

**Patterns of Host Exploitation by the Parasitoid Wasp  
*Trichogramma minutum* (Hymenoptera:  
Trichogrammatidae) when Attacking  
Eggs of the Spruce Budworm  
(Lepidoptera: Tortricidae)  
in Canadian Forests**

BARRY B. BAI AND SANDY M. SMITH

Faculty of Forestry, University of Toronto, 33 Willcocks Street,  
Toronto, Ontario, Canada M5S 3B3

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**ABSTRACT** We examined patterns of host exploitation by natural populations of the parasitoid *Trichogramma minutum* Riley parasitizing eggs of the spruce budworm, *Choristoneura fumiferana* (Clemens), in Canadian boreal forests in an effort to identify aspects to improve inundative releases. Egg masses of spruce budworm were sampled from eight different sites in Ontario and New Brunswick during the period of oviposition in 1992. Parasitoids did not necessarily fully exploit a discovered egg mass; 35% of parasitized egg masses were completely parasitized by naturally occurring *T. minutum*, but the remaining 65% were only partially parasitized. Not all parasitized host eggs produced viable parasitoid offspring. Natural mortality of immature *T. minutum* was as high as 52% in one site. This high mortality was not correlated with the degree of superparasitism. The size of adult *T. minutum* as estimated by wing length varied among different localities, but females were always larger than males from the same site. Females were usually mated before they discovered spruce budworm eggs and produced a female-biased sex ratio when allocating progeny in the field. Field patterns of host exploitation can help us to predict what to expect from inundative release programs and, more important, to identify aspects that need to be enhanced so that a better level of control of spruce budworms can be achieved.

**KEY WORDS** *Trichogramma minutum*, *Choristoneura fumiferana*, host exploitation

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THE WAY IN WHICH PARASITOIDS forage and exploit their hosts in the field can have potential implications in biological control programs in which these parasitoids are released to search for and exploit hosts. Although many parasitoid species have been studied intensively in the laboratory before being used as biological control agents, there has been relatively little investigation on how parasitoids exploit their hosts in the field (Waage 1983, Walde & Murdoch 1988). Even in classical biological control programs, field populations of parasitoids and hosts are often not closely followed after the establishment of the parasitoids, and mechanisms by which parasitoids regulate host populations are not clearly understood (see Murdoch et al. 1985). Studies of parasitoids interacting with their hosts in the natural habitat are important because they provide valuable information that not only enables theoreticians to formulate, correct, and further ecological theory, but also enables practitioners to improve biological control.

The minute egg parasitoid, *Trichogramma minutum* Riley, is widely distributed in North American forest and parasitizes a number of forest pests including the spruce budworm, *Choristoneura fumiferana* (Clemens) (Houseweart et al. 1984). Although common, this parasitoid is generally considered unimportant in the natural control of the spruce budworm (Anderson 1976) because of its low occurrence and lack of response to increases in the pest population during an outbreak (Miller 1963). Because of the economic importance of the spruce budworm to the forest industry (Moody 1992) and governmental restrictions on the use of chemical insecticides, forest managers and entomologists have long been searching for new alternatives in management of this pest (Morris 1963, Sanders et al. 1985). Since the 1980s, a biological control program using inundative releases of *T. minutum* to suppress budworm populations in Canadian forests has shown some promising results (Smith et al. 1990). Inundative releases augment naturally occurring parasitoids at critical times to achieve

the goal of suppression of pest populations. In such programs, large numbers of parasitoids are released in the field, and these parasitoids are expected to search for and exploit hosts (pests) effectively and efficiently.

Although a considerable amount of work has been done on various aspects of *T. minutum*, including its potential application against spruce budworm and other forest pests (Houseweart 1985, Smith et al. 1990; B.B.B., unpublished data), relatively little is known about how naturally occurring parasitoids exploit their hosts in the field. Early reports on natural control of spruce budworm by *Trichogramma minutum* in the forests described mainly levels of parasitism (Morris 1963). It is not known whether females of *T. minutum* respond to the size of egg masses in a density-dependent fashion or whether a female can fully exploit an egg mass once she encounters it. Information on progeny and sex allocation by wasps in the field and the natural mortality of *T. minutum* on spruce budworm is also lacking. In this article, we report natural patterns of host exploitation by *T. minutum* when parasitizing eggs of spruce budworm in the forest. We focus on patterns of host exploitation within egg masses (i.e., what happens after [rather than before] parasitoids discover an egg mass). Parasitization of naturally laid egg masses of spruce budworm from different sites in central and eastern Canadian forests was examined and characterized. Findings from these natural parasitoids attacking host eggs will help us to identify aspects of host exploitation that may be improved in biological control programs or to predict how released parasitoids might behave and what might be an optimal level of parasitism to expect using inundative releases.

### Materials and Methods

**Patterns of Host Exploitation by Naturally Occurring *T. minutum* in the Field.** We sampled naturally occurring egg masses of spruce budworm during the period of budworm oviposition, July to August 1992, to determine parasitization by *T. minutum* in the field. Parasitized budworm egg masses were collected from one site in New Brunswick and seven sites in Ontario. The sites in Ontario included A, B, and C, all from the Dryden area (49.8° N, 92.8° W). Of these, B and C were about 10 km apart; both were about 40 km from site A. The other sites included Kenora (49.8° N, 94.5° W), Kirkwood (46.3° N, 83.5° W), Sault Ste. Marie (46.5° N, 84.3° W) and Alliston (44.2° N, 79.9° W). The site in New Brunswick was located near St.-Quentin (47.5° N, 67.3° W). These sites represent a wide range of forest inhabited by spruce budworm from about 67° to 95° W longitude, ≈2,000 km. All sampled areas were experiencing moderate to severe spruce budworm outbreaks during 1992; population density

of budworm egg masses was high across all sites. Our estimated percentage parasitism of total egg masses by *T. minutum* in the field was low, <10% in all sites.

Egg masses collected from all sites were laid by naturally occurring spruce budworms in the field. At the Sault Ste. Marie site, we also put out sentinel budworm egg masses. Spruce twigs with one or several egg masses laid in the laboratory were transported to the field and twist-tied to branches of white spruce, *Picea glauca* (Moench) Voss, trees. After 5 d of exposure to possible parasitization by naturally occurring *Trichogramma* in the field, these twigs were recovered and brought to the laboratory for examination. Evidence from laboratory studies suggests that sentinel egg masses are attacked as often as, if not more than, natural egg masses by females of *T. minutum* (Song 1993). Those females also allocated a similar number of progeny per egg, and the progeny had similar rates of survival in sentinels and natural egg masses. We included sentinels in this site to compare differences, if any, in patterns of host exploitation by naturally occurring parasitoids on two types of hosts in the field. Unfortunately, only four of the naturally occurring budworm egg masses collected from this site were parasitized, and none of the four produced adult *T. minutum*. Therefore, our data at the Sault Ste. Marie site represented only the information on sentinels.

In all sites, white spruce and balsam fir, *Abies balsamea* (L.) Mill., with obvious spruce budworm damage were chosen as sample trees. Because female spruce budworm adults lay eggs in masses on tree needles, usually on new growth in the middle and upper crown levels (Morris 1963), we sampled twigs from the middle and upper crown of each tree with an extendable pole pruner. One twig was usually cut from each side (east, west, north, south) of a tree to obtain a total of four twigs per tree. Total number of trees sampled per site varied with the abundance of budworm populations, and usually >10 trees were sampled from a single site. The number of parasitized and unparasitized budworm egg masses obtained per tree or per site also varied because of the uneven distribution of budworm and parasitoid populations in the field. Parasitoid populations were relatively high at site A around the Dryden area and very low at three of the other sites (Kenora, Kirkwood, and Alliston). Pruned twigs were placed in plastic bags, labeled, transported to the laboratory, and stored at 4°C until examined.

Needles bearing budworm egg masses with at least one parasitized egg were removed from sampled twigs, placed individually in a glass vial (6.0 by 1.5 cm), and held at 20°C, with a photoperiod of 16:8 (L:D) h for emergence of parasitoids. Parasitization of the egg masses was recognized by the dark appearance of the eggs

(Jennings & Houseweart 1983). Usually a needle contained only one egg mass; however, when two egg masses occurred on one needle, the needle was cut into two pieces so that only a single egg mass was placed in each vial.

All vials were examined after 20 d. This ensured that all parasitoids had emerged, because developmental time from egg to adult for *T. minutum* at 20°C and 16:8 (L:D) h is  $\approx$ 14 d (Lawrence et al. 1985, Laing & Eden 1990). For each egg mass, we recorded its size (i.e., number of spruce budworm eggs in one egg mass), the number of host eggs parasitized per egg mass, and the number of emerged parasitoids, including both females and males. We dissected all parasitized hosts to determine the number of parasitoids that died inside the host chorion. We measured wing lengths from a subsample ( $n = 10$  for both sexes at all except two sites where  $n < 10$  because of limited numbers of adults emerged) of emerged parasitoids to obtain size distribution of naturally occurring *T. minutum* from different field sites (Bourchier et al. 1993).

**Progeny and Sex Allocation by *T. minutum* in the Field and the Laboratory.** We examined and compared patterns of progeny and sex allocation by *T. minutum* in the field and the laboratory. To determine patterns in the field, we counted the number of parasitoid progeny emerged (survived) and the corresponding sex ratio (percentage of males) from each parasitized budworm egg mass collected from the field. We counted the number of eggs parasitized in an egg mass and dissected all the parasitized eggs to determine number of parasitoids that failed to emerge. From this information, we calculated the number of parasitoid offspring that were found (i.e., numbers emerged + numbers died) and that survived per host egg. Before parasitoid emergence, we also dissected a subsample ( $n = 2$  egg masses per site) of parasitized budworm egg masses from each site to count the number of parasitoids developing inside each host egg. Pupae and pre-adults of the parasitoids could be easily recognized by their resemblance to the adults. This information generated a frequency distribution of progeny allocated by *T. minutum* in each host egg under natural conditions.

To determine patterns in the laboratory, we used a colony of parasitoids that had been collected from site A near Dryden and maintained on spruce budworm eggs for >10 generations in the laboratory. The colony was maintained by providing newly emerged parasitoids with fresh budworm egg masses in a glass vial (2.5 by 9.5 cm) for 24 h and then incubating parasitized host eggs at 25°C and 16:8 (L:D) h for emergence of parasitoid progeny. Each generation of parasitoids was started with wasps emerged within a 24-h period to synchronize development. We obtained our weekly shipments of fresh, laboratory-reared spruce budworm eggs from the Forest

Pest Management Institute (Forestry Canada), Sault Ste. Marie, Ontario, Canada.

Honey-fed wasps 2 d old were used in our laboratory test of progeny and sex allocation. A female was introduced into a petri dish (5.0 by 1.0 cm) containing a single budworm egg mass on a needle. The female was observed using a stereomicroscope for 30 min or until she laid 10 eggs, whichever came first. We recorded the number of eggs deposited into each host and the corresponding sex of the eggs using a behavioral criterion (Suzuki et al. 1984) in which a continuous movement of the abdomen during oviposition signaled male offspring and an abrupt movement, female offspring. The parasitized host eggs were reared in the laboratory until parasitoid emergence, whereupon the number of progeny emerged and the sex ratio of the emergents were recorded. Laboratory emergence data confirmed our behavioral judgment about progeny and sex allocation of females.

Voucher specimens of *T. minutum* were deposited in the Department of Entomology, Royal Ontario Museum, Toronto, Ontario, Canada.

**Statistical Analysis.** Comparisons of various measurements among different sites were conducted using a one-way analysis of variance (ANOVA) followed by Tukey's studentized range test. Correlation analysis was performed between the rate of host exploitation by parasitoids and size of egg masses and between the rate of mortality and degree of superparasitism. A Student's *t*-test was used to compare differences in wing length between sexes for wasps collected from each site. We used an IBM-PC version of the SAS computer package (SAS Institute 1990) to analyze all data.

## Results

**Patterns of Host Exploitation by Naturally Occurring *T. minutum* in the Field.** The average size of naturally occurring, parasitized budworm egg masses was similar among sites (Table 1) despite some within-site variation. In site A near Dryden, we found that the smallest egg mass contained only one host egg, whereas the largest contained 44 eggs. Sentinel egg masses placed at the Sault Ste. Marie site contained more eggs than those naturally occurring from other sites ( $F = 12.72$ ;  $df = 4, 82$ ;  $P = 0.0001$ ; one-way ANOVA with Tukey's studentized range test) and had up to 54 eggs in a single egg mass.

An egg mass can be completely parasitized. We found that in 34.5% ( $n = 87$ ) of the field-collected, parasitized budworm egg masses all eggs were blackened and parasitized. The majority ( $\approx$ 65%) of these egg masses, however, was only partially exploited by parasitoids in the field (Table 1). The mean percentage of eggs parasitized in an egg mass did not vary significantly from site to site ( $F = 1.63$ ;  $df = 4, 82$ ;  $P = 0.175$ ;

**Table 1.** Variation in patterns of host exploitation and body size (mean  $\pm$  SE) of *T. minutum* in the field when parasitizing *C. fumiferana* eggs

Site	n <sup>a</sup>	No. spruce budworm eggs per egg mass	No. eggs parasitized	No. parasitoids emerged	No. parasitoids died	Wing length of emerged parasitoids, mm			
						♀		♂	
						n	Length	n	Length
Dryden area									
A	50	19.7 $\pm$ 1.2b	12.3 $\pm$ 1.5a	17.5 $\pm$ 2.5a	3.5 $\pm$ 0.7b	10	0.66 $\pm$ 0.02ab	10	0.61 $\pm$ 0.02ab
B	14	20.2 $\pm$ 1.2b	13.4 $\pm$ 2.0a	15.1 $\pm$ 3.2a	5.4 $\pm$ 2.3b	10	0.70 $\pm$ 0.01a	10	0.65 $\pm$ 0.02a
C	8	21.0 $\pm$ 2.8b	17.9 $\pm$ 3.2a	22.4 $\pm$ 6.6a	7.4 $\pm$ 3.3ab	10	0.63 $\pm$ 0.02ab	6	0.55 $\pm$ 0.02bc
Sault Ste. Marie <sup>b</sup>	11	38.6 $\pm$ 3.3a	16.0 $\pm$ 3.1a	13.8 $\pm$ 3.2a	13.7 $\pm$ 3.0a	10	0.60 $\pm$ 0.02b	10	0.54 $\pm$ 0.02bc
St.-Quentin	10	—	—	21.6 $\pm$ 7.0a	—	8	0.64 $\pm$ 0.02ab	8	0.53 $\pm$ 0.04bc
Others <sup>c</sup>	4	17.0 $\pm$ 3.1b	13.5 $\pm$ 2.4a	11.8 $\pm$ 2.1a	9.0 $\pm$ 4.3ab	10	0.62 $\pm$ 0.03ab	10	0.51 $\pm$ 0.01c

In each column, means followed by the same letter are not significantly different ( $P = 0.05$ ; Tukey's studentized range tests).

<sup>a</sup> Sample size (n) = number of parasitized spruce budworm egg masses collected per site.

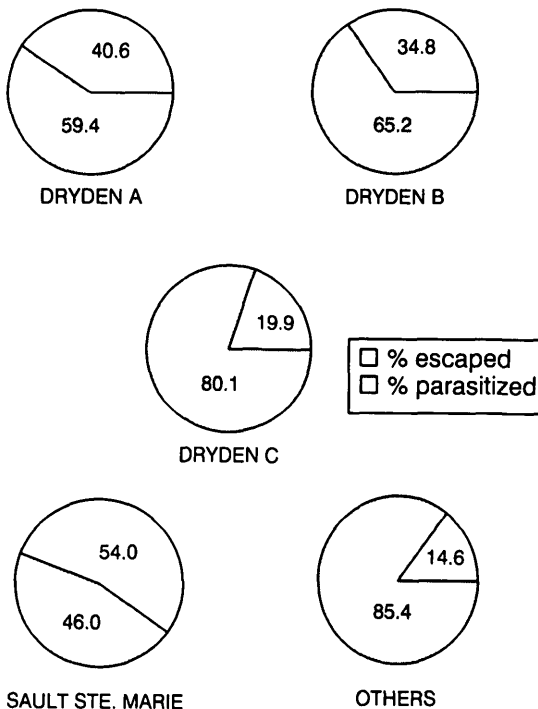
<sup>b</sup> Egg masses collected from the Sault Ste. Marie site were laid on foliage in the laboratory and then exposed to parasitoids in the field.

<sup>c</sup> These four egg masses were collected from three sites in Ontario: two from Kenora, one from Kirkwood, and one from Alliston.

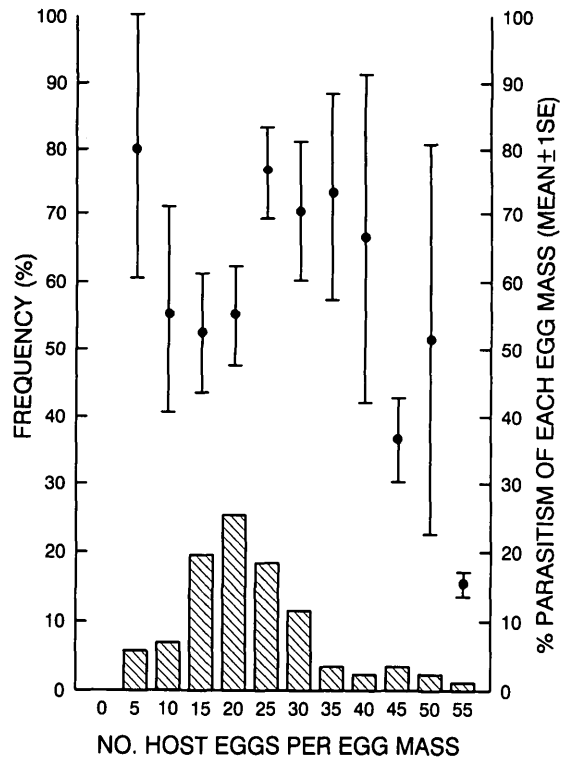
one-way ANOVA on arcsine transformed data), although it ranged from 46 to 85% (Fig. 1). Among all egg masses having at least one parasitized egg, an average of 62% ( $n = 87$ ) of eggs were parasitized. Although percentage parasitism appeared to vary with the number of eggs in an egg mass (Fig. 2), an analysis failed to detect a significant correlation between the two parameters ( $r = -0.04, P = 0.68$ ) (i.e., a larger egg mass did not have a greater percentage of eggs parasitized than a smaller egg mass or vice versa). Size of spruce budworm egg masses was normally distributed ( $G = 10.48, df = 5, P > 0.05$ ;

goodness-of-fit test); there were few very small or very large egg masses, and most (74.7%,  $n = 87$ ) contained 15 to 30 eggs.

Not all parasitized host eggs produced viable parasitoid offspring. Natural mortality varied among sites and was heaviest at the Sault Ste. Marie location (Table 1). Between 20.8 and 51.6% of parasitoid offspring found inside spruce budworm eggs collected from the field failed to emerge. Parasitoids died as pupae or preadults



**Fig. 1.** Mean proportion of eggs in a field-collected spruce budworm egg mass parasitized by *T. minutum* (hatched area) and that escaped parasitism (open area).



**Fig. 2.** Frequency distribution of size of field-collected spruce budworm egg masses (hatched bars) and the relationship between egg mass size and percentage parasitism by *T. minutum* (solid circles).

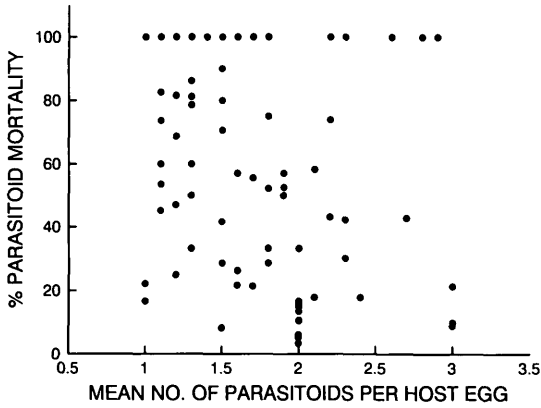


Fig. 3. Relationship between mean number of *T. minutum* found per spruce budworm egg and percentage mortality of the parasitoid in the field.

inside the blackened chorion of host eggs. Some of the eggs that contained dead parasitoids also had emergence holes, indicating that some individuals had emerged successfully from the same host. It was not clear what caused the mortality. Mortality was independent of the mean number of parasitoids contained inside each host egg (Fig. 3; correlation analysis,  $r = -0.19$ ,  $P = 0.08$ ,  $n = 87$ ). This suggests that superparasitism is not a significant mortality factor. Size, as estimated by wing length, of parasitoids collected from the field varied among different sites (Table 1), although females, on average, were always larger than males from the same site ( $t > 2.142$ ,  $P < 0.05$  for all sites, with the exception of site A in which  $t = 1.964$ ,  $P = 0.065$ ;  $df = 18$  for sites A, B, Sault Ste. Marie, Others, and = 14 for sites C, St.-Quentin;  $t$ -test). The size of males was generally more variable than that of females among sites.

**Progeny and Sex Allocation by *T. minutum* in the Field and the Laboratory.** In the field, *T. minutum* produced a female-biased sex ratio from all sites. The sex ratio (percentage of males) of emergents ranged between 20 and 34% (Table 2). Most females that parasitized egg masses in the field were mated, because 97% of the parasitized egg masses ( $n = 97$ ) yielded offspring of both sexes. In the laboratory, *T. minutum* females also had a female-biased sex ratio (28% males), which fell within the range of the field sex ratio. Our dissections indicated that 62.1% of the field-parasitized spruce budworm eggs contained a single *Trichogramma*, although in one case, seven parasitoid progeny were found in one host egg. The frequency of hosts decreased with an increasing number of parasitoids contained per host (Fig. 4). The number of parasitoid offspring found inside each host was similar among different field sites ( $F = 1.01$ ;  $df = 4, 82$ ;  $P = 0.41$ ; one-way ANOVA) and averaged 1.7 parasitoids per host (Table 2). In the laboratory, we found that a greater proportion of parasitized budworm eggs contained only a single parasitoid offspring. Females were never observed in the laboratory to lay more than three eggs in a single host, on average, they allocated 1.3 offspring per host. In both the field and laboratory, however, mortality was observed regardless of the average number of progeny allocated inside each host. This mortality did not correlate with the degree of superparasitism at any site (Table 2).

## Discussion

Our results show that parasitoids in the field do not necessarily fully exploit discovered egg masses. About 35% of the parasitized egg masses were completely parasitized, the remaining 65%,

Table 2. Progeny and sex allocation (mean  $\pm$  SE) of *T. minutum* in the field and laboratory when parasitizing *C. fumiferana* eggs

Site	$n^a$	No. <i>T. minutum</i> progeny		$r^b$ between progeny no. and mortality	Sex allocation per spruce budworm egg mass		
		Found per host egg	Survived per host egg		♀	♂	Sex ratio (% ♂)
Dryden area							
A	50	1.8 $\pm$ 0.1a	1.5 $\pm$ 0.1a	-0.32 ns	14.0 $\pm$ 2.2	3.5 $\pm$ 0.8	20.0 $\pm$ 3.4a
B	14	1.5 $\pm$ 0.1ab	1.1 $\pm$ 0.1ab	0.29 ns	12.0 $\pm$ 2.6	3.1 $\pm$ 1.0	20.4 $\pm$ 4.4a
C	8	1.8 $\pm$ 0.2a	1.3 $\pm$ 0.3ab	-0.62 ns	19.3 $\pm$ 6.0	3.1 $\pm$ 0.7	20.0 $\pm$ 6.2a
Sault Ste. Marie <sup>c</sup>	11	1.8 $\pm$ 0.1a	0.8 $\pm$ 0.1b	0.42 ns	10.1 $\pm$ 2.9	3.7 $\pm$ 0.9	33.5 $\pm$ 7.8a
St.-Quentin	10	—	—	—	14.0 $\pm$ 2.3	7.6 $\pm$ 5.2	22.1 $\pm$ 5.2a
Others <sup>d</sup>	4	1.5 $\pm$ 0.2ab	0.9 $\pm$ 0.2ab	0.60 ns	8.7 $\pm$ 1.9	3.0 $\pm$ 1.2	23.7 $\pm$ 4.2a
Laboratory	69	1.3 $\pm$ 0.1b	1.2 $\pm$ 0.1ab	0.08 ns	5.7 $\pm$ 0.3	2.1 $\pm$ 0.1	27.5 $\pm$ 2.0a

In each column, means followed by the same letter are not significantly different ( $P = 0.05$ ; Tukey's studentized range tests).

<sup>a</sup> Sample size ( $n$ ) = number of parasitized spruce budworm egg masses collected per site. In the laboratory, each egg mass was parasitized by a single wasp; in the field, an egg mass may or may not have been parasitized by a single wasp.

<sup>b</sup> Pearson correlation coefficients between number of parasitoids found in each host egg (degree of superparasitism) and rate of mortality. Numbers followed by ns are not significantly different from the null hypothesis of a zero correlation coefficient.

<sup>c</sup> Egg masses collected from the Sault Ste. Marie site were laid on foliage in the laboratory and then exposed to parasitoids in the field.

<sup>d</sup> These four egg masses were collected from three sites in Ontario: two from Kenora, one from Kirkwood, and one from Alliston.

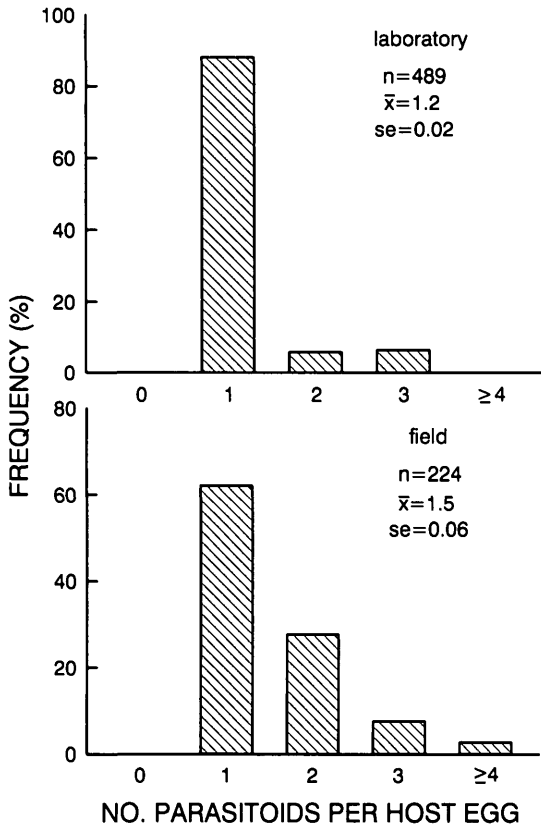


Fig. 4. Frequency distribution of the number of *T. minutum* progeny allocated per spruce budworm egg in the laboratory and the field.

including small egg masses (<10 eggs), were only partially parasitized. There can be at least four possible explanations for partial rather than full exploitation in the field. These four can act either alone or in concert to produce the same result. First, a parasitoid may parasitize an egg mass partially as a result of inferior quality of some eggs in the egg mass. Second, she may be disturbed by an event such as wind or predators before completing exploitation. Third, a female may not have enough eggs in her ovaries to exploit the egg mass completely. Last, it may be advantageous for a wasp to distribute her egg complement in several host egg masses under certain circumstances (e.g., when predation rate or other mortality factors of the host are high).

The percentage parasitism on each egg mass was not correlated with the number of host eggs contained in that mass. This paralleled a previous cage study (Smith et al. 1986) that indicated that parasitism of (sentinel) egg masses was not dependent on the number of egg masses available in the cage. Other studies generally show a common density-independent response by *Trichogramma* to host densities (e.g., Thomas 1966, Pena & Waddill 1983, Pak et al. 1989).

Our results also indicate that parasitized host eggs did not always produce viable parasitoid offspring. There was frequent immature mortality of *T. minutum* under both field and laboratory conditions when parasitizing spruce budworm eggs. This mortality was not associated with the degree of superparasitism (more eggs laid in a host than can successfully develop) because in the laboratory there was no superparasitism and yet there was mortality. Females were seen to lay a maximum of three eggs in a host egg, and a single host egg is large enough to support the complete development of three parasitoids (Miller 1953; B.B.B., unpublished data). For the sake of comparison, we also offered eggs of the Mediterranean flour moth, *Anagasta kuehniella* (Zeller) (Lepidoptera: Pyralidae), one of the facultitious hosts used in commercial insectaries for *Trichogramma* production, to individual *T. minutum* to determine the rate of progeny mortality. We found that out of 200 individually parasitized host eggs, there were only two that failed to issue an adult wasp. Therefore, *T. minutum* had a much higher immature mortality when parasitizing spruce budworm than when parasitizing Mediterranean flour moth.

Females allocated an average of 1.7 and 1.3 eggs per host egg when parasitizing egg masses of spruce budworm in the field and laboratory, respectively. The difference in level of (super) parasitism could be because in the laboratory, only one female was involved whereas in the field, several females could discover an egg mass. Although a single budworm egg can support at least three *T. minutum*, the majority of host eggs parasitized in the field (62%) and laboratory (88%) contained only one parasitoid offspring. Such an underexploitation may be a result of circumstantial abundance in host resources. Being in the form of an egg mass, eggs of spruce budworm once found present a bonanza of resources for a foraging *T. minutum*. The circumstantial abundance of hosts may lead to under- rather than overexploitation. Overexploitation of hosts (for example, superparasitism) typically occurs when hosts are scarce or limited (Alphen & Visser 1990).

The size of field-collected parasitoids, as measured by wing length, varied among different sites and showed a general trend (i.e., females on average were always larger than males). Southard et al. (1982) found that although females reared from spruce budworm in both field and laboratory were generally larger than their male counterparts, those reared from a smaller host, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae), had no size differences between sexes. Size differences between sexes have also been found in other species of *Trichogramma* and in hymenopteran species in general (Trivers & Hare 1976, Charnov et al. 1981, Waage & Ming 1984). Size of facultatively gregarious parasitoids

such as *Trichogramma* is generally influenced by the degree of superparasitism. Crowding is known to produce small parasitoids (e.g., Bai et al. 1992).

The sex ratio of *T. minutum* collected from the different field sites was fairly consistent and showed a female bias among all sites. Wasps produced 66–80% female progeny in either field or laboratory when parasitizing the budworm eggs. These percentages are all secondary sex ratios after discounting for immature mortality. Using the behavioral criterion of Suzuki et al. (1984), we determined the primary sex ratio of *T. minutum* in the laboratory through direct observation. Our laboratory studies showed a similar pattern for the primary sex ratio (i.e., females allocated 69% [70 females tested, a total of 579 eggs laid] female progeny). In a previous laboratory study (Bai & Smith 1993), we found that young females of *T. minutum* (<7 d old) produced a female-biased sex ratio, whereas old ones produced a male-biased sex ratio. If we assume parasitoids in the field have relatively short lives and lay eggs at a young age, it is then not surprising to see the female-biased sex ratio in the field.

Parasitoids from the Sault Ste. Marie site were distinct in two characters, a higher mortality per egg mass and a lower survival rate per egg than those from naturally laid eggs. This may be a result of the larger size of the sentinel egg masses. Host acceptance and parasitoid survival were similar between sentinel and natural hosts in a laboratory study (Song 1993), where two types of egg masses with the same number of eggs were used. All other parameters of host exploitation by parasitoids in the field were similar among the sentinels and natural hosts.

The knowledge obtained from this study on patterns of host exploitation by *T. minutum* could be used to improve the rate of exploitation for wasps inundatively released in the field in biological control programs. Both increasing the exploitation rate of the egg mass and reducing mortality of parasitoid progeny are important to consider. If a whole egg mass, instead of part of it, can be exploited, there will be a greater reduction in the number of spruce budworms. Retention of parasitoids on an egg mass long enough so that most or all of the eggs in the mass will be parasitized can be achieved by chemical means (e.g., Lewis et al. 1982, Zaborski et al. 1987). Scales of some lepidopteran moths have been shown to act like kairomones to attract parasitoids and retain them in the vicinity of a host patch (Schmidt & Carter 1992). Products derived from host insects and those from plants on which host insects feed have been demonstrated to serve as cues for parasitoids in finding hosts (Tumlinson et al. 1993a, b). Immature mortality of parasitoids in the natural host will reduce the number of progeny produced in the next gener-

ation. However, this immature mortality may not be critical when *T. minutum* is inundatively released, because spruce budworm usually has only one generation per year in North America, and hosts that contained dead immature parasitoids were killed by the parasitoid.

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