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Assessment of *Trichogramma* species for biological control of forest lepidopteran defoliators

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Abstract

In a laboratory study, we determined the potential of three *Trichogramma* (Hymenoptera: Trichogrammatidae) species, *T. brassicae* Bezdenko, *T. minutum* Riley and *T.* nr. *sibiricum* Sorokina, for biological control against six species of forest lepidopteran pests, black army cutworm, hemlock looper, eastern spruce budworm, western spruce budworm, white-marked tussock moth, and gypsy moth. Females of each parasitoid species were offered eggs from each of the six host species. Parasitization and the effect of the host species on the emerging progeny were examined and recorded. *Trichogramma minutum* had the broadest host range and successfully parasitized four host species out of the six offered. *Trichogramma* nr. *sibiricum* had the narrowest host range and parasitized only two species of hosts. Of the six host species, black army cutworm was the most preferred by all three *Trichogramma* species; white-marked tussock moth and gypsy moth were not parasitized by any parasitoids. There was a positive correlation between the size of female offspring and their corresponding egg complement in all three parasitoid species. The developmental time of parasitoids from egg to adult was influenced by both the parasitoid and host species. Our results suggest that *T. minutum* has the greatest potential for biological control against various forest lepidopteran pests and that the black army cutworm may be the best target candidate for further study.

Introduction

Trichogramma is a large genus of hymenopteran parasitoids which attack insect, primarily lepidopteran, eggs (Nagarkatti & Nagaraja, 1977). Inundative releases of *Trichogramma* against forest insect pests have been tried in several countries, including *T. dendrolimi* Matsumura against pine lasiocampids (*Dendrolimus* spp.) in China (Sun & Yu, 1988), *Trichogramma* spp. against the European pine shoot moth (*Rhyacionia buoliana*) in the former USSR (Tsankov *et al.*, 1981) and several *Trichogramma* spp. against the teak skeletonizer (*Pyrausta machaeralis*) in India (Patil & Thontadarya, 1984). In North America, very little research had been conducted in forestry on the use of *Trichogramma* prior to 1978 despite the severity of insect defoliators. Recent restrictions on the use of chemical insecticides in the forest environment have resulted in a steady replacement of chemicals with new control tactics. One of these alternatives has been the development of *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae) as a biological control agent against the serious forest defoliator, the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae) in Canada (Smith *et al.*, 1990) and the northeastern United States (Houseweart, 1985).

Species of *Trichogramma* are regarded as generalist parasitoids, attacking a wide range of host species (Muesebeck *et al.*, 1951). Many species of forest pests can be parasitized by *Trichogramma* (Houseweart *et al.*, 1984) and may be candidates for biological control through inundative releases. The preliminary success of using *T. minutum*, an indigenous species widely distributed in North American forests, against the spruce budworm has raised the question as to whether this species and perhaps other *Trichogramma* species can be used against a number of forest insects.

Three species of *Trichogramma* were available to us. The first two, *T. brassicae* Bezdenko and *T. minutum* occur in both forest and agricultural environments, while the third, *T.* nr. *sibiricum* Sorokina is a newly discovered species (Li *et al.*, 1993) from cranberry fields in British Columbia, Canada. We wanted to examine their potential for parasitizing a number of economically important forest defoliators and to determine if they could be used as biological control agents. As a first step in the application of these parasitoids, we evaluated the potential host range of the three species by providing each with eggs of six species of forest defoliators; black army cutworm, *Actebia fennica* Tauscher (Lepidoptera: Noctuidae), hemlock looper, *Lambdina fiscellaria* Guenee (Lepidoptera: Geometridae), eastern spruce budworm, *Choristoneura fumiferana* western spruce budworm, *C. occidentalis* Freeman (Lepidoptera: Tortricidae), white-marked tussock moth, *Oryia leucostimata* Smith and gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae). Although the ability of *T. minutum* to parasitize the eastern spruce budworm has been well documented (Houseweart, 1985; Smith *et al.*, 1990), the ability of this species to parasitize other forest lepidopterans or the potential of the other *Trichogramma* species to parasitize such forest pests has been poorly studied. We chose the three *Trichogramma* species for this study because *T. minutum* is the commonest *Trichogramma* species found in the forests of North America and *T. brassicae* is one of the most frequently collected species of *Trichogramma* in Europe. Both species are commercially produced, readily available and have relevance to future applications. *Trichogramma* nr. *sibiricum* is uniparental and reproduces asexually. The potential of such asexual *Trichogramma* species against forest lepidopterans has not been tested. Herein we report our results on the host range and reproductive potential of these three species of *Trichogramma*.

Materials and methods

Insect cultures. The three species of *Trichogramma* used in our experiments were from different sources. *Trichogramma minutum* (identified by J. D. Pinto, University of California, Riverside) was collected originally from parasitized egg masses of the eastern spruce budworm in Ontario during 1988. This species was reared in the laboratory on the Angoumois grain moth, *Sitotroga cerealella* Olivier (Lepidoptera: Gelechiidae) until 1990 and then switched to the Mediterranean flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) until completion of the experiments. *Trichogramma brassicae* was obtained from Bio-Logicals, Ciba-Geigy Canada, Guelph, Ontario, Canada. This species was collected initially from parasitized eggs of the European corn borer, *Ostrinia nubilalis* Hubner (Lepidoptera: Pyralidae) in Moldavia and was reared by Bio-Logicals on *E. kuehniella* since 1992. *Trichogramma* nr. *sibiricum* was collected from parasitized eggs of the blackheaded fireworm, *Rhopobota naevana* Hübner (Lepidoptera: Tortricidae), in Richmond, British Columbia, Canada (Dr. D. E. Henderson, E. S. Cropconsult Ltd., Vancouver, British Columbia). All parasitoids were reared on eggs of the Mediterranean flour moth for a minimum of three generations in the laboratory before initiation of the experiments. Fresh eggs of the flour moth were supplied weekly by the Biological Control Laboratory, Department of Environmental Biology, University of Guelph, Ontario, Canada.

Eggs of the six host species, *Actebia fennica*, *Lambdina fiscellaria*, *Choristoneura fumiferana*, *C. occidentalis*, *Orgyia leucostimata* and *Lymantria dispar*, were obtained from laboratory colonies maintained in the Forest Pest Management Institute, Forestry Canada, Sault Ste. Marie, Ontario. Moth scales covering egg masses of *O. leucostimata* and *L. dispar* were removed before experiments to eliminate possible effects of scale coverage on parasitism. All experiments were conducted and parasitoid colonies were maintained under laboratory conditions at 25±1 °C, L16:D8 and 50±10% r.h.

Assessment of host range and reproductive potential of parasitoids. To determine the host range and reproductive potential of each parasitoid species, we designed the following experiment. Newly-emerged females (<6 h old) from the same cohort of a parasitoid species were randomly assigned to one of the six host species. For each parasitoid species, an individual female ($n = 20$) was provided in a glass vial (1.0 cm diameter by 3.5 cm height) with an egg card that had >40 host eggs. The female and egg card were confined together with a stopper and the vial streaked with diluted honey to provide a food source for the parasitoid. After 24 h, the egg card was removed and placed in a new vial which was incubated under laboratory conditions until emergence of the parasitoid offspring. The original vials were placed in a freezer for 10 min to kill the parasitoids. Half of the females (n = 10) from each parasitoid species were dissected individually on a microscope slide to count the number of mature eggs left in their ovaries. This information enabled us to distinguish between a 'true' host rejection due to physiological dislike of the host and a 'false' host rejection due to a shortage of mature eggs in the female. The length of each females' front wing, an index of parasitoid size (Bourchier *et al.*, 1993), was then measured using an ocular micrometer mounted in the eyepiece of a microscope.

For each combination of parasitoid and host species, we recorded the number of host eggs parasitized by counting the number of eggs which had turned black on the egg card. When the estimated emergence time of parasitoid offspring approached, we examined the egg cards daily to record the number of parasitoid offspring emerged and the corresponding sex ratio (% females) of emergents. This provided a distribution of emergence for each parasitoid/host combination over the period of emergence. The total number of parasitoid offspring emerged and the overall sex ratio of the offspring for a particular parasitoid and host combination were obtained by pooling the data over all emergence days.

Wing length, egg complement and longevity of the emerged offspring were also measured to determine whether there had been a host effect on the parasitoid progeny. The wing length of female offspring was measured as above. The egg complement of one-day old female progeny (who had never laid eggs) was obtained by counting mature eggs squeezed out from the ovaries of individual females onto a microscope slide (Bai *et al.*, 1992). The longevity of female progeny was measured by providing individual wasps with diluted honey (without hosts) in a glass vial and recording the number of days lived.

Statistical analysis. We used an IBM PC version of the SAS computer package (SAS, 1990) to analyze all data. Effects of parasitoid and host species on various parameters were analyzed by a 2-way analysis of variance using the general linear models procedure (PROC GLM). This procedure was followed by T tests (LSMEANS with PDIFF option) when comparisons of various measurements for the effects of parasitoid and host species were necessary. Data on sex ratios were transformed to ArcSin(Sqrt(sex ratio)) before applying analysis of variance. Correlation analysis was performed between wing length and egg complement for female offspring of all three *Trichogramma* species reared from accepted hosts.

Results

Trichogramma brassicae and *T. minutum* parasitized and their offspring successfully emerged from eggs of four host species, *A. fennica*, *L. fiscellaria*, *C. fumiferana* and *C. occidentalis* whereas *T.* nr. *sibiricum* attacked and reproduced in only two host species, *A. fennica* and *L. fiscellaria*, out of the six offered (Table 1). All three *Trichogramma* species failed to parasitize and reproduce in eggs of either white-marked tussock moth or gypsy moth. Although females of the three parasitoid species were observed to attack (drilling) the eggs of these two hosts, none of the eggs blackened and no parasitoid progeny emerged. Dissection of attacked hosts showed no sign of *Trichogramma* eggs. This suggests that the three *Trichogramma* species did not use either white-marked tussock moth or gypsy moth as their hosts and therefore, these results were not included in the table. The females of the three *Trichogramma* species used in the experiment were similar in size (ANOVA, F = 2.78; df = 2,117; P = 0.066) when reared from eggs of the Mediterranean flour moth. Dissection of their ovaries upon completion of a 24-h oviposition period indicated that all of these females had some mature eggs retained in their abdomen. Those that did not parasitize hosts or that parasitized only a few hosts had more eggs in their ovaries than those that parasitized greater number of hosts (Table 1). Of the three parasitoid species, *T. minutum* parasitized the greatest number of eggs and produced the highest number of offspring on the four species of hosts accepted, followed by *T. brassicae*; *T.* nr. *sibiricum* did the poorest on all the hosts except black army cutworm (ANOVA followed by comparison tests for number of host eggs parasitized, F = 27.14; df = 2,217; P = 0.0001, for number of parasitoid offspring produced, F = 3310; df = 2,217; P = 0.0001). Of the four host species that were accepted, *A. fennica* was the most preferred by all three *Trichogramma* species (Table 1).

Although all the parasitoid eggs were laid within a 24-h period, the developmental time of the progeny from egg to adult varied over a wide range of

Table 1. Parasitization, size variation and egg retention in females of three *Trichogramma* species when exposed to four species of hosts in the laboratory for 24 h[1]

Host species	No. host eggs parasitized		No. parasitoid offspring emerged	Wing length of females (mm)		No. eggs left in ovary/female
	n[2]	mean ± se	mean ± se	n	mean ± se	mean ± se
	Trichogramma brassicae					
Actebia fennica	20	39.4 ± 1.4a	45.9 ± 2.3a	10	0.496 ± 0.006ab	17.2 ± 3.5c
Lambdina fiscellaria	20	0.9 ± 0.3d	1.9 ± 0.8d	10	0.485 ± 0.006ab	52.2 ± 2.8a
Choristoneura fumiferana	20	0.9 ± 0.6d	1.4 ± 1.0d	10	0.490 ± 0.007ab	51.9 ± 4.3a
Choristoneura occidentalis	20	0.3 ± 0.1d	0.3 ± 0.2d	10	0.483 ± 0.006b	52.8 ± 3.6a
	Trichoglamma minutum					
Actebia fennica	20	32.2 ± 1.2b	35.5 ± 1.5b	10	0.490 ± 0.007ab	18.3 ± 2.9c
Lambdina fiscellaria	20	7.1 ± 0.8c	15.5 ± 1.7c	10	0.477 ± 0.006b	35.0 ± 2.0b
Choristoneura fumiferana	20	8.6 ± 1.5c	16.6 ± 3.1c	10	0.483 ± 0.006b	41.1 ± 5.6b
Choristoneura occidentalis	20	5.9 ± 1.2c	11.8 ± 2.5c	10	0.481 ± 0.008b	39.1 ± 4.2b
	Trichogramma nr. *sibiricum*					
Actebia fennica	20	31.2 ± 1.3b	36.3 ± 2.1b	10	0.504 ± 0.006a	25.9 ± 3.3c
Lambdina fiscellaria	20	0.7 ± 0.3d	1.8 ± 0.7d	10	0.494 ± 0.006ab	55.1 ± 3.2a
Choristoneura fumiferana	20	0.0 ± 0.0d	0.0 ± 0.0d	10	0.492 ± 0.007ab	57.6 ± 3.3a
Choristoneura occidentalis	20	0.0 ± 0.0d	0.0 ± 0.0d	10	0.485 ± 0.006ab	54.1 ± 3.2a

[1] In each column, means followed by the same letter are not significantly different at 0.05 level by T tests.
[2] Sample size (n) = number of female parasitoids tested or measured.

time. A variation of about 4 to 5 days in developmental time of parasitoid offspring was observed for most combinations of parasitoid and host species (Fig. 1). *Trichogramma minutum* had the shortest developmental time (mean±se = 11.0±0.1 days, n = 234) in the four host species parasitized, followed by *T. brassicae* (12.6±0.1 days, n = 105). *Trichogramma* nr. *sibiricum* had the longest developmental time (14.3±0.2 days, n = 86), especially in eggs of hemlock looper (ANOVA followed by comparison tests, F = 275.88; df = 2,422; P = 0.0001). Host species also affected developmental time. The three *Trichogramma* species developed in the four hosts, from the slowest to fastest, in the order of *L. fiscellaria* (mean±se = 13.5±0.2 days, n = 116)>*A. fennica* (12.0±0.1 days, n = 200)>*C. fumiferana* (10.6±0.2 days, n = 57) = *C. occidentalis* (10.4±0.2 days, n = 52) (ANOVA, F = 123.39; df = 3,421; P = 0.0001). The daily sex ratio of the emerged *T.* nr. *sibiricum* was 100% female over all days. This species was known to be thelytokous, i.e., virgin females produced female offspring without mating with males (uniparental). The sex ratio of emerged *T. minutum* was always female-biased (75.9–100% females) and varied insignificantly over the period of emergence (Fig. 1, F = 1.84; df = 6,191; P = 0.094). In *T. brassicae* the sex ratio was influenced significantly by the time of emergence (F = 7.15; df = 5,87; P = 0.0001) and by the interaction between host species and the day of emergence (F = 4.83; df = 7,85; P = 0.0002). Generally, more female offspring emerged earlier than males while more males emerged later than females when the parasitoid developed in all species of hosts except in *C. occidentalis*.

The species of host in which the parasitoid offspring had developed significantly affected their size (F = 18.30; df = 3,91; P = 0.0001) and egg complement (F = 14.96; df = 3,91; P = 0.0001) for all three *Trichogramma* species (Table 2). Female progeny of all parasitoid species emerging from *Actebia fennica* had the longest wing length and carried the largest number of mature eggs in their ovaries, followed by those emerging from the two *Choristoneura* species (Table 2). Those parasitoids emerging from *Lambdina fiscellaria* had the shortest wing length and the smallest egg complement. Egg complement was positively correlated with size in female offspring of all three *Trichogramma* species reared from

Table 2. Offspring size, egg complement, longevity and sex ratio of three *Trichogramma* species emerging from eggs of four host species[1]

Host species	Wing length of females (mm)		No. eggs in ovary/female	Female longevity (days)		Progeny sex ratio (% females)	
	n[2]	mean ± se	mean ± se	n	mean ± se	n	mean ± se
	Trichogramma brassicae						
Actebia fennica	10	0.621 ± 0.009ab	107.8 ± 5.9ab	20	8.6 ± 0.7c	20	71.2 ± 2.0c
Lambdina fiscellaria	10	0.562 ± 0.011c	82.4 ± 3.3cd	15	9.2 ± 0.8bc	6	74.8 ± 8.9bc
Choristoneura fumiferana	10	0.600 ± 0.008ab	92.3 ± 4.6bcd	10	8.7 ± 1.1bc	2	82.1 ± 3.6b
Choristoneura occidentalis	5	0.608 ± 0.010ab	92.0 ± 7.6bcd	–		3	61.1 ± 20.0c
	Trichogramma minutum						
Actebia fennica	10	0.621 ± 0.009ab	106.5 ± 5.3ab	20	10.2 ± 0.8bc	20	86.5 ± 1.0b
Lambdina fiscellaria	10	0.560 ± 0.011c	79.1 ± 3.4d	20	11.3 ± 0.7ab	20	85.5 ± 2.8b
Choristoneura fumiferana	10	0.600 ± 0.013ab	95.3 ± 5.3bc	20	11.7 ± 0.9ab	14	86.2 ± 1.8b
Choristoneura occidentalis	10	0.593 ± 0.011b	90.8 ± 4.6cd	20	10.6 ± 0.9abc	14	87.5 ± 2.5b
	Trichogramma nr. *sibiricum*						
Actebia fennica	10	0.629 ± 0.009a	109.4 ± 6.8a	20	12.4 ± 0.9a	20	100 ± 0.0a
Lambdina fiscellaria	10	0.570 ± 0.009c	82.8 ± 3.2cd	16	8.3 ± 0.8c	5	100 ± 0.0a
Cholistoneura fumiferana	–		–	–		–	
Choristonuera occidentalis	–		–	–		–	

[1] In each column, means followed by the same letter are not significantly different at 0.05 level by T tests.

[2] Sample size (n) = number of female parasitoids measured.

each host (Fig. 2, for all combinations of parasitoids and hosts, $R \geq 0.87$, $P \leq 0.001$). Surprisingly, all three *Trichogramma* species had similar wing length and egg complement when they developed in the same host species (Table 2). Thus, size and egg complement of female parasitoids were more influenced by the species of the hosts in which they developed than by the species of *Trichogramma* to which they belonged. However, the longevity of female offspring was more influenced by the parasitoid species (F=4.71; df=2,158; P=0.010) than by the host species (F=0.60; df=3,157; P=0.618). *Trichogramma minutum* lived longer than *T. brassicae* regardless of the host from which they emerged (F=10.18; df=1,123; P=0.002). The longevity of *T.* nr *sibiricum* varied with host species (Table 2). The overall sex ratio of the progeny was more female-biased in *T. minutum* than in *T. brassicae* whereas *T.* nr. *sibiricum* produced all female offspring (Table 2, F=42.70; df=2,122; P=0.0001). This conforms to the daily patterns of sex ratio described earlier (Fig. 1).

Discussion

Of the three *Trichogramma* species, *T. minutum* had the broadest host range. This species parasitized and reproduced well in eggs of four species of lepidopteran hosts out of the six that were offered. *Trichogramma* nr. *sibiricum* had the narrowest host range and parasitized and successfully reproduced in only two species of the hosts. Although females of *T. brassicae* could parasitize the same four host species as *T. minutum* the number of hosts parasitized and that of parasitoid offspring produced were low in all but one host (Table 1). None of the three *Trichogramma* species successfully parasitized and reproduced in eggs of the white-marked tussock moth or gypsy moth. Therefore, these two host species could not be included in the list of potential hosts for any of the three *Trichogramma* species. It should be noted that moth scales covering egg masses of tussock moth and gypsy moth were removed before the eggs were presented to parasitoids. Thus, negative parasitism on eggs of these two hosts could not be attributed to the scale coverage.

The observed patterns of host range in our experiments apparently conform to the habitat location and

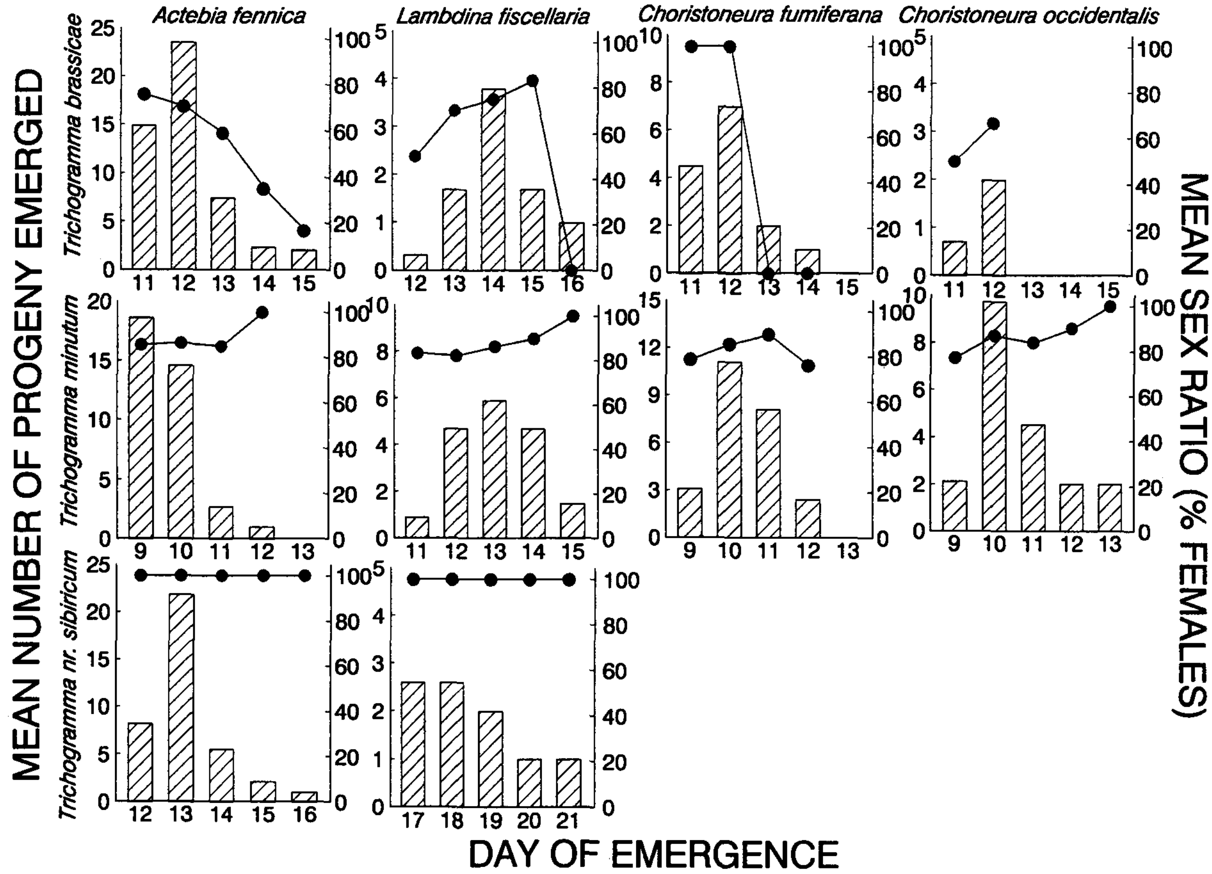

Fig. 1. Frequency distribution of adult emergence (hatched bars) and corresponding sex ratio (solid circles) for three *Trichogramma* species emerging from eggs of four host species.

natural distribution of these parasitoid species. All hosts used in our experiments are forest insects. *Trichogramma minutum* is commonly found throughout forest environments (Anderson, 1976) as well as in agricultural fields (Thorpe, 1984). It is naturally expected that this parasitoid will attack forest insects and have a relatively wide host range. *Trichogramma brassicae* is frequently collected from agricultural fields (Voegelé & Pintureau, 1982; Pintureau, 1987) and thus, may not parasitize as many forest insects as a forest-dwelling species such as *T. minutum*. *Trichogramma* nr. *sibiricum* is a poorly-known and perhaps a new species in Canada. Its closest relative, *T. sibiricum* was originally collected and described from apple trees in Siberia (Sorokina, 1981). *Trichogramma* nr *sibiricum* has two reproductive modes, arrhenotoky (fertilized eggs give rise to females and unfertilized eggs males) and thelytoky (Li *et al.*, 1993). The colony we examined was thelytokous. Unpublished evidence suggests that thelytokous forms of *Trichogramma* tend to have narrower host ranges than their arrhenotokous conspecifics (Wang & Smith, unpubl.).

Of the six host species tested, black army cutworm was most preferred by all three *Trichogramma* species. Parasitoids attacked the greatest number of eggs of this host and produced the largest number of progeny from this host. Offspring emerging from this host were also largest in size and had the greatest egg complement. Our results suggest that the black army cutworm may be a good candidate for biological control using *Trichogramma*, however, the biology of this host may hinder or prevent the potential success of *Trichogramma*. Black army cutworm is a sporadic defoliator of herbaceous agricultural crops and planted conifer seedlings (Ross & Iinytzky, 1977). Female moths lay their eggs on the surface of the soil and *Trichogramma* must search this area to locate such hosts. It is unknown how efficient *Trichogramma* females are at foraging on soil.

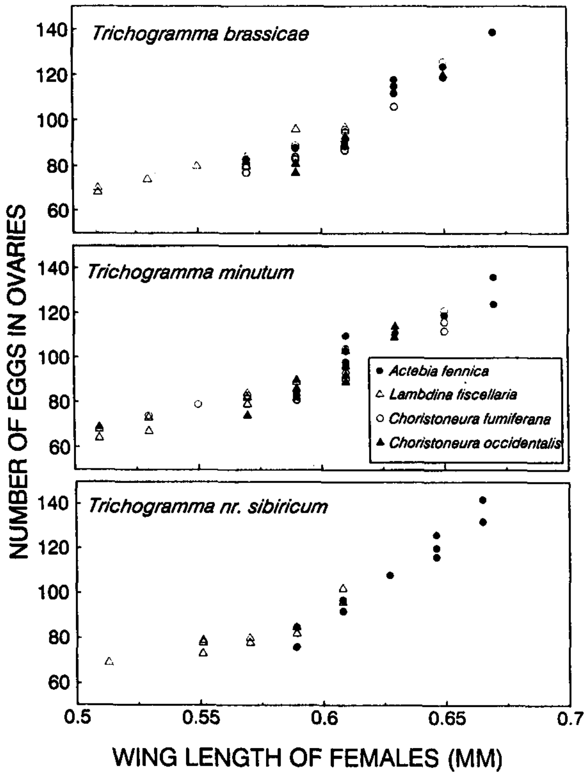

Fig. 2. Relationship between wing length and egg complement in females of three *Trichogramma* species reared from four host species.

After being exposed to host eggs for 24 h, female parasitoids had more eggs left in their ovaries if they parasitized few or no hosts than if they parasitized a number of hosts. This indicates that females did not parasitize certain hosts because they did not like or use them as hosts, not because they were short of eggs. Parasitoids normally had more than 50 eggs in their abdomen if they parasitized few or no hosts. Those that parasitized the greatest number of hosts still had more than 17 eggs left in their ovaries by the end of the exposure period. Therefore, females always had an adequate supply of eggs. Previous studies have shown that egg production in *Trichogramma* is highest during the first day after female emergence (Hohmann *et al.*, 1988; Bai & Smith, 1993)

The effect of the host on the size and egg complement of the parasitoid offspring was uniform and consistent in all three *Trichogramma* species. All three species had a similar size if they were reared from the same host species. The length of the female wing ranked from largest to smallest when wasps emerged from: *A. fennica*>*C. fumiferana* and *C. occidentalis*>*L. fiscellaria*. Egg complement (and potential fecundity) of female offspring was positively correlated with wing length in all parasitoids regardless from which hosts they emerged. Studies of other *Trichogramma* species show a similar positive correlation between the size of the host and that of the parasitoids (Hohmann *et al.*, 1988; Bai *et al.*, 1992). The size of adult parasitoids is affected by the size of the host and the number of parasitoids developing in that host (Bai *et al.*, 1992).

It is worth noting that the developmental time of parasitoid offspring varied greatly even in the same host species. *Trichogramma minutum* on average, had the shortest developmental time among the three parasitoid species. All the parasitoid species took the longest time to develop when reared in *Lambdina fiscellaria*. Both rearing host and parasitoid species influenced the developmental time. Internal composition and nutritional value of host eggs have been suggested to influence parasitoid development (Qin & Wu, 1988; Barrett & Schmidt, 1991). The mechanism of reproduction by parasitoids (i.e., arrhenotoky versus thelytoky) may also cause differences in developmental times in *Trichogramma* (Wang & Smith, unpubl.).

The sex ratio of the progeny is characteristic of the parasitoid species rather than the host species. *Trichogramma* nr. *sibiricum* produced all female offspring whereas *T. minutum* produced offspring with a female-bias. Although the progeny of *T. brassicae* were also female-biased, the sex ratio was more variable when reared from different hosts than that of *T. minutum* (Table 2, Fig. 1). Parasitoid sex ratio has been shown to be influenced by a number of factors, including clutch size (e.g. Waage & Godfray, 1985), mode of reproduction (arrhenotoky versus thelytoky) (e.g. Stouthamer & Luck, 1993), female parental age (e.g. Bai & Smith, 1993) and host size (e.g. van Dijken *et al.*, 1991).

Our results indicate that *T. minutum* is the best egg parasitoid for forest lepidopteran defoliators among the three *Trichogramma* species tested. This species not only attacked the spruce budworm, as demonstrated by other researchers (Houseweart, 1985; Smith *et al.*, 1990), but also parasitized two other species, black army cutworm and hemlock looper. Further work is warranted using this species against these two hosts in the field. Although *T. brassicae* has been widely used in agricultural fields against lepidopterans such as corn borers and cabbage moth (Pak *et al.*, 1989; Frandon *et al.*, 1991), our results suggest that it is a poor candidate for use against forest lepidopterans. The potential of *T.* nr. *sibiricum* as a biological control agent in suppressing forest insects is even more limited. One should note that the three *Trichogramma* species in our experiments were reared on the Mediterranean flour moth for at least 3 generations before they were tested. Rearing the parasitoids on their target hosts, e.g., any of the tested hosts, may increase their efficiencies in parasitizing these targets (e.g. Bergeijk *et al.*, 1989). From the host perspective, black army cutworm is perhaps the most promising pest against which *Trichogramma* species can be used. All three *Trichogramma* species achieved high levels of parasitism in this host. This is consistent with the fact that this species belongs to the Noctuidae, a family commonly attacked by most *Trichogramma* species (Pak *et al.*, 1990).

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