

# Exogenous and Endogenous Factors Inducing Diapause in *Trichogramma principium* Sug. et Sor. (Hymenoptera, Trichogrammatidae)

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**Abstract**—Maternal control of prepupal diapause in the progeny of the egg parasitoid *Trichogramma principium* Sug. et Sor. was studied in laboratory. Pre-maternal ( $G_1$ ) and maternal ( $G_2$ ) generations were reared at 20°C and photoperiods L : D = 3 : 21, 6 : 18, 9 : 15, 12 : 12, 15 : 9, 18 : 6, 21 : 3, or 24 : 0. The tendency to diapause in the progeny ( $G_3$ ) was determined by rearing at 13°C in the dark. The experiments revealed a response of a long-day type with a threshold zone of 12–15 h. The photoperiodic conditions of rearing of both  $G_1$  and  $G_2$  generations significantly influenced the prepupal diapause in the progeny ( $G_3$ ), the maternal influence being much stronger than the pre-maternal influence. Experiments with individual females which were offered several batches of host eggs demonstrated that the incidence of diapause in the progeny also depended on endogenous factors, such as the maternal age and duration of the egg retention period.

To date, the factors inducing diapause have been studied in many insect species from various taxa. The leading role of the photoperiod, temperature, food, and other environmental factors in the regulation of development and reproduction of insects was clearly demonstrated by both field observations and experimental studies (Danilevskii, 1961; Tyshchenko, 1977; Tauber *et al.*, 1986; Zaslavski, 1984, 1996). The choice between diapause and active development in some insects depends to a large extent on endogenous factors, and primarily age-related changes (Mousseau and Dingle, 1991; Denlinger, 1998; Fox and Mousseau, 1998).

The object of our work, *Trichogramma principium* Sug. et Sor., belongs to the group of egg parasitoids that are commonly used as biological agents of agricultural and forest pest control, and also as model objects of various studies in the field of insect ecology and physiology (Smith, 1996). The experimental study of factors inducing diapause is especially important in this case since it constitutes an essential element of the mass rearing techniques (Voegelé *et al.*, 1986; Boivin, 1994).

The seasonal cyclicality in *Trichogramma* is characterized by temperature of larval development being the main factor inducing the prepupal diapause, while the effect of photoperiod is relatively small (Maslennikova, 1959; Bonnemaïson, 1972; Boivin, 1994; Laing and Corrigan, 1995; Garcia *et al.*, 2002). In most of

the studied *Trichogramma* species the fraction of diapausing progeny was shown to depend on the photoperiodic conditions of development of maternal individuals and on their age (Zaslavski and Umarova, 1981, 1990; Mai Fu Kwi and Zaslavski, 1983; Sorokina and Maslennikova, 1986, 1987; Reznik *et al.*, 2002). The maternal age effect on the progeny diapause in *T. principium* is made more complicated by the fact that when eggs of a non-preferred host, such as the grain moth *Sitotroga cerealella* Oliv. (Lepidoptera, Gelechiidae), are offered to the *Trichogramma* females, oviposition starts immediately in some females, but in a considerable fraction it is delayed for 2 days or longer (up to 8–10 days). Thus, the females that hatched simultaneously do not all start ovipositing at the same time. Therefore, two relatively independent factors can be distinguished: the age of a female and the egg retention period. In this feature, *T. principium* clearly differs from the previously studied *T. embryophagum* Htg., in which nearly all individuals start ovipositing soon after contact with the host (Reznik *et al.*, 2002).

This study had two main goals. The first one was to study the dependence between the diapausing fraction in *T. principium* progeny and the photoperiods acting upon the maternal and pre-maternal generations (i.e., to make the photoperiodic response curves). The second goal was to study the effect of endogenous factors, such as the female age and the duration of the egg

retention period, on the tendency toward diapause in the progeny.

## MATERIALS AND METHODS

Experiments were performed using a laboratory strain of *T. principium* which had been reared for many generations on grain moth eggs at L : D = 18 : 6 and 20°C. In the experiments, the maternal generations G<sub>1</sub> and G<sub>2</sub> developed at 20°C and the photoperiods L : D = 3 : 21, 6 : 18, 9 : 15, 12 : 12, 15 : 9, 18 : 6, 21 : 3, and 24 : 0. The test for prepupal diapause (generation G<sub>3</sub>) was performed in the dark at 13°.

### *Mass Infestation*

The photoperiodic response was studied using the mass infestation technique. The necessary number of batches of grain moth eggs (500–1000 each), corresponding to the number of regimes studied, were selected from a single sample. Each batch was glued onto a separate sheet of cardboard, and all the cardboards together were offered for 24 h to trichogramma females from a single generation of the main laboratory strain, the parasitoid-to-host ratio being about 1 : 10. The cardboard sheets with infested eggs (the pre-maternal generation G<sub>1</sub>, or “grandmothers”) were then placed into separate tubes, and each group was allowed to develop under a specific photoperiodic regime.

Approximately 24 h after G<sub>1</sub> generation started to emerge (i.e., 19–20 days after infestation at 20°C), cardboard sheets with 100–200 fresh grain moth eggs were placed for 24 h in each tube. After this period, sheets with freshly infested eggs (the maternal generation G<sub>2</sub>) were also transferred into separate tubes and subjected to different photoperiodic regimes. Approximately 24 h after the emergence of the maternal generation, sheets with 200–300 grain moth eggs were placed for 24 h in each tube, and then all the cardboard sheets with freshly infested eggs (generation G<sub>3</sub>, or the progeny) were transferred into a low-temperature chamber (13°C, darkness). At this temperature active development of *T. principium* was completed 3 months after infestation. At the end of this period all infested host eggs were dissected and the number of developed adults and diapausing prepupae of the parasitoid was determined; the larvae which died at various stages of development were not counted. Data for each cardboard sheet were treated as a single trial of the experiment.

### *Individual Infestation*

To study the incidence of diapause in the progeny in relation to the maternal age and the egg retention period, 50 randomly selected freshly emerged females of the maternal generation were placed in separate tubes and then kept at the same photoperiodic regime at which they had developed. Each female was offered 50–60 grain moth eggs. Every 2 days during the experiment, the egg batches were replaced with fresh ones, and the infested eggs (the next generation) were placed in a low-temperature chamber (13°C, darkness). The duration of each experiment was determined by the individual adult’s lifespan, which in most cases did not exceed 13–15 days. The fraction of diapausing individuals was determined from summarized data for each 2-day period.

### *Data Processing*

The number of trials and the sample sizes are given below, together with the descriptions of each experiment. In the mass infestation experiments, the fractions of diapausing individuals, determined for each trial, were transformed by the formula  $Y = \arcsin(\sqrt{X})$  and then used for analysis of variance and for comparison of means (Tukey test). In the individual infestation experiments, non-transformed fractions of diapausing individuals were compared using  $\chi^2$  criterion, and the maternal age effect was estimated using the Spearman test for rank correlation. Data transformation and further processing were performed using the SYSTAT software. All the figures show original (non-transformed) data.

## RESULTS AND DISCUSSION

### *Effect of the Conditions of Development of the Maternal Generation*

Figure 1 shows the results of the first experiment, in which generation G<sub>1</sub> developed at the same day length at which the main laboratory strain was kept (L : D = 18 : 6). Females of 6 generations of the laboratory strain were used for the experiment. A total of 30 trials were made for each photoperiod (4–6 trials per generation), with no less than 100 infested grain moth eggs examined in each trial. ANOVA including the whole body of data showed the fraction of diapausing individuals in the progeny (generation G<sub>3</sub>) to depend significantly on the photoperiod at which the maternal generation G<sub>2</sub> had developed ( $F = 97.3$ ,  $p < 0.001$ ). Development of maternal individuals at short day

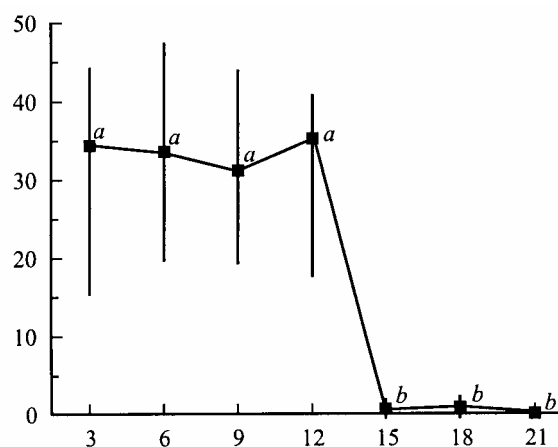
(3–12 h) induces diapause in 30–40% of the progeny, whereas 15 h of light result in practically no diapause at all. Changes in the incidence of diapause within the short-day and long-day segments of the photoperiodic scale were shown by the Tukey test to be non-significant. *T. principium* evidently shows a typical long-day photoperiodic response with a threshold positioned between 12 and 15 h. Very similar results were obtained earlier for other *Trichogramma* species studied (Bonnemaïson, 1972; Zaslavski and Umarova, 1981; Mai Fu Kwi and Zaslavski, 1983; Maslennikova and Sorokina, 1986; Sorokina and Maslennikova, 1986, 1987; Reznik *et al.*, 2002), and also for most other egg parasitoids (Jackson, 1963; van den Berg, 1971; Anderson and Kaya, 1974; Boivin, 1994).

It should be noted that the fractions of diapausing progeny differed significantly between the laboratory strain generations as well ( $F = 6.5$ ,  $p < 0.001$ ). The considerable variability of the results obtained for these consecutive generations may have been caused by endogenous processes, which were previously observed in other *Trichogramma* species (Zaslavski and Umarova, 1981; Reznik *et al.*, 2002; Voinovich *et al.*, 2003).

As concerns the mechanism of the “maternal effect” on the tendency to prepupal diapause in the progeny, one may assume, by analogy with other insect species, that the hormonal status of the female, determined by the photoperiod, has some influence on the oocytes and thus affects the hormonal system of the developing larva (Vinogradova, 1991; Mousseau and Dingle, 1991).

#### *Effect of the Conditions of Development of the Pre-maternal Generation*

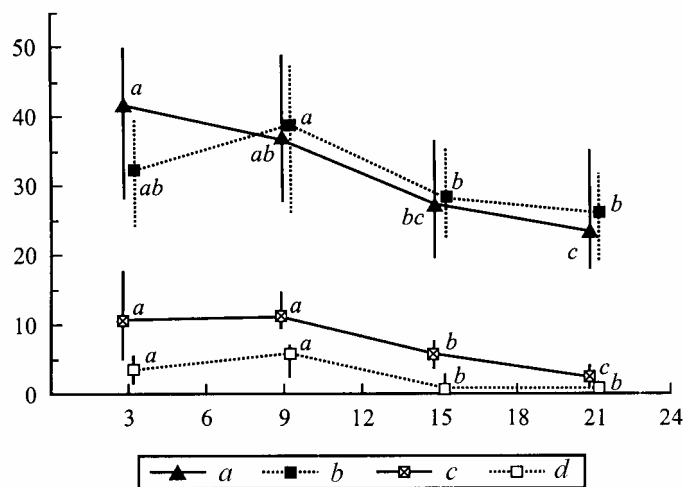
In the second experiment, devoted to the effect of “grandmothers” on the incidence of diapause, generations  $G_1$  and  $G_2$  developed at photoperiods  $L : D = 3 : 21$ ,  $9 : 15$ ,  $15 : 9$ , and  $21 : 3$ , for a total of 16 different treatments (Fig. 2). Eleven generations of the laboratory strain were involved. Each variant was studied with 4 trials for each generation, and each trial included no less than 100 infested grain moth eggs. The fraction of diapausing individuals in progeny  $G_3$  was shown by ANOVA to depend very significantly ( $p < 0.001$ ) on the conditions of development of generations  $G_2$  and  $G_1$ , the effect of “mothers” being much stronger than that of “grandmothers” ( $F = 1223.4$  and  $F = 101.8$ , respectively). The “generation factor” was much weaker but still significant ( $F = 8.3$ ,  $p < 0.001$ ).



**Fig. 1.** Dependence of the fraction of diapausing progeny on the photoperiodic conditions of development of the maternal generation of *Trichogramma principium*. Abscissa: photoperiod affecting females of the maternal generation  $G_2$  (day length, h); ordinate: fraction of diapausing prepupae in the progeny  $G_3$ , %. Median values (squares) and quartiles (vertical bars) are shown. The points marked with different letters correspond to the values found to be significantly ( $p < 0.05$ ) different by the Tukey test for arcsine-transformed data.

The response of generation  $G_3$  to the photoperiod affecting generation  $G_1$  evidently depended on the conditions of development of generation  $G_2$  (Fig. 2). For example, if the maternal generation  $G_2$  had developed under long-day conditions  $L : D = 15 : 9$  or  $21 : 3$ , the fraction of diapausing individuals in the progeny was relatively low regardless of the photoperiod affecting  $G_1$ . Still, in both cases (Figs. 2c and 2d) the fraction of diapausing individuals decreased significantly over the day length interval from 9 to 15 h. The same phenomenon was observed when generation  $G_2$  developed at  $L : D = 3 : 21$  (Fig. 2a). Thus, the response to the conditions of development of the “grandmothers” and the “mothers” revealed approximately the same threshold zone (compare Figs. 1 and 2).

The maternal influence on the diapause in the progeny often extends beyond the two consecutive generations and can be traced in rather long sequences (Vinogradova, 1973; Zaslavski, 1984; Mousseau and Dingle, 1991). One of the most vivid and best studied examples is induction of larval diapause in the blowfly *Calliphora vicina* R.-D. (Vinogradova, 1991). A rather common variant of long-term modifications due to maternal influence consists in the lack of sensitivity to diapause-inducing factors in several generations following the diapausing one; this phenomenon was observed in egg parasitoids as well (Jackson, 1963;



**Fig. 2.** Dependence of the fraction of diapausing progeny of *Trichogramma principium* on the photoperiodic conditions of development of the maternal and pre-maternal generations. Abscissa: photoperiod affecting females of the pre-maternal generation  $G_1$  (day length, h); ordinate: fraction of diapausing prepupae in the progeny  $G_3$ , %. Photoperiod affecting females of the maternal generation  $G_2$  (L : D) : (a) 3 : 21, (b) 9 : 15, (c) 15 : 9, (d) 21 : 3. Median values and quartiles are shown. The points of the same line marked with different letters correspond to the values found to be significantly ( $p < 0.05$ ) different by the Tukey test for arcsine-transformed data.

Voegelé *et al.*, 1986). The influence of the development conditions of the pre-maternal generation on the incidence of diapause in the progeny was reported earlier for *T. evanescens* Westw. (Zaslavski and Umárova, 1981) and *T. euproctidis* Gir. (Mai Fu Kwi and Zaslavski, 1983), but only by comparing 2 or 3 contrasting photoperiods. The investigation of the “maternal effect upon maternal effect” over a broad range of day lengths in *Trichogramma* species, reported here, is to the best of our knowledge the first study of this kind.

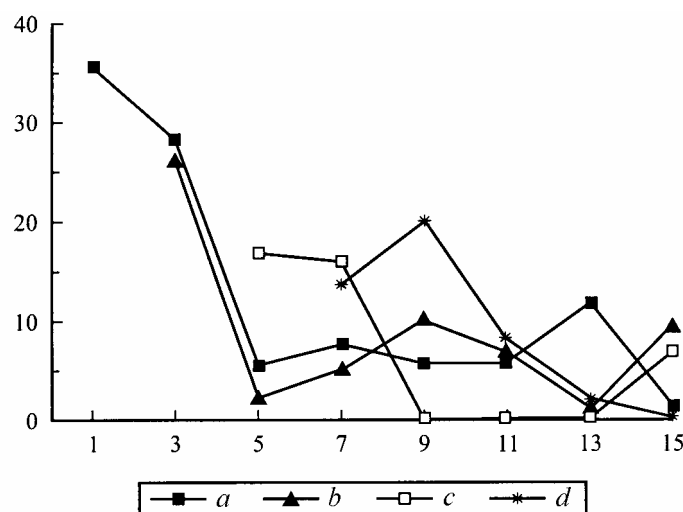
It is very interesting to compare the photoperiodic responses obtained for the maternal generations that had developed at day lengths 3 h and 9 h. It is evident (Figs 2a, 2b) that development of the “grandmothers” at L : D = 9 : 15, 15 : 9 and 21 : 3 result in almost identical photoperiodic curves, the 9-h short-day conditions being slightly “stronger” than 3-h ones (i.e., inducing diapause in a somewhat greater fraction of the progeny). The first experiment (Fig. 1) also demonstrated the almost identical effect of short-day conditions L : D = 3 : 21 and 9 : 15. However, the fraction of diapausing individuals in generation  $G_3$  was smaller when  $G_1$  developed at 3h L and  $G_2$  at 9h L, as compared to the variant when both  $G_1$  and  $G_2$  developed at 3h L (Fig. 2, initial points of graphs a and b). This difference was found to be significant by Tukey’s test ( $p = 0.034$ ).

The above effect is most probably explained by the stepwise short-long-day response to day length

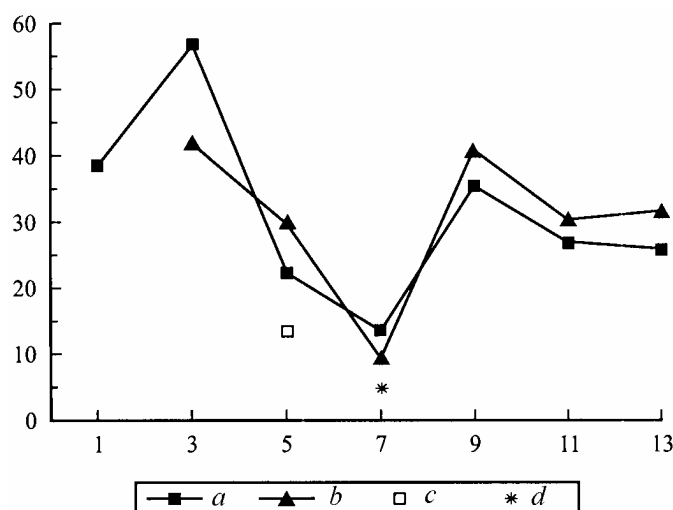
changes, which is common to many insects (Zaslavski, 1984). Transition from 3-h day length (development of generation  $G_1$ ) to 9-h day length (development of generation  $G_2$ ) is probably perceived as an increase in day length and reduces the fraction of diapausing individuals, even though both photoperiods are in fact “short-day” ones (Fig. 1). The possibility of response to day length changes was proposed for species of the genus *Trichogramma* over 20 years ago (Zaslavski and Umárova, 1981), but it is only now that this phenomenon has been experimentally confirmed. In our experiments the relatively long and short day lengths affected two consecutive generations of trichogrammas. However, it is interesting that the stepwise response revealed in these experiments is very similar to that observed in many other insects over a single individual’s lifespan (Zaslavski, 1984). This fact may be regarded as one more manifestation of the endogenous processes that “continue” from one generation to another (Reznik *et al.*, 1996; Voinovich *et al.*, 2002, 2003).

#### *Effect of the Age of Maternal Individuals*

The two preceding experiments employed the mass infestation technique to determine the percentage of diapausing individuals in the progeny hatching from the eggs laid by the females during the first 24 h after their contact with the host. In other experiments, in order to characterize the possible relation between the age of the female and the fraction of diapausing progeny, individual infestation was used. Four variants of



**Fig. 3.** Dependence of the fraction of diapausing progeny of *Trichogramma principium* on the age of maternal individuals (development at L : D = 3 : 21) and the egg retention period. Abscissa: age of females of the maternal generation  $G_2$  at the moment of infestation (days); ordinate: fraction of diapausing prepupae in the progeny  $G_3$ , %. Egg retention period: (a) 0, (b) 2, (c) 4, (d) 6 days.



**Fig. 4.** Dependence of the fraction of diapausing progeny of *Trichogramma principium* on the age of maternal individuals (development at L : D = 9 : 15) and the egg retention period. Designations as in Fig. 3.

photoperiod affecting the maternal generation were used: L : D = 3 : 21, 9 : 15, 18 : 6, and 24 : 0. The results (number of diapausing and active prepupae for each batch of eggs) were broken down into groups by 2 parameters of the maternal individual, namely its age and the time from contact with the host to laying of the first egg (because of the egg retention typical of most *T. principium* females). Then the results for each group were summarized, and data for small groups (less than 5 females or less than 10 eggs laid) were discarded.

Results of the experiment with maternal individuals developing at L : D = 3 : 21 are shown in Fig. 3. The fraction of diapausing progeny obviously decreases

with the age of the maternal individual. In addition, it can be seen from the figure that the 2-day egg retention has almost no effect on this trend (compare Figs. 3a and 3b); at the same time, among the progeny produced during the first two days of reproduction, the incidence of diapause in the progeny of females with an egg retention period of 4 or 6 days is significantly higher ( $p < 0.001$  and  $p < 0.05$ , respectively) than in the progeny of females with a shorter retention period (compare Figs. 3a–3b and 3c–3d). The difference between the data for the females aged 11–15 days is non-significant; these data show a substantial spread which is probably related to a smaller sample size due to mortality.

An entirely different dynamics of the fraction of diapausing progeny is observed for the females developing at  $L : D = 9 : 15$  (Fig. 4). First, the age-related pattern in itself is more complicated: it includes a significant ( $p < 0.01$ ) increase from the 1st to the 3rd day, followed by a decrease with a distinct minimum by the 7th day, after which there is another increase and finally stabilization. Secondly, this pattern is practically not affected by egg retention: graphs *a* and *b* in Fig. 4 almost overlap, and the difference between *c* and *d* is non-significant (data for females with egg retention period of 4–6 days represent only the first batch of eggs, which is also the largest; subsequent batches are not represented because of the insufficient sample size). It should be noted that the incidence of diapause in the progeny produced during the first days of life by the females that have developed at  $L : D = 3 : 21$  and  $9 : 15$  (initial parts of the graphs in Figs. 3*a* and 4*a*) is nearly the same. This observation agrees well with the results of the first experiment (Fig. 1, day length 3 and 9 h).

The relation between the incidence of diapause in the progeny and the age of females developing at long day ( $L : D = 18 : 6$ ) and at constant light is difficult to characterize because the fraction of diapausing progeny in these variants is very small. Still, this fraction was found to decrease significantly ( $p < 0.001$ ) in both variants as the age of maternal individuals increased (Spearman's rank correlation is  $r = -0.28$  and  $r = -0.20$ ,  $n = 221$  and  $n = 300$ , respectively).

The very existence of the maternal effect indicates the presence of a special mechanism of the progeny's response to the physiological state of the female. The same mechanism may be responsible for the observed dependence of the incidence of diapause on maternal age. Previous studies of the "age-related component of maternal effect" in various insects revealed different trends in the incidence of diapause in the progeny in relation to the age of females (Vinogradova, 1973, 1991; Mousseau and Dingle, 1991); still, authors of the latest reviews (Denlinger, 1998; Fox and Mousseau, 1998) conclude that the fraction of diapausing progeny usually increases with maternal age. The age dynamics of the fraction of diapausing progeny in relation to the photoperiodic conditions of development of females was previously studied in considerable detail, for example in the blowfly *C. vicina* (Saunders, 1987; Vinogradova, 1991; Vinogradova and Reznik, 2000, 2002) and the pea aphid *Acyrtosiphon pisum* Harris (Erlykova, 1997, 1999). The dynamics in *Trichogramma* is described here for the first

time. In general, our data agree well with the conclusion made earlier on the basis of similar experiments with *C. vicina* (Vinogradova and Reznik, 2000). Namely, the maternal effect has two components: the primary one, which is exogenous and determined by the photoperiodic response, and the secondary one, which is endogenous and related to the female's age. The primary (photoperiodic) component affects the nature of the secondary (age-related) component.

Of special interest is the interaction between the age-related changes in the maternal effect and egg retention. Our experiments (Fig. 3) have shown that this interaction is certainly more complicated than mere summation. Both ageing of females and egg retention do not simply increase or decrease the fraction of diapausing progeny, but exert some influence that clearly depends on the photoperiod. To explain such nonlinear interactions, it would be logical to assume the existence of some general mechanism integrating the effects of three factors: photoperiod, age-related changes, and the processes accompanying the onset of oviposition. This assumption also allows one to explain the mechanism of transition from egg retention to infestation of the host. Experimental studies (Reznik *et al.*, 2001a, 2001b) have shown that infestation starts abruptly and cannot be stopped under certain conditions. Such behavioral changes in insects may be effected by two kinds of mechanisms: either "purely behavioral" ones, for example various forms of learning (Lewis *et al.*, 1990; Vet and Groenewold, 1991; Papaj and Lewis, 1992; Reznik, 1993; Vinson, 1998), or more profound changes with participation of the neuroendocrine system (Barton Browne, 1993; Vinson, 1998). It was previously supposed (Reznik *et al.*, 1998, 2001b, 2003) that transition from egg retention to infestation could be based on a neuroendocrine mechanism. Results of the present study confirm this hypothesis. Both components of the maternal effect (photoperiodic response and age-related changes) are known to be based on a neuroendocrine mechanism (Vinogradova, 1991; Mousseau and Dingle, 1991; Fox and Mousseau, 1998). Considering their close interaction with egg retention and induction of oviposition, one may assume that these two phenomena are also, at least partly, governed by endocrine processes.

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## REFERENCES

1. Anderson, J.F. and Kaya, H.K., Diapause Induction by Photoperiod and Temperature in the Elm Spanworm Egg Parasitoid *Ooencyrtus* sp., *Ann. Entomol. Soc. Amer.*, 1974, vol. 67, no. 6, pp. 845–849.
2. Barton Browne, L., Physiologically Induced Changes in Resource Oriented Behavior, *Ann. Rev. Entomol.*, 1993, vol. 38, pp. 1–25.
3. Berg, M.A. van den, Studies on the Induction and Termination of Diapause in *Mesocomys pulchriceps* Cam. (Hymenoptera: Eupelmidae), an Egg Parasite of Saturniidae (Lepidoptera), *Phytophylactica*, 1971, vol. 3, no. 1, pp. 85–88.
4. Boivin, G., Overwintering Strategies of Egg Parasitoids, Wajnberg, E. and Hassan, S.A., Eds., *Biological Control with Egg Parasitoids*, Wallingford, UK: CAB Int., 1994, pp. 219–244.
5. Bonnemaïson, L., Diapause et superparasitisme chez *Trichogramma evanescens* Westw. (Hymenoptera, Trichogrammatidae), *Bull. Soc. Entomol. France*, 1972, vol. 77, nos. 5–6, pp. 122–132.
6. Danilevskii, A.S., *Fotoperiodizm i sezonnoe razvitiye nasekomykh* (Photoperiodism and Seasonal Development of Insects), Leningrad: Nauka, 1961.
7. Denlinger, D.L., Maternal Control of Fly Diapause, Mousseau, T.A. and Fox, C.W., Eds., *Maternal Effects as Adaptations*, Oxford Univ. Press, 1998, pp. 275–287.
8. Erlykova, N.N., Peculiarities of Photoperiodic Response of Unisexual Clone of Pea Aphid *Acyrtosiphon pisum* Harris (Homoptera, Aphididae), *Entomol. Obozr.*, 1997, vol. 76, no. 3, pp. 497–507; English translation: *Entomol. Rev.*, 1997, vol. 77, no. 3, pp. 301–308.
9. Erlykova, N.N., Effect of Photoperiod and Maternal Age on the Progeny Pattern of the Pea Aphid *Acyrtosiphon pisum* Harris (Homoptera, Aphididae) from the Volga Area, *Entomol. Obozr.*, 1999, vol. 78, no. 2, pp. 275–286; English translation: *Entomol. Rev.*, 1999, vol. 79, no. 9, pp. 1098–1106.
10. Fox, C.W. and Mousseau, T.A., Maternal Effects as Adaptations for Transgeneration Phenotypic Plasticity in Insects, Mousseau, T.A. and Fox, C.W., Eds., *Maternal Effects as Adaptations*, Oxford Univ. Press, 1998, pp. 159–177.
11. Garcia, P.V., Wajnberg, E., Pizzol, J., and Olivejra, M.L.M., Diapause in the Egg Parasitoid *Trichogramma cordubensis*: Role of Temperature, *J. Insect Physiol.*, 2002, vol. 48, no. 2, pp. 349–355.
12. Jackson, D.J., Diapause in *Caraphractus cinctus* Walker (Hymenoptera: Mymaridae), a Parasitoid of the Eggs of Dytiscidae (Coleoptera), *Parasitology*, 1963, vol. 53, no. 2, pp. 225–251.
13. Laing, J.E. and Corrigan, J.E., Diapause Induction and Post-Diapause Emergence in *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae): the Role of Host Species, Temperature, and Photoperiod, *Canad. Entomol.*, 1995, vol. 127, no. 1, pp. 103–110.
14. Mai Fu Kwi and Zaslavski, V.A., Photoperiodic and Temperature Reactions in *Trichogramma euproctidis* (Hymenoptera, Trichogrammatidae), *Zool. Zh.*, 1983, vol. 62, no. 11, pp. 1676–1680.
15. Maslennikova, V.A., On Overwintering and Diapause in *Trichogramma evanescens* Westw., *Vestnik Len. Gos. Univ.*, 1959, no. 3, pp. 91–96.
16. Maslennikova, V.A. and Sorokina, A.P., The Effect of Host Physiological State on the Diapause and Infection Intensity of *Trichogramma cacoeciae* March., *T. evanescens* Westw., and *T. embryophagum* Htg. (Hymenoptera, Trichogrammatidae), *Inf. Byull. VPS MOBB*, 1986, vol. 14, pp. 33–38.
17. Mousseau, T.A. and Dingle, H., Maternal Effects in Insect Life Histories, *Ann. Rev. Entomol.*, 1991, vol. 36, pp. 511–534.
18. Papaj, D.R. and Lewis, A.C., *Insect Learning: Ecological and Evolutionary Perspectives*, London: Chapman and Hall, 1992.
19. Reznik, S.Ya., Learning in the Host Specialization of Insects, *Trudy Zool. Inst. Ross. Akad. Nauk*, 1993, vol. 193, pp. 5–72.
20. Reznik, S.Ya., Voinovich, N.D., and Umarova, T.Ya., Experimental Study of the Proportion of Infesting Females and Their Fecundity in Consecutive Generations of *Trichogramma* (Hymenoptera, Trichogrammatidae), *Zool. Zh.*, 1996, vol. 75, no. 3, pp. 375–382.
21. Reznik, S.Ya., Umarova, T.Ya., and Voinovich, N.D., Egg Retention in the Presence of a Host in *Trichogramma* females, *J. Appl. Entomol.*, 1998, vol. 122, no. 9–10, pp. 555–559.
22. Reznik, S.Ya., Voinovich, N.D., and Umarova, T.Ya., Comparative Behavioral Analysis of Ovipositing Females and Females with Egg Retention in *Trichogramma principium* Sug. et Sor. (Hymenoptera, Trichogrammatidae), *Entomol. Obozr.*, 2001a, vol. 80, no. 3, pp. 545–555; English translation: *Entomol. Rev.*, 2001, vol. 81, no. 8, pp. 895–903.
23. Reznik, S.Ya., Voinovich, N.D., and Umarova, T.Ya., Long-Term Egg Retention and Parasitization in *Trichogramma principium* (Hymenoptera, Trichogrammatidae), *J. Appl. Entomol.*, 2001b, vol. 125, no. 4, pp. 169–175.
24. Reznik, S.Ya., Kats, T.S., Umarova, T.Ya., and Voinovich, N.D., Maternal Age and Endogenous Variation in Maternal Influence of Photoperiodic Response in the Progeny Diapause in *Trichogramma embryophagum* (Hymenoptera: Trichogrammatidae), *Eur. J. Entomol.*, 2002, vol. 99, no. 2, pp. 175–179.
25. Reznik, S.Ya., Umarova, T.Ya., and Voinovich, N.D., Egg Retention in *Trichogramma* (Hymenoptera: Chalcidoidea: Trichogrammatidae): Learning or Diapause?, *Acta Soc. Zool. Bohem.*, 2003, vol. 67, no. 1, pp. 25–33.
26. Saunders, D.S., Maternal Influence on the Incidence and Duration of Larval Diapause in *Calliphora vicina*, *Physiol. Entomol.*, 1987, vol. 12, no. 3, pp. 331–338.

27. Smith, S.M., *Biological Control with Trichogramma: Advances, Successes, and Potential of Their Use*, *Ann. Rev. Entomol.*, 1996, vol. 41, pp. 375–406.
28. Sorokina, A.P. and Maslennikova, V.A., Photothermic Reactions in Some Species of the Genus *Trichogramma* (Hymenoptera, Trichogrammatidae), *Vestnik Len. Gos. Univ. Ser. 3*, 1986, no. 1, pp. 9–14.
29. Sorokina, A.P. and Maslennikova, V.A., Thermal Optimum of Diapause in Species of the Genus *Trichogramma* Westw. (Hymenoptera, Trichogrammatidae), *Entomol. Obozr.*, 1987, vol. 66, no. 4, pp. 689–699.
30. Tauber, M.J., Tauber, C.A., and Masaki, S., *Seasonal Adaptations of Insects*, New York, Oxford: Oxford Univ. Press, 1986.
31. Tyshchenko, V.P., Physiology of Photoperiodism in Insects, *Trudy Vses. Entomol. O-va*, 1977, vol. 59, pp. 1–155.
32. Vet, L.E.M. and Groenewold, A.M., Semiochemicals and Learning in Parasitoids, *J. Chem. Ecol.*, 1991, vol. 16, no. 11, pp. 3119–3155.
33. Vinogradova, E.B., Maternal Effect on the Progeny Diapause in Insects, *Doklady na 23 ezhgodnom chtenii pamyati N.A. Kholodkovskogo* (Proc. 23rd Annual Meet. in Memory of N.A. Kholodkovskii), Leningrad: Nauka, 1973, pp. 39–66.
34. Vinogradova, E.B., Diapause in Flies and Its Regulation, *Trudy Zool. Inst. Akad. Nauk SSSR*, 1991, vol. 214, pp. 1–255.
35. Vinogradova, E.B. and Reznik, S.Ya., Influence of Female Age on Larval Diapause in Progeny of the Blowfly *Calliphora vicina* R.-D. (Diptera, Calliphoridae), *Entomol. Obozr.*, 2000, vol. 79, no. 2, pp. 296–302; English translation: *Entomol. Rev.*, 2000, vol. 80, no. 2, pp. 185–189.
36. Vinogradova, E.B. and Reznik, S.Ya., Influence of a Single (Stepwise) Change in Photoperiod and Female Age on Larval Diapause in the Blowfly *Calliphora vicina* R.-D. (Diptera, Calliphoridae), *Entomol. Obozr.*, 2002, vol. 81, no. 4, pp. 785–794; English translation: *Entomol. Rev.*, 2002, vol. 82, no. 9, pp. 1190–1196.
37. Vinson, S.B., The General Host Selection Behavior of Parasitoid Hymenoptera and a Comparison of Initial Strategies Utilized by Larvaphagous and Oophagous Species, *Biological Control*, 1998, vol. 11, no. 1, pp. 79–96.
38. Voegelé, J., Pizzol, J., Raynaud, B., and Hawlitzky, N., La diapause chez les Trichogrammes et ses avantages pour la production de masse et la lutte biologique, *Meded. Fac. Landbouw. Rijksuniv. Gent.*, 1986, vol. 51, no. 3a, pp. 1033–1039.
39. Voinovich, N.D., Umarova, T.Ya., Kats, T.S., and Reznik, S.Ya., The Role of Endogenous Factors in Diapause Induction in *Trichogramma embryophagum* (Hymenoptera, Trichogrammatidae), *Zool. Zh.*, 2002, vol. 81, no. 5, pp. 584–589; English translation: *Entomol. Rev.*, 2002, vol. 82, no. 9, pp. 1233–1237.
40. Voinovich, N.D., Umarova, T.Ya., Kats, T.S., and Reznik, S.Ya., Variation of the Photoperiodic Reaction in *Trichogramma embryophagum* (Hymenoptera, Trichogrammatidae), *Entomol. Obozr.*, 2003, vol. 82, no. 2, pp. 264–269; English translation: *Entomol. Rev.*, 2003, vol. 83, no. 7, pp. 779–782.
41. Zaslavski, V.A., Photoperiodic and Temperature-Related Control of Insect Development, *Trudy Zool. Inst. Akad. Nauk SSSR*, 1984, vol. 120, pp. 1–180.
42. Zaslavski, V.A., Diversity of Environmental Factors Controlling the Seasonal Development in Insects and the Possible Unity of the Physiological Mechanism, *Entomol. Obozr.*, 1996, vol. 75, no. 2, pp. 233–243.
43. Zaslavski, V.A. and Umarova, T.Ya., Photoperiodic and Temperature Control of Diapause in *Trichogramma evanescens* Westw. (Hymenoptera, Trichogrammatidae), *Entomol. Obozr.*, 1981, vol. 60, no. 4, pp. 721–731.
44. Zaslavski, V.A. and Umarova, T.Ya., Environmental and Endogenous Control of Diapause in *Trichogramma* Species, *Entomophaga*, 1990, vol. 35, no. 1, pp. 23–29.