Oviposition by the Forest Tent Caterpillar (Lepidoptera: Lasiocampidae) and Acceptability of Its Eggs to *Trichogramma minutum* (Hymenoptera: Trichogrammatidae)

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Environ. Entomol. 22(6): 1375–1382 (1993)

ABSTRACT Studies were conducted to assess the availability and acceptability of eggs of forest tent caterpillar, *Malacosoma disstria* Hubner, to *Trichogramma minutum* Riley for use in inundative releases. Oviposition by the forest tent caterpillar occurred 4–19 July and lasted 7–10 d in southern Ontario. At least 50% of the egg-laying activity occurred during the first 3–4 d. Oviposition was initiated on the same day as female moth emergence, 2 d after male moth emergence. Pheromone traps baited with two-component lures predicted oviposition within 2 d. No *Trichogramma* emerged successfully from 0- to 7-d-old host eggs, although the survival of tent caterpillar embryos exposed at this age to the parasitoids was reduced significantly (from 97.5 to 42.3%). The greatest number of *Trichogramma* emerging from caterpillar egg masses (72.7%) was observed in those eggs exposed to parasitoids 21 d after oviposition, with 43.5 and 12.5% emergence from egg masses exposed at 14 and 28 d after oviposition, respectively. A tent caterpillar egg mass contained 109.8 ± 14.8 (mean ± SE) eggs; parasitoids emerged from 14.4 ± 3.5 of these eggs (13.1% egg parasitism). The number of parasitoids emerging from each parasitized egg ranged from 5.0 to 11.0; 69.5% were female and development at 20°C took 14.2 ± 0.2 d. Removal of the spumaline layer from the egg masses increased emergence of parasitoids very slightly. No *Trichogramma* successfully overwintered in forest tent caterpillar eggs, although a single dead parasitoid (0.2%) was observed infrequently in eggs simultaneously with a dead pharate larva. *Trichogramma* possibly can be used in inundative releases against *M. disstria*; however, further studies are needed to determine why the parasitoid kills but does not emerge from tent caterpillar eggs <14 d old.

KEY WORDS *Malacosoma disstria, Trichogramma minutum,* biological control

THE FOREST TENT CATERPILLAR, *Malacosoma disstria* Hubner, is a polyphagous insect native to North American forests. Extensive outbreaks of this insect occur regularly throughout much of its range causing defoliation of trembling aspen, *Populus tremuloides* Michx., balsam poplar, *Populus balsamifera* L., sugar maple, *Acer saccharum* Marsh., and red oak, *Quercus rubra* L. (Witter et al. 1975, Sippell 1962). In Ontario, outbreaks last about 4–5 yr and occur with moderate periodicity every 6–16 yrs. The eventual collapse of an outbreak is considered the result of a complex of natural mortality factors including weather, resource availability, disease, parasitoids, and genetic quality (Hodson 1941, Wellington 1960, Witter & Kulman 1972).

Aesthetic damage, growth reduction, and losses in sap flow in deciduous stands have sometimes necessitated control of the forest tent caterpillar (Gross 1991) and a number of strategies have been used, each with its own limitation. Pruning egg masses from infested branches, although effective in protecting selected high-value trees, is labor intensive. Contact chemical insecticides have been used effectively against the larval stage, however; public acceptance of these chemicals is diminishing (Jones et al. 1988). Today, the most widely used control agent is the bacterial pathogen, *Bacillus thuringiensis* Berliner, which must be ingested by the larvae to be effective (van Frankenhuyzen 1990). In recent years, there has been concern about bacterial contamination in some of the commercial products of *B. thuringiensis* and the possibility of nontarget effects in the forest environment (Jones et al. 1988). A major limitation with *B. thuringiensis* for the forest manager is that it is currently the sole option available for control.

Parasitoids attacking the egg stage of an insect pest are mobile biological control agents which reduce pest populations before the damaging larval stage appears. They generally are more selective than insecticides or *B. thuringiensis* and may be particularly effective when used in an

0046-225X/93/1375–1382$02.00/0

integrated program with these control measures. A few species, including *Trichogramma,* have been reported from forest tent caterpillar eggs (Houseweart et al. 1984) and, when this parasitoid was released inundatively, caused suppression of forest lepidopteran species such as the spruce budworm, *Choristoneura fumiferana* (Clemens) (Smith et al. 1990).

The goal of our research was to determine the potential for using inundative releases of *Trichogramma minutum* Riley for biological control of the forest tent caterpillar. To assess the feasibility of inundative releases, two considerations were addressed: (1) the temporal occurrence of tent caterpillar eggs in the field (the oviposition period), and (2) the length of time tent caterpillar eggs were acceptable to parasitism by *T. minutum.* No information is currently available on acceptability of forest tent caterpillar eggs by *Trichogramma* spp. Although oviposition by the tent caterpillar has been documented in a general manner (Hodson 1941, Witter et al. 1975), specific relationships between moth emergence, flight, and oviposition, as well as the predictive effect of pheromone traps under field conditions, are lacking.

Materials and Methods

Field work was carried out in southern Ontario at Six-Mile Lake Provincial Park (45°N, 79.5°W) in 1988 and at Awenda Provincial Park (45°N, 80°W) in 1989. Both sites were comprised of white oak, *Quercus alba* (50%), aspen or poplar, *Populus tremuloides* (15%), and other nonhost species (35%) and were experiencing severe defoliation in the third year of a forest tent caterpillar outbreak. On-site daily maximum and minimum temperatures and relative humidity were recorded using a hygrothermograph placed inside a Stephenson screen (Environment Canada, Atmospheric Environment Services, Downsview, Toronto).

Pheromone Traps. Pheromone traps were used to detect the presence of male moths, adult flight, and oviposition. Two types of lures were used in the traps. One contained the primary and secondary components of the forest tent caterpillar sex pheromone (Z)-5,(E)-7-dodecadienal and (Z)-5,(E)-7-dodecadien-l-ol (Chisholm et al. 1980) and one contained the three components (Z)-7,(E)-9-dodecadienal, (Z)-7,(Z)-9-dodecadienal, and (Z)-7 dodecanal (Chisholm et al. 1986). The pheromones were prepared by the Research and Productivity Council, Fredericton, New Brunswick, and were mounted individually in A-form cardboard traps.

The traps were placed in the field during the pupation period of the tent caterpillar (third week in June). They were suspended from lower tree branches (≈4 m high, at least 40 m apart) and were changed daily. In 1988, 6 traps were used, three each of the two- and three-component lures; in 1989, 10 traps were used, all with the two-component lures.

Branch Sampling. Branches were sampled for egg masses to determine the cumulative oviposition curve of the tent caterpillar during each year. Fifty dominant or codominant (10–20 m high) white oak trees were selected throughout a 10-ha stand at each site. One foliated branch (1 m long) was clipped from the mid- to upper crown of each sample tree daily between 0900 and 1400 h (EST). Branch sampling (n = 50 per d) was initiated when male moths were first detected in the pheromone traps. All twigs on each branch were examined, and egg masses laid only in the current year were tabulated.

Sampling of Young Aspen. In 1989, 100 sapling aspen trees (0.5 ha) were selected to provide a measure of egg mass deposition that could be related to the branch sampling and pheromone traps. The area was located near the same oak-maple forest used for branch sampling. Trees selected for the study were 3–6 cm in diameter at breast height (dbh) with a maximum height of 5 m, and foliated branches of which were available for tent caterpillar oviposition. After the first male moth was collected in the pheromone traps, the top of each aspen sapling was bent over and the branches were examined daily for new egg masses. Freshly laid egg masses were flagged so that a daily measure of oviposition could be made.

Walk-In Cage. A walk-in cage (Dining Shelter, Canadian Tire, Toronto, Ontario) was used in both years to determine the emergence pattern of adult moths relative to the temporal distribution of freshly laid egg masses. The cage (3.7 by 3.7 by 2 m) had an opaque top of blue polyethylene with screened sides sealed at ground level. The cage surrounded a single white oak sapling (2.0 m tall) in 1988; four saplings (white oak, sugar maple *Acer saccharum,* trembling aspen, and eastern white pine *Pinus strobus,* (0.5–1.5 m tall) in 1989. The cages and the Stephenson screen were situated in the understory of the stand used for branch sampling in both years. The stand used in 1988 was severely defoliated by tent caterpillar feeding, whereas it was only partially defoliated in 1989.

Pupae of forest tent caterpillar (with cocoons and foliar webs intact) were collected from locations near each field site in late June of each year. In 1988, 600 of the collected pupae were placed in three translucent plastic boxes (0.75 by 0.5 by 0.2 m) with screened lids, and 3,000 collected pupae were placed in three screened wood-frame boxes (1 by 1 by 0.4 m) in 1989. The boxes were placed on the bottom of the cage and examined each morning for emergence of adult moths. The sex of the adults was determined, and adults were counted and released into the walk-in cage. Once emergence had begun, the

inner portions of the cage were checked twice daily for the presence of new egg masses; this included branches of the saplings, grasses, and sedges, as well as the sides and ceiling of the cage. Oviposition dates of new egg masses were noted and locations were marked with tape.

Egg Acceptability to *Trichogramma*. Tent caterpillar egg masses of different ages were exposed to female *T. minutum* to determine the influence of egg mass age on parasitism. The egg masses were obtained by collecting 400–600 pupae near Awenda Provincial Park, Ontario, in June 1990. Adult moths were allowed to emerge inside 3–4 screened cages (each 0.125 m^3) under laboratory conditions (20°C, 60% RH). The cages were misted twice daily, and small branches were set inside to provide oviposition sites. Each cage was checked for fresh egg masses twice each day. As the egg masses appeared, they were collected and the spumaline layer was removed with finely pointed tweezers from half of the eggs in each mass. This allowed for a comparison between attack rates on the same egg mass with and without spumaline and provided a larger sample size than would have been possible if each treatment had been applied to an entire egg mass.

The egg masses were allowed to develop at 20°C, 60% RH, and 16:8 (L:D) h until the specified treatment age was reached. An equal number of egg masses was allocated daily to each treatment age group as they were collected. The age groups were assigned as 0, 2, 7, 14, 21, and 28 d after oviposition, based on preliminary results from the previous year. Exposure of egg masses to parasitism also depended upon the availability of similarly aged (<48 h old) female parasitoids, and because this was sometimes irregular, development of some egg masses had to be delayed at 4°C until parasitoids were available. It was assumed that essentially no development occurred at this temperature.

The egg masses, with half their spumaline removed, were kept individually in screen-topped, glass vials (15 by 45 mm) and were exposed to 10 honey-fed female *T. minutum* for 48 h. The parasitoids were obtained from spruce budworm eggs in northwestern Ontario during 1988 and had been reared in the laboratory for 32 generations on eggs of the Angoumois grain moth, *Sitotroga cerealella* (Olivier). After exposure to the parasitoids, the egg masses were held at 20°C, 60% RH, and 16:8 (L:D) h until emergence of parasitoid progeny. To obtain controls for larval development, 10 egg masses were treated in the manner as described above except they were not exposed to parasitoids. The time from exposure to the parasitoids until emergence of progeny was considered the development time and was compared between ages using log-transformed data in one-way analysis of variance (ANOVA) and Tukey's range test (Systat-Mglh; Wilkinson 1990).

All egg masses were held at room temperature (20°C) for an additional 8 wk, whereupon they were placed at 4°C for 17 wk to meet diapause requirements for the host and possible parasitoids. After removal from the cold, the egg masses were held at 20°C and again examined for parasitoid emergence. The proportion of egg masses with parasitoids emerging was compared for each host age using Pearson's χ^2 statistic (Systat-Tables; Wilkinson 1990). In parasitized egg masses, counts were made of the number of eggs and number of parasitoid emergence holes in each of the spumaline and nonspumaline areas as well as the total number of male and female parasitoids emerging from each egg mass. Data for the number of caterpillar eggs in each area and the number of parasitoid emergence holes for each egg mass age were log-transformed and analyzed using two-way ANOVA within spumaline and nonspumaline areas. One-way ANOVA and Tukey's range test were used to compare the transformed number of males, females, and total progeny emerging from parasitized egg masses of each age (Systat-Mglh; Wilkinson 1990).

To determine whether there was an effect of egg location within the egg mass on parasitoid development and success, 10 egg masses were selected randomly in each age class; within each of these egg masses, 10 eggs were selected from each of four zones: (1) spumaline retained and from the margin, (2) spumaline retained and from the interior, (3) spumaline removed and from the margin, and (4) spumaline removed and from the interior. These eggs were dissected to determine the number of host eggs which were: fertile (eggs from which caterpillar larvae had emerged); partially developed (translucent grey-green fluid with or without a partially developed larva); undeveloped (waxy orange fluid); or parasitized (eggs with emergence holes or dead *T. minutum*). Data from the 10 eggs per egg mass zone were log-transformed and analyzed using a three-way ANOVA with factors of egg mass age (6), spumaline presence (2), and egg location (2); contrast matrices identified the significant differences (Systat-Stats; Wilkinson 1990). The percentage of tent caterpillar larvae emerging was log-transformed and compared within each age group using a one-way ANOVA and Tukey's range test (Systat-Stats; Wilkinson 1990).

Results

Pheromone Traps. Male moths always appeared in the pheromone traps before egg masses were collected on the branch samples (Fig. 1). In 1988, the two-component lures collected males 2 d before egg masses appeared, and the three-component lures collected males

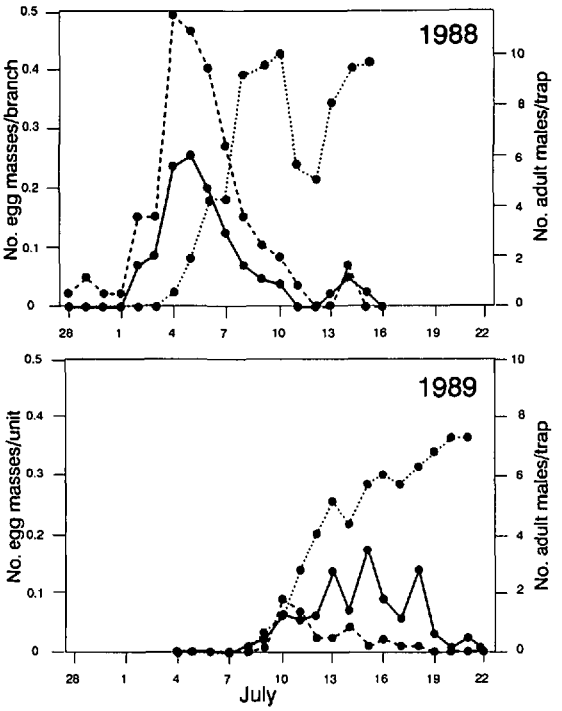

Fig. 1. Mean number of forest tent caterpillar egg masses per sample laid on white oak and aspen trees and mean number of adult males collected in pheromone traps in southern Ontario during 1988 and 1989. ●——●, number of adult males collected in pheromone traps with two-component lures; ●----●, number of males collected in traps with three-component lures in 1988 and the number of egg masses found on 100 aspen trees in 1989; and ●· · · ·●, number of egg masses laid on 50 branches of white oak.

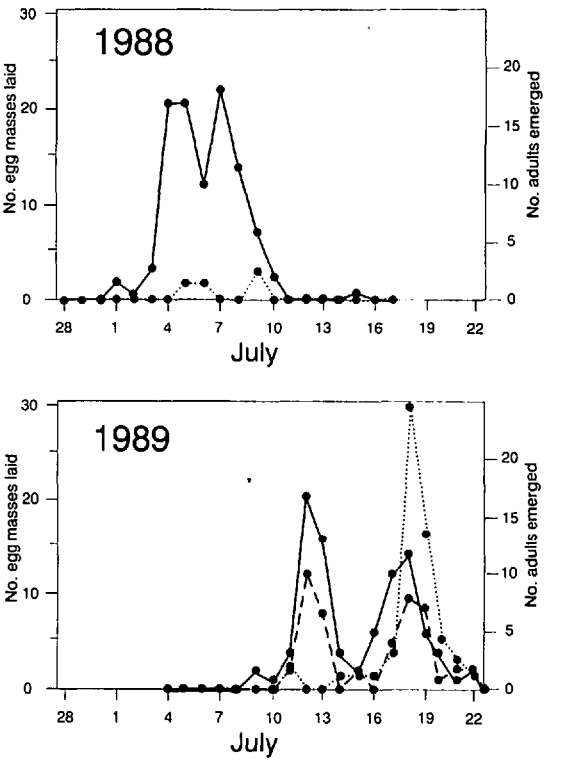

Fig. 2. Total number of male and female tent caterpillar adults emerging and total number of egg masses laid in a walk-in cage during 1988 and 1989. ●——●, number of adult moths emerging in 1988 and the number of adult males emerging in 1989; ●----●, number of adult females emerging; and ●· · · ·●, number of egg masses laid in the cage.

6 d, before egg masses appeared (Fig. 1). The peak in male catch for both lures occurred ≈4–5 July, 3–6 d after the first male appeared. Males were collected in the traps for 18 d from 27 June until 15 July. Males appeared in the pheromone traps during 1989 only 1 d before the first egg mass was collected on the branch samples (8 July) (Fig. 1). Peak male catch occurred on 15 July, 7 d after flight was initiated. Males were collected in the traps for 15 d from 8 to 22 July.

Branch Sampling. Newly laid egg masses were collected by branch sampling in 1988 for ≈6 d (4–10 July) with almost 50% of the egg masses being laid in the first 3 d (Fig. 1). The average temperatures throughout the oviposition period during 1988 were warm (maximum, 29 ± 1.1°C [mean ± SE]; minimum, 14 ± 1.0°C).

Egg masses were collected on branch samples in 1989 for ≈10 d from 9 to 19 July with 50% of the egg masses again being laid in the first 3 d of oviposition (Fig. 1). Daily temperatures for the oviposition period in 1989 were cooler than in 1988, averaging 21 ± 1.0°C (maximum) and 10 ± 1.0°C (minimum).

Sampling of Young Aspen. Oviposition on aspen saplings in 1989 peaked on the second and third days of egg-laying, with 50% of the oviposition occurring in the first 4 d (Fig. 1). As with the branch samples from the white oak, the oviposition period on young aspen lasted ≈10 d.

Walk-In Cages. Peak emergence of the 86 surviving pupae in 1989 occurred during 4–8 July; the first adults emerged on 1 July (Fig. 2). No emergence was observed after 10 July. Egg masses were laid inside the cage during 5–9 July during the peak emergence period. The first egg mass laid on 5 July appeared 4 d after the beginning of adult emergence.

Bimodal curves were observed for adult emergence and oviposition in the walk-in cages during 1989 (Fig. 2). The initial rise in emergence and oviposition was synchronous with that from the pheromone traps, white oak branches, and aspen saplings. The first adult males appeared on 9 July and female emergence and oviposition began on the same day, 2 d later. The distinct reduction in emergence and egg-laying during 14–16 July coincided with a 3-d period of cooling; daily temperatures averaged 18 ± 1.1°C

Table 1. Parasitism of forest tent caterpillar egg masses of various ages by *T. minutum*, including numbers, sex ratio, and development time of successfully emerged progeny

Age of egg mass, d	No. egg masses exposed (*n*)	Eggs masses from which parasitoids emerged		No. parasitoids/egg mass, mean (SE)[b]			Development time, d, mean (SE)[b,c]	No. eggs with parasitoid holes, mean (SE)[b]
		No.	%	♂♂	♀♀	Total		
0	23	0	0a	—	—	—	—	—
2	21	0	0a	—	—	—	—	—
7	24	1	4.2a	2.0 (–)	4.0 (–)	6.0 (–)	12.0 (–)	6.0 (–)
14	23	10	43.5b	26.5 (5.3)a	65.2 (12.5)a	91.7 (17.2)a	14.5 (0.2)a	11.0 (2.9)a
21	22	16	72.7c	24.3 (4.5)a	57.3 (10.0)a	81.5 (15.2)a	14.2 (0.3)a	5.0 (0.3)b
28	24	3	12.5ab	6.3 (0.3)b	10.7 (2.3)b	17.0 (2.0)b	14.0 (0.0)a	6.4 (1.8)b
Control	10	0	0a	—	—	—	—	—
F			G = 63.28	2.93	5.60	4.74	0.88	4.92
df			6	2,26	2,26	2,26	2,26	2,26
P			<0.001	0.07	0.01	0.02	0.43	0.02

[a] Means followed by the same letter are not significantly different when log-transformed (Pearson's χ^2 test).
[b] Means followed by the same letter in the same column are not significantly different when log-transformed (1-way ANOVA; Tukey's range test).
[c] Development time, number of days from the first day that tent caterpillar egg masses were exposed to 10 female parasitoids until the first day progeny emerged when maintained at 20°C and L:D = 16:8.

(maximum) and 7 ± 0.9°C (minimum). For the next 5 d after 16 July, temperatures rose to 23 ± 1.0°C (maximum) and 12 ± 1.1°C (minimum), and both emergence and egg-laying resumed to a peak on 18 July.

Egg Acceptability to *Trichogramma*. In total, 147 tent caterpillar egg masses were laid and available for testing in the laboratory. When egg masses of various ages were exposed to *T. minutum* females, the percentage from which parasitoids emerged increased as the age of the host eggs increased up to 21 d (Table 1). Although females were observed drilling into the chorion of eggs in all treatment ages, few progeny emerged from younger egg masses (<14 d old). The greatest emergence of *T. minutum* from egg masses occurred on those masses exposed to parasitoids 21 d after oviposition (72.7% of the egg masses).

Similar numbers of male or female progeny emerged from egg masses parasitized at days 14 and 21 (Table 1). Based on a weighted average, 69.5% of the progeny were female with a development time at 20°C of 14.2 ± 0.3 d. The number of parasitoids emerging from a single parasitized host egg ranged from 5.0 to 11.0, with no clear relationship to the age of the host egg (Table 1).

Within those egg masses that were parasitized, no interaction was observed between the age of the host egg and the presence or absence of a spumaline cover (F = 0.69–0.79; df = 2, 44; P = 0.46–0.51) (Table 2). On average, the number of host eggs was similar in the spumaline and nonspumaline areas (54.9 ± 7.4) and the spumaline covering had no effect on the number of eggs (7.5 ± 1.8) or the percentage of eggs (16.1 ± 3.8) with parasitoid emergence holes (see footnote, Table 2). A slightly greater percentage of spumaline-covered eggs had parasitoid emergence holes in 14- and 21-d-old eggs than in 7- or 28-d-old eggs (Table 2). Combined values for both spumaline-covered and nonspumaline areas show that there averaged 109.8 ± 14.8 tent caterpillar eggs per egg mass from which 14.4 ± 3.5 eggs had parasitoids emerge; providing an average of 13.1% egg parasitism.

Three-way factorial analysis of the dissected subsample of eggs (n = 2,400 eggs; 10 eggs from

Table 2. Number of tent caterpillar eggs per egg mass, number of eggs with parasitoid emergence holes, and percentage eggs with parasitoid holes in spumaline-covered and nonspumaline areas according to host age

Age of egg mass, d	No. parasitized egg masses	Spumaline-covered, mean (SE)[a]			No. spumaline covering, mean (SE)		
		No. host eggs	No. eggs with parasitoid holes	% with holes	No. host eggs	No. eggs with parasitoid holes	% with holes
7	1	84.1 (–)	1.0 (–)	1.2 (–)	62.6 (–)	0 (–)	0 (–)
14	10	58.1 (8.0)a	7.4 (3.0)a	12.4 (4.1)a	43.7 (4.6)a	7.9 (1.9)a	18.7 (4.6)a
21	16	49.2 (5.6)a	8.5 (1.8)a	19.8 (4.3)a	50.1 (6.6)a	7.7 (1.6)a	17.6 (3.7)a
28	3	73.0 (27.2)a	1.7 (0.3)b	3.2 (1.3)b	89.0 (–)	5.0 (–)	5.6 (–)
F		0.95	3.18	5.14	1.28	0.01	0.37
df		2,22	2,22	2,22	2,22	2,22	2,22
P		0.40	0.06	0.02	0.30	0.99	0.59

[a] No differences were observed between spumaline-covered and nonspumaline area of the same egg mass for number of host eggs (F = 0.01; df = 1,44; P = 0.94), number of eggs with parasitoid holes (F = 0.93; df = 1,44; P = 0.34), or percentage of eggs with parasitoid holes (F = 0.81; df = 1,44; P = 0.37) (two-way ANOVA test). Means followed by the same letter within the same column are not significantly different when log-transformed (two-way ANOVA; Tukey's range test).

Table 3. Effect of host age on mean number of forest tent caterpillar eggs with larval emergence holes, partially developed, undeveloped, or parasitoid emergence holes, and percentage of eggs with emerging caterpillar larvae from egg dissections

Age of egg mass, d	No. subsamples of 10 eggs (*n*)	No./10 eggs/egg mass, mean (SE)[a]				% Larvae[b] emerging, mean (SE)
		Larval holes	Partially developed	Undeveloped	Parasitoid holes	
0	40	2.0 (0.5)a	7.2 (10.6)b	0.3 (0.1)a	0.0 (0.0)a	21.3 (5.4)ab
2	40	0.7 (0.3)a	9.2 (0.3)a	0.2 (0.1)a	0.0 (0.0)a	6.6 (3.2)a
7	40	4.1 (0.7)b	5.7 (0.7)bc	0.1 (0.0)a	0.0 (0.0)a	42.3 (7.0)bc
14	40	6.6 (0.6)b	3.1 (0.6)c	0.0 (0.0)a	0.2 (0.1)b	67.8 (6.1)c
21	40	9.4 (0.2)c	0.5 (0.2)d	0.0 (0.0)a	0.1 (0.1)ab	94.3 (2.3)d
28	40	9.0 (0.4)c	0.6 (0.3)d	0.0 (0.0)a	0.0 (0.0)a	96.2 (1.6)d
Control	40	9.5 (0.3)c	0.4 (0.2)d	0.0 (0.0)a	0.0 (0.0)a	97.5 (3.6)d
F		16.91	11.31	1.19	7.74	16.91
df		5,216	5,216	5,216	5,216	5,216
P		<0.001	<0.001	0.32	<0.001	<0.001

[a] Means followed by the same letter within the same column are not significantly different when log-transformed (three-way ANOVA; contrast tests).

[b] Means followed by the same letter are not significantly different when log-transformed (one-way ANOVA; Tukey's range test).

each of the four zones of 10 egg masses for each of the six age classes) showed that none of the parameters was affected by the zone (interior or margin of the egg mass) in which the host eggs were located ($F = 0.52$; df = 5, 216; $P = 0.76$). Thus, further analysis was based on pooling the four subsamples of 10 eggs per location per egg mass (Table 3).

The number of undeveloped eggs did not vary with the age at which the eggs were exposed to the parasitoids. However, the number of eggs with larval holes, partially developed or with parasitoid holes, was significantly influenced by the age of the host egg (Table 3). The number of larval holes increased with the age of the host egg up to 21 d whereas the number of partially developed eggs declined with host age. The most rapid change in these two parameters occurred before 21 d of age; no significant differences were observed between 21- and 28-d-old treatments and the controls. The number of eggs with parasitoid emergence holes was significantly higher when the host egg was 14 d old than at any other age. The percentage of caterpillar larvae successfully emerging increased significantly with the age at which the egg mass was exposed to *Trichogramma* (Table 3). Larval emergence was maximum when egg masses 21–28 d old were exposed to the parasitoids; this was not significantly different from the 10 control egg masses not exposed to *Trichogramma*.

The number of parasitoid emergence holes was the only parameter in the dissected eggs which varied between the spumaline-covered and nonspumaline areas of the egg mass ($F = 7.52$; df = 1, 216; $P = 0.01$). When spumaline was removed, the number of eggs with successfully emerging parasitoids was higher in 14- and 21-d-old egg masses than in egg masses of similar age where the spumaline was not removed. No parasitoids emerged from eggs with a spumaline covering, whereas without the covering, one parasitoid each emerged from six 14-d-old egg masses and three parasitoids emerged from one 21-d-old egg mass.

No parasitoids emerged from host eggs that had developed for 2 mo at room temperature and had then been placed in the cold to break possible diapause. When host eggs within each of these egg masses were dissected, a few fully developed, dead parasitoids were observed: on average, 1.0 ± 0.4 dead parasitoids per egg mass. Both a single dead adult parasitoid and a dead pharate larva were observed within the same egg in six of the 30 egg masses where parasitoids emerged (14–28 d old).

Discussion

Oviposition Activity in the Field. Distribution of males in the pheromone traps (with two-component lures) was similar in both years and provided a consistent prediction of oviposition (1–2 d). Although the overall trap catch was lower in 1989 than in 1988, the fact that the oviposition period also was shorter in the first year (7 d) than in the second year (10 d) suggests that this was a result of warmer temperatures in 1988. Although the exact effect of cooling on the activity of adult tent caterpillars is not known (Hodson & Weinman 1945), adult activity is thought to be promoted by warm, sunny weather (Ives 1973). The effects of cool weather could also be observed in the delayed emergence and oviposition by moths in the cage experiment during the second year.

The most notable characteristic of the forest tent caterpillar was the very short time (7–10 d) it took to complete oviposition. Most of the oviposition (50%) in each year occurred within the first 3 d after female emergence. Females oviposited within the first day of adult life, and the emergence pattern of the population was compressed sufficiently, despite different weather patterns

between years, to allow all egg masses to be deposited within 7–10 d.

Egg Acceptability to *Trichogramma*. Only 13.1% of the 137 tent caterpillar egg masses exposed to *Trichogramma* had parasitoids emerge under ideal laboratory conditions. Removal of the spumaline layer appeared to improve parasitoid success only slightly. This was unexpected because *Trichogramma* spp. have been reported to successfully parasitize and emerge from field-collected forest tent caterpillar eggs, even at low levels (Hodson 1939, Houseweart et al. 1984). It may be that *Trichogramma* parasitizing forest lepidopteran eggs are more specialized than previously thought. One of the species described from tent caterpillar egg masses by Houseweart et al. (1984), *Trichogramma* spp. near *nubilale*, had a longer ovipositor (which was hypothesized to improve access to spumaline-covered eggs) than *T. minutum* collected from spruce budworm. This relatively unknown species may be much more successful at exploiting tent caterpillar eggs than *T. minutum*.

The *T. minutum* colony used in our experiment was reared for 32 generations in the laboratory on a factitious host. It is possible that the fitness or quality of the female parasitoids was reduced compared to natural field populations through inbreeding, selection, and genetic drift of traits such as host acceptance and oviposition behavior. This shift has been in observed in at least one other *Trichogramma* system (Bergeijk et al. 1989). The original population of *Trichogramma* used in this experiment was collected from spruce budworm eggs rather from those of forest tent caterpillar. Budworm eggs, as well as those of the factitious host, are relatively soft-shelled compared with those of forest tent caterpillar, and continuous culture of such eggs may have selected for small females that could not penetrate the chorion of the tent caterpillar eggs. Parasitoids collected relatively recently from the field or from a different species of *Trichogramma* may lead to higher levels of parasitism on tent caterpillar eggs.

The highest number of *Trichogramma* emerged from older egg masses (>7 d old); the highest level of emergence was from egg masses exposed 21 d after oviposition. This also was unexpected because most reports of parasitism by this genus suggest that younger eggs (0–2 d old) are preferred over older eggs (>2 d old) (Pak 1986). It is surprising that eggs <14 d of age would not allow parasitoids to develop successfully because eggs older than this are known to contain pharate larvae (Hodson 1939), and *Trichogramma* have not been previously reported to develop in hosts with fully developed larvae. Although we found fully developed parasitoids in conjunction with fully developed larvae, neither emerged successfully.

Successful parasitism must be assessed in terms of attack (host acceptance) as well as success of progeny emergence (host suitability). When tent caterpillar eggs were removed from cold storage and dissected, no undeveloped *T. minutum* were observed. In the younger age classes, the majority of forest tent caterpillar eggs exposed to parasitoids were classified as partially developed. This led to low tent caterpillar emergence (<40%) compared with egg masses not exposed to *Trichogramma*. It appears, therefore, that young tent caterpillar eggs were selected and attacked by the parasitoids but that parasitoids failed to emerge unless the egg masses were between 7–14 d old (at 20°C). Eggs of *T. minutum* would not have been visible during our examination of the dissected host eggs and, thus, it is unknown whether female parasitoids could puncture the host chorion and insert venom but not lay eggs, or whether their eggs were laid in the host and failed to develop. Injecting venom and calyx fluid by parasitoids have been shown to disrupt larval development of some hosts (Strand & Dover 1991). Barrett & Schmidt (1991) suggested that an imbalance in amino acid concentrations may prevent parasitoid development in unsuitable host eggs. This also may be true for different ages of the same host egg.

Feasibility of Using *Trichogramma* for Release. If an egg parasitoid such as *Trichogramma* were to be released inundatively against the tent caterpillar, it appears that there would be relatively little time to predict oviposition from males caught in pheromone traps with two-component lures (2 d); three-component lures may provide more lead time. It may be possible to provide better prediction by using sampling schemes for late instars or pupae. Fortunately, the long period of time the eggs are available for parasitism (up to 14–21 d after oviposition) means there is a 2- or 3-wk period over which releases could be made. Because the greatest mortality to the host egg occurred during the first 14 d after oviposition (≈92% at 2 d of age), any proposed biocontrol strategy should be directed at this stage. The fact that *T. minutum* mass-reared in the laboratory cannot emerge successfully from such eggs means that no carryover effects will be present. Although this lack of long-term parasitism may be more socially acceptable for controlling the forest tent caterpillar, additional studies are needed to determine why *T. minutum* kill but do not emerge from young tent caterpillar eggs.

Acknowledgments

We thank Nalayini Maheswaren and Heather Sutton, University of Toronto, for technical assistance, and R. Goyer (University of Georgia, Athens), E. Forsse, R. Bourchier (University of Toronto), and an anonymous

reviewer for suggested revisions. The production of pheromone lures by Research & Productivity Council and the donation of pheromone traps from Agriculture Canada were also appreciated. This research was funded through a grant to S.M.S. from the Ontario Pesticides Advisory Committee, Ontario Ministry of the Environment.

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Received for publication 28 February 1992; accepted 15 June 1993.