the same proportion of individuals diapaused at 15°C and the threshold lies between 15L : 9D and 18L : 6D (Reznik et al., 2002). Thus, it is conceivable that in October–November, when the last *Trichogramma* females are still active but their lepidopteran hosts are already scarce (Falkovich, 1979) it is maladaptive to postpone parasitization "hoping" to find a better host.

This tendency to speed up the life cycle and, in particular, to reduce the pre-oviposition period at the end of a favourable season is reported for other insect species (e.g. Tanaka et al., 1993; Kawano & Ando, 1997), although it is certainly not a general rule (Hodek, 1979; Ando, 1991; Ruberson et al., 1991; Canard et al., 1994; Kawano & Ando, 1997; Musolin & Saulich, 1999, 2000; Inoue, 2001; Luker et al., 2002; Tommasini & Van Lenteren, 2003). However, a comparative study of several *Trichogramma* species from various climatic zones is needed to test this hypothesis.

Delayed oviposition in the presence of a less preferred host is also recorded in other parasitoids (Donaldson & Walter, 1988; Tepedino, 1988; Vinson, 1998; Kim, 1999; Beck et al., 2001; Hirose et al., 2003), predators (Evans, 2003) and phytophages (Withers et al., 2000). Hence, a photoperiodic response similar to that described in the present paper possibly occurs in other insects. And finally, the dependence of oviposition activity on photoperiod could be important for developing methods of mass rearing *Trichogramma*.

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