

DIAPAUSE INDUCTION AND POST-DIAPAUSE EMERGENCE IN *TRICHOGRAMMA MINUTUM* RILEY (HYMENOPTERA: TRICHOGRAMMATIDAE): THE ROLE OF HOST SPECIES, TEMPERATURE, AND PHOTOPERIOD

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Abstract

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Trichogramma minutum Riley entered diapause, in the prepupal stage, in eggs of *Lambdina fiscellaria fiscellaria* Guenée held at 15°C, 12L:12D, but failed to do so in eggs of *Ephestia kuehniella* (Zeller), *Sitotroga cerealella* (Olivier), or *Choristoneura fumiferana* (Clemens) held under these conditions. The parasitoids emerged without diapause from eggs of all host species held at 25°C, 16L:8D, indicating a role of temperature or photoperiod, or both, in the diapause of the parasitoids in eggs of *L. fiscellaria* held at 15°C, 12L:12D. Percentage emergence of parasitoids from eggs of *L. fiscellaria* was virtually the same (>80%) after passing the winter outdoors or after approximately 3 months at 2°C in the laboratory as it was when reared indoors in this host at 25°C, 16L:8D. Emergence of *T. minutum* was very poor (<20%) after long-term, low-temperature storage in eggs of *C. fumiferana*, *E. kuehniella*, or *S. cerealella*. Apparently, *T. minutum* must parasitize diapause host eggs in order to enter diapause, and good survival after long-term low-temperature storage is possible only when *T. minutum* is in diapause. *Trichogramma minutum* will enter diapause in *L. fiscellaria* after 14 days at 15°C, 12L:12D, but the parasitoids need a period of storage at 2°C, 0L:24D for a high percentage of emergence to happen. Over 50% emergence was recorded for *T. minutum*, held for 300 days in eggs of *L. fiscellaria*.

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Résumé

Des *Trichogramma minutum* Riley sont entrés en diapause avant la nymphose dans des oeufs de *Lambdina fiscellaria fiscellaria* Guenée gardés à 15°C, à une photopériode 12L:12O, mais n'ont pas subi de diapause dans des oeufs d'*Ephestia kuehniella* (Zeller), *Sitotroga cerealella* (Olivier) ou *Choristoneura fumiferana* (Clemens) gardés dans les mêmes conditions. Tous les parasitoïdes ont émergé sans subir de diapause des oeufs de toutes les espèces hôtes gardés à 25°C, à une photopériode de 16L:8O, ce qui indique que la température et (ou) la photopériode ont un rôle à jouer dans le déclenchement de la diapause des parasitoïdes dans les oeufs de *L. fiscellaria* gardés à 15°C, 12L:12O. Le pourcentage de parasitoïdes émergés des oeufs de *L. fiscellaria* s'est avéré à peu près le même (>80%) après l'hiver à l'extérieur ou après une période de 3 mois en laboratoire à 2°C qu'après un hiver à l'intérieur à 25°C, 16L:8O. Très peu de guêpes (<20%) ont réussi à parvenir à l'émergence après un long séjour à température froide dans des oeufs de *C. fumiferana*, *E. kuehniella* ou *S. cerealella*. Il semble que *T. minutum* doive parasiter les oeufs en diapause de son hôte avant de pouvoir entrer en diapause et que le taux de survie après un long séjour à température faible dans les oeufs de l'hôte ne puisse être élevé que lorsque la guêpe est en diapause. *Trichogramma minutum* peut entrer en diapause dans les oeufs de *L. fiscellaria* après 14 jours à 15°C, à une photopériode 12L:12O, mais les parasitoïdes ont besoin d'une période à 2°C, 0L:24O, pour que leur taux d'émergence soit élevé. Plus de 50% des *T. minutum* gardés durant 300 jours dans des oeufs de *L. fiscellaria* sont parvenues à l'émergence.

[Traduit par la Rédaction]

Introduction

Diapause is a state of suppressed development enforced by a physiological mechanism rather than by unfavourable environmental conditions (Beck 1968). The ability to induce, maintain and terminate diapause in the laboratory has important implications for the use of parasitoids as biological control agents (Tauber et al. 1986; Voegelé et al. 1986; Voegelé et al. 1988; Laing and Eden 1990; Boivin 1994). *Trichogramma maidis* Pintereau and Voegelé (Hymenoptera: Trichogrammatidae), *T. embryophagum* Hartig, and *T. cacoeciae* Marchal have been induced to enter diapause in eggs of the Mediterranean flour moth, *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae), *T. cacoeciae* having been maintained in diapause for more than 200 days with a mortality of less than 10% (Quednau 1957; Voegelé et al. 1988).

Trichogramma minutum Riley, a polyphagous egg parasitoid native to temperate, boreal North America, must pass prolonged periods in the northern portion of its range in a state of quiescence or diapause. For example, this species was reported to overwinter without diapause in Missouri (Parker and Pinnell 1971), but in diapause in Maine (Houseweart et al. 1984). Peterson (1930) reported that *T. minutum* overwintered outdoors in eggs of *E. kuehniella* in New Jersey, but the parasitoids were probably not in diapause, because they emerged on warm days in December and January.

Repeated attempts to induce diapause of *T. minutum* in factitious hosts such as *E. kuehniella* have failed, although a wide range of conditions has been used (Schread and Garman 1934; Laing, Eden, and Corrigan, unpublished). As a result of these attempts we became convinced that *T. minutum* was a species of *Trichogramma* that would not enter diapause in the commonly used factitious host species, under any set of temperature–photoperiodic conditions. Without diapause, *T. minutum* must be kept in continuous culture for mass-rearing programs that use this parasitoid as a biological control agent. Under these circumstances, most of the annual parasitoid production is not marketable, because the generation time is ca. 10 days at 25°C but field releases of *T. minutum* take place over a period of only a few weeks per year. Continuous rearing greatly increases the cost of production of parasitoids, because personnel, equipment and supplies must be maintained year-round. In addition, the parasitoids must be reared through at least 30 generations per year in factitious hosts prior to a field release. Bigler et al. (1982) showed that prolonged rearing on a factitious host can adversely affect the ability of *Trichogramma* to attack their target host in the field.

Trichogramma minutum attacks and completes development in the eggs of many species of Lepidoptera; it probably also overwinters in lepidopteran eggs. Relatively few species of Lepidoptera overwinter in the egg stage within the boreal forest of North America (Houseweart et al. 1984). Among these species is the hemlock looper, *Lambdina fiscellaria fiscellaria* Guenée (Lepidoptera: Geometridae), a univoltine species that passes the winter in diapause in the egg stage (Rose and Lindquist 1977; Singh and Moore 1985); this species could be a potential overwintering host for *T. minutum*.

Our research determines the roles of temperature–photoperiod and host species in diapause induction for *T. minutum*, the influence of low temperature on post-diapause emergence, and the length of time that the parasitoids can be stored at low temperatures with a high percentage survival after storage.

Materials and Methods

The population of *T. minutum* used in these experiments was originally collected from five egg masses of *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) found on balsam fir (S.M. Smith, pers. comm.). Specimens, reared from these initial collections, were sent to John Pinto (University of California, Riverside) for confirmation of species identity and voucher specimens were deposited in the University of Guelph collection. The

TABLE 1. Percentage emergence of *Trichogramma minutum* from parasitized eggs of *E. kuehniella*, *S. cerealella*, *C. fumiferana*, and *L. fiscellaria* after various treatment regimens of temperature (°C), daylength (hL:hD), and storage time (days). Sample sizes (*n*) are the number of blackened eggs per treatment

Treatment	Rearing-host species			
	<i>Ephestia kuehniella</i>	<i>Sitotroga cerealella</i>	<i>Choristoneura fumiferana</i>	<i>Lambdina fiscellaria</i>
I (25°C, 16:8, to emergence)	70.1 (234)*	83.4 (307)*	78.3 (92)	86.5 (111)
II (25°C, 16:8, 1 day; 15°C, 12:12, to emergence)	72.5 (302)	83.4 (586)	18.8 (32)	0 (170)
IIa (<i>L. fiscellaria</i> only — 25°C, 16:8, 1 day; 15°C, 12:12, 46 days; 2°C, 0:24, 70 days; 25°C, 16:8, to emergence)				80.7 (88)
III (25°C, 16:8, 1 day; outside in November to emergence)	26.4 (72)	38.5 (65)	1 male†	86.8 (152)
IV (25°C, 16:8, 1 day; 10°C, 0:24, 26 days; outside in December to emergence)	17.2 (704)	12.0 (769)	2 males†	82.1 (196)

* For these samples, the number of eggs counted is a subsample of the total number of parasitized eggs.

† Due to their poor condition, it was impossible to determine the number of parasitized SBW eggs in treatments III and IV.

parasitoids used in our experiments had been kept in continuous culture for approximately 30 generations.

Female *T. minutum* were presented simultaneously with eggs of two factitious host species, *E. kuehniella* and *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae), and two species attacked by *T. minutum* in the field, *C. fumiferana* and *L. fiscellaria fiscellaria*. Eggs of *E. kuehniella*, *S. cerealella*, and *C. fumiferana* (diapause strain) were taken from laboratory cultures, and had been stored at 2°C for less than 1 week prior to use. Eggs of *L. fiscellaria*, in diapause, were obtained from individuals that had been field collected as pupae in Newfoundland and allowed to emerge and oviposit in the laboratory; the eggs were stored at 2°C for 3 weeks prior to use.

After exposure to parasitoid attack for 1 h the eggs were allowed to develop for 23 h (25°C, 16L:8D), and then were divided among different treatments with respect to temperature, daylength, and storage time (Table 1). Parasitized eggs, held at 25°C and 16L:8D (treatment I), served as the control to evaluate other treatments with respect to adult emergence. We chose to test the combination of 15°C and 12L:12D because this set of conditions had evoked diapause in *T. evanescens* Westwood parasitizing eggs of *E. kuehniella* (Bonnemaison 1972). Thus, we held parasitized eggs from all host species under these conditions (treatment II). Parasitoids in eggs of *L. fiscellaria* did not emerge after 46 days at 15°C, 12L:12D; subsequently we placed them in storage at 2°C, 0L:24D, for 70 days (treatment IIa). After this, the eggs were returned to 25°C, 16L:8D, and held until emergence of the parasitoids. All indoor treatments were conducted at ambient relative humidity (50–80%).

Eggs of all four hosts, parasitized by *T. minutum*, were put outside for the winter at Guelph, Ontario, Canada, 43°34'N, 80°16'W. Half of the eggs were placed outside in

November, 1 day after parasitism, prior to the eggs turning black (treatment III). Host eggs, parasitized by *Trichogramma* spp., turn black when the parasitoid is in the prepupal stage (Flanders 1937). The other half were held at 10°C in darkness until they had turned black, then were put outside in December, 26 days after parasitism (treatment IV). The samples were left outside until emergence was completed in the spring (early to mid-May).

Percentage emergence was determined by dividing the number of blackened (parasitized) host eggs with emergence holes by the total number of blackened eggs. Several days after emergence had ceased, dissections were made to determine the fate of individuals that failed to emerge.

To examine the influence of cold conditions on post-diapause emergence by *T. minutum* in eggs of *L. fiscellaria*, we exposed eggs to parasitism by *T. minutum* for 30 min, held them at 25°C, 16L:8D, until 24 h after parasitism, then placed them at 15°C, 12L:12D, for 14, 28, or 42 days. After each of these initial treatments, samples were placed at 2°C, 0L:24D, for 0, 28, 42, or 56 days after which all samples were moved to 25°C, 16L:8D, to allow the adult parasitoids to emerge. Five replications of this experiment were undertaken and the arcsine transformed mean emergences for each temperature–time combination were compared using ANOVA procedures followed by LSD tests (SAS Institute 1985).

To estimate the length of time that *T. minutum* could be held in diapause in eggs of *L. fiscellaria*, parasitized eggs were held at 2°C, 0L:24D for 84, 207, and 272 days after developing for 28 days at 15°C, 12L:12D. After storage, the parasitized eggs were returned to 25°C, 16L:8D, to allow the adult parasitoids to emerge; the proportion of parasitized eggs with emergence holes was recorded after emergence was completed.

Results

At 25°C (16L:8D), 70–87% of the *T. minutum* emerged from the parasitized eggs of all host species within 9–13 days of parasitism (Table 1). Dissections of unemerged, parasitized eggs revealed only dead and desiccated individuals, of which 20–60% had died in the pupal or adult stage.

At 15°C (12L:12D), individuals held in eggs of *E. kuehniella*, *S. cerealella*, and *C. fumiferana* began to emerge 28–30 days after parasitism. Similar percentages of adult parasitoids emerged from the two factitious host species at 15°C as did at 25°C, but greatly reduced levels of emergence were recorded from parasitized eggs of *C. fumiferana* (Table 1). All parasitized eggs of *C. fumiferana* from which no parasitoids emerged were dissected, revealing only dead and desiccated individuals, mainly in the larval stage. After 46 days, no parasitoids had emerged from parasitized eggs of *L. fiscellaria* kept at 15°C, 12L:12D. At this time, a sample of 10 eggs was dissected and virtually all (60 of 62) of the parasitoids in these eggs were found to be alive and in the prepupal stage. The sample of *L. fiscellaria* then was put into cold conditions (2°C, 0L:24D) for an additional 70 days. After this period, and the subsequent return of the sample to 25°C (treatment IIa — see Table 1 for details), 80.7% emergence was recorded (Table 1).

Emergence of the parasitoids was low from the two factitious host species and *C. fumiferana* that had been placed outside 1 day after parasitism (treatment III) or 26 days after parasitism (treatment IV) (Table 1). The proportion of parasitoids emerging from blackened eggs of *E. kuehniella* and *S. cerealella* was higher from treatment III than from treatment IV, but the numbers of blackened eggs were very low in treatment III, as approximately 90% of the parasitoids died before they developed to the point at which they induced the host eggs to turn black.

The percentage emergence from parasitized eggs of *L. fiscellaria* held outside overwinter was over 80% (Table 1), with first emergence occurring after 6 months outside (November to mid-May) from treatment III and after 5 months from treatment IV (December to early May). Unlike the other host species, placing eggs of *L. fiscellaria* outside 1 day after

TABLE 2. Percentage emergence of *Trichogramma minutum* from parasitized eggs of *Lambdina fiscellaria* returned to 25°C, 16L:8D, after being held at 15°C, 12L:12D, for 14, 28, or 42 days followed by storage at 2°C, 0L:24D, for 0, 28, 42, or 56 days. Sample sizes (*n*) are the number of replications of each time–temperature combination

Days at 15°C, 12L:12D	Days at 2°C, 0L:24D			
	0	28	42	56
14	42.8±13.9 ab* (5)	80.6±14.9 cd (5)	83.3±28.9 de (5)	99.0±2.2 e (5)
28	13.6±14.1 a (5)	79.2±19.1 cd (5)	88.6±12.6 de (5)	83.3±28.9 de (4)
42	45.6±37.3 bc (5)	97.8±3.2 de (5)	89.3±19.6 de (4)	100.0±0.0 e (3)

* Means followed by the same letter are not significantly different ($P < 0.05$, LSD test).

parasitism (treatment III) did not affect parasitoid survival, based on the number of blackened eggs of *L. fiscellaria* found in treatment III relative to the other treatments (Table 1).

Trichogramma minutum in eggs of *L. fiscellaria* appeared to enter diapause if they were held at 15°C, 12L:12D, for 14, 28, or 42 days, although emergence was less than 50% for those samples not subsequently exposed to low temperatures (Table 2). Emergence levels of approximately 80% or higher were recorded for all samples that were held at 2°C, 0L:24D, for at least 28 days after the initiation of diapause (Table 2). Relatively high levels of emergence were recorded for *T. minutum*, stored for long periods at 2°C, 0L:24D, after developing for 28 days at 15°C, 12L:12D (94% emergence after 84 days of storage; 68% emergence at 207 days of storage; 53% emergence at 282 days of storage).

Discussion

Diapause responses vary among species of *Trichogramma*. Some species of *Trichogramma* exhibit a relatively intense, photoperiodically controlled diapause, others have a thermally controlled arrest of development of some part of the population, and some species or strains of *Trichogramma* appear to lack diapause altogether (Tauber et al. 1986). For some species of *Trichogramma*, diapause induction is a function of temperature and photoperiod acting on the parasitoids themselves or on their parental generation or both; rearing them on a factitious host species does not hinder diapause induction (*T. cacoeciae* in *E. kuehniella*—Quednau 1957; *T. evanescens*, *T. euproctidis* Girault, *T. acheae* Nagaraja and Nagarkatti in *E. kuehniella*—Voegelé 1976; *T. pinto* Voegelé, *T. embryophagum*, *T. principium* Sugonjaev and Sorokina, *T. semblidis* Aurivillius in *S. cerealella*—Zaslavski and Umarova 1990). Other species and populations have failed to enter diapause in factitious hosts even when exposed to low temperatures or short photoperiod, or both (*T. minutum* in *E. kuehniella*—Peterson 1930; *T. minutum* in *S. cerealella*—Peterson 1931; *T. pallida* Meyer in *S. cerealella*—Telenga 1956; *T. pretiosum* Riley in *S. cerealella*—Lopez and Morrison 1980).

In our experiments, the ability of *T. minutum* to enter diapause and withstand long periods of low-temperature storage depended on the host species. *Trichogramma minutum*, held in eggs of *L. fiscellaria* at 15°C, 12L:12D, were found to be alive and in the prepupal stage, after parasitoids in the other three host species had emerged or died. The prepupa was the diapause stage recorded for other *Trichogramma* species (Marchal 1936 in Askew 1971; Telenga 1956; Quednau 1957; Voegelé 1976; Zaslavski and Umarova 1981, 1990). The parasitized eggs of *L. fiscellaria* subsequently were subjected to a prolonged exposure to low temperatures (2°C, 0L:24D, for 70 days). This exposure did not have an adverse effect on emergence of the parasitoids from eggs of *L. fiscellaria* relative to emergence from the

control, reared at 25°C, 16L:8D. We conclude that diapause of *T. minutum* was induced in eggs of *L. fiscellaria* held at 15°C, 12L:12D.

Diapause induction in other species of *Trichogramma* is affected by the host species attacked (Howard 1937; Bonnemaïson 1972). The parasitoids did not enter diapause in eggs of the two factitious host species, or in eggs of *C. fumiferana*. Populations of *T. minutum* apparently overwintered without diapause in eggs of *E. kuehniella* in New Jersey (Peterson 1930) and in eggs of *Peridroma saucia* (Hübner) (Lepidoptera: Noctuidae) in Missouri (Parker and Pinnell 1971). These two host species do not overwinter in the egg stage; *E. kuehniella* does not have an overwintering stage and *P. saucia* overwinters as a pupa (Metcalf et al. 1962). Houseweart et al. (1984) found *T. minutum* that had parasitized eggs of *Malacosoma disstria* Hübner in the fall were in diapause, and we were successful in inducing diapause of *T. minutum* in eggs of *L. fiscellaria*. Individuals of *L. fiscellaria* overwinter in diapause in the egg stage (Rose and Lindquist 1977; Singh and Moore 1985) and those of *M. disstria* overwinter as diapause larvae inside the egg (Rose and Lindquist 1982; Stehr and Cook 1968). We concluded that diapause in our population of *T. minutum* was induced when the parasitoids attacked host eggs that were themselves in a diapause state. This phenomenon has been observed for several other species of egg parasitoids (Boivin 1994).

Photoperiod and temperature are thought to be major factors influencing diapause induction in many species of egg parasitoids (Boivin 1994). *Trichogramma minutum* did not enter diapause when held in eggs of *L. fiscellaria* at 25°C, 16L:8D, indicating that short days or low temperatures, or both, interacted with the host species characteristics to promote diapause induction in *T. minutum*.

Fewer eggs of either *E. kuehniella* or *S. cerealella* blackened when the parasitized host eggs were put outside 1 day after parasitism (treatment III) relative to being put out 26 days after parasitism (treatment IV). Because all eggs were exposed simultaneously to a single group of parasitoids, we expected that similar numbers of eggs were parasitized in all treatments. Therefore, most of the parasitoids in the eggs of the factitious host species in treatment III must have died before they developed sufficiently to turn the host eggs black. In the same treatment, however, parasitoids in eggs of *L. fiscellaria* survived well, even though they had not developed to the diapause (prepupal) stage prior to being placed outside for the winter. Some factor in the eggs of *L. fiscellaria* allowed the parasitoids to survive at low temperatures or it is possible that the ability to overwinter in eggs of *L. fiscellaria* is a result of some other attribute, such as their greater relative resistance to desiccation.

Embryonic diapause in the Lepidoptera has been most extensively studied in the silkworm, *Bombyx mori* L. (Lepidoptera: Bombycidae). A diapause hormone, produced in the subesophageal ganglion of the mother, exerts its influence on the developing ovaries, causing the oöcytes to take up high levels of glycogen (Yamashita and Yaginuma 1991). At the initiation of diapause, glycogen is converted into the cryoprotectants, sorbitol and glycerol (Yamashita and Yaginuma 1991). We speculate that the diapause eggs of *L. fiscellaria* contain cryoprotectants similar to those found in eggs of *B. mori*; the presence of these compounds allows *T. minutum* to survive long periods at low temperatures in these eggs. The cryoprotectants of the host may be a factor in triggering diapause of the parasitoid, or they may allow the immature parasitoids to survive low-temperature conditions long enough to receive the sufficient photoperiodic or temperature, or both, cues to induce diapause.

Emergence levels below 50% were recorded for parasitoids held in eggs of *L. fiscellaria* at 15°C, 12L:12D, for 14, 28, or 42 days without subsequent exposure to 2°C, 0L:24D conditions. If held for at least 28 days at 2°C, 0L:24D, the emergence rates were generally above 80%. These findings suggest that a cold period of 28 days was sufficient to complete diapause development for *T. minutum*.

We observed that the parasitoids developed to the prepupal stage while being held at 10°C in the laboratory. These results suggest that the developmental threshold of ca. 10°C, calculated for *T. minutum* by Peterson (1930) and Yu et al. (1984), is too high.

Our results suggest that it may not be possible to induce diapause in *T. minutum* when *E. kuehniella* and *S. cerealella* are used as hosts. The use of these hosts may preclude the long-term storage of parasitized host material, an important consideration for economical mass production of the parasitoid.

Lambdina fiscellaria can be reared on both natural and artificial diets (Singh and Moore 1985), yet it may be too expensive to keep in culture relative to the commonly used factitious host species. Producers of *T. minutum* should compare the cost of occasional production of *L. fiscellaria*, to allow storage of *T. minutum* in diapause, with the potential saving that could be accrued if year-round culture of the parasitoid and the factitious host species could be avoided. Alternatively, using *L. fiscellaria* as the principal host species in a rearing program would allow producers to stockpile parasitoids for release in the field season. This ability, combined with the fact that *T. minutum* produced from eggs of *L. fiscellaria* are superior in their reproductive performance compared with those produced from *E. kuehniella* or *S. cerealella* (Corrigan and Laing 1994), may more than compensate for the greater cost of culture of *L. fiscellaria*.

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