Effect of host diet on acceptance of eastern spruce budworm eggs by *Trichogramma minutum*

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Abstract

The acceptance behaviour of the parasitic wasp, *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae), was studied on two types of egg masses of eastern spruce budworm (SBW), *Choristoneura fumiferana* Clemens. Host eggs were obtained from moths that had been fed balsam fir or artificial diet during their larval stages. Parasitoids were reared from both types of hosts. Host acceptance assays were conducted where females were provided with a single egg mass and with a choice between egg masses. Regardless of the parasitoid's rearing host, females parasitised hosts reared from artificial diet more often than those from balsam fir. Response was consistent in both no-choice and choice assays. Rejection of hosts tended to occur during the examining stage of behaviour, suggesting that acceptability is judged externally. If a host was accepted, the same number of eggs were laid per egg mass regardless of treatment.

Introduction

Host acceptance is the process where a female parasitoid evaluates the host for oviposition (Arthur 1981). The female begins to assess acceptability upon approach and contact with the host and continues until the host is rejected or eggs are deposited (Pak & de Jong, 1987). Research on host acceptance behaviour of the polyphagous egg parasitoid, *Trichogramma*, has focused on the second trophic level, the host (e.g. Salt, 1935; van Dijken et al. 1986; Pak & de Jong, 1987). Host acceptance is based on the ability of *Trichogramma* to recognise a host and on the quality of the host for progeny development (Pak & de Jong, 1987). Attributes of both the female *Trichogramma* and the host egg can affect host acceptance behaviour (e.g. Salt, 1935; Pak et al., 1986; Pak & de Jong, 1987; van Bergeijk et al., 1989).

T. minutum Riley is a potential candidate for control of spruce budworm via inundative release into infested areas (Smith et al., 1990). In outbreak pop-ulations, budworm causes extensive damage to balsam fir and spruce stands that are valued for pulp and paper resources and for aesthetic and biological reasons. Understanding the role of host diet on host acceptance by *T. minutum* could improve the success of biological control programmes by increasing the predictability of parasitoid performance in an inundative release.

Little is known about the impact of the first trophic level, the host plant, on host acceptance, particularly once it has been consumed by the host herbivore. To examine the interaction between parasitoid and host plant, the behaviour of *T. minutum* is studied using a natural host, eastern spruce budworm, *Choristoneura fumiferana* Clemens, and a principal host plant of budworm, balsam fir, *Abies balsamea* L. Balsam fir contains terpenes and other allelochemicals that affect the development and fecundity of spruce budworm (Mattson et al., 1983). If plant diet affects the host egg, acceptance by parasitoids may vary in response to the presence of these chemicals or other changes to phys-

ical characteristics of the host caused by balsam fir consumption. In laboratory studies, spruce budworm eggs used in studies of parasitoid behaviour are usually from hosts reared on artificial diet (e.g., Zaborski et al., 1987; Bourchier et al., 1993; Bourchier & Smith, 1996), while in field studies, budworm hosts feed on a natural diet such as balsam fir, *Abies balsamea* (e.g., Smith et al., 1990). This study investigates the influence of these two host diets on acceptance of spruce budworm egg masses by *T. minutum*.

Materials and methods

Insect rearing. *T. minutum* females were originally collected from eastern spruce budworm (SBW), *Choristoneura fumiferana* Clemens, and were reared on the factitious host, Mediterranean flour moth (MFM), *Ephestia kuehniella* Zeller, for more than 100 generations. MFM hosts were reared at the Biological Control Laboratory, Department of Environmental Biology, University of Guelph, Ontario. All parasitoids were reared for one generation at 25 °C and L16:D8 photoperiod on SBW hosts provided with balsam fir or artificial diet; these SBW egg masses were obtained as described below. Female *T. minutum* used in the experiments were less than 6 h old and had never oviposited. Males and females were kept together before use to allow mating (Forsse et al., 1992).

Larvae of eastern spruce budworm were obtained from the Canadian Forest Service in Sault Ste. Marie, Ontario. All larvae were fed artificial diet during their first five instars (McMorran, 1965). During their sixth (final) instar, when they do the majority of their feeding (Morris, 1963), larvae either continued to feed on artificial diet or were fed with balsam fir buds. Balsam fir buds were collected fresh from the Sault Ste. Marie and Dryden, Ontario area, frozen and then thawed before being fed to insects. Spruce budworm eggs, laid in an overlapping mass, were collected every 24 h from laying female moths to ensure even-aged hosts (<24 h old). Females moths were provided balsam fir foliage for oviposition regardless of the diet they had fed upon as larvae. Egg masses resulting from SBW reared on artificial diet are referred to as AD-SBW; egg masses resulting from SBW reared on balsam fir are referred to as BF-SBW hosts. Diet also affected egg mass colour: AD-SBW eggs were blue and BF-SBW eggs were green. For all studies, SBW egg masses were kept on the balsam fir needle on which they had been laid.

No-choice host acceptance assays. Assays were designed to test if the host diet of balsam fir or artificial diet affected acceptance of the host by *T. minutum* presented with only one type of host egg. In the field, *Trichogramma* probably encounters hosts in a no-choice scenario the majority of the time (Courtney et al., 1989). All assays compared the effects of source host (i.e. the host from which the maternal female emerged) and target host (i.e. the host presented to the female for attack) in four treatments: females emerged from AD-SBW or BF-SBW egg masses and were presented with either AD-SBW or BF-SBW egg masses for attack. No-choice experiments evaluated the absolute acceptability of the host (Singer, 1986).

The number of egg masses parasitised and the number of parasitoid eggs laid per SBW egg mass during a fixed 2-h exposure period were used to measure host acceptance. Female *T. minutum* were placed individually in a $\frac{1}{2}$ dram vial with either an AD-SBW egg mass or a BF-SBW egg mass; both egg mass types averaged 14.8 ± 0.8 (SE) eggs/egg mass. Each assay was run using 12 females given AD-SBW hosts and 12 females given BF-SBW hosts. After exposure, female *T. minutum* were removed and hosts were placed in 25 °C for 24 h and then in saline at 4 °C until dissection. Assays using differing source hosts were run on alternate days. *T. minutum* eggs were dissected from the SBW egg mass in a saline and dish soap solution and counted. Due to the difficulty of separating SBW eggs in an egg mass, parasitoid egg counts were per egg mass and not per egg. Thirteen and eight assays were run with parasitoids emerged from BF-SBW and AD-SBW egg masses, respectively, at the rate of one assay per day.

Choice host acceptance assays – Indirect observations. The relative acceptability of hosts was obtained by measuring host parasitism for a large number of *T. minutum* females presented with a choice of the 2 hosts for a fixed period of time. Choice experiments evaluated preference or relative acceptability of hosts relative to each another (Singer, 1986). Females reared from AD-SBW or BF-SBW hosts were placed individually into $\frac{1}{2}$ dram vials for 2 h with both an AD-SBW and a BF-SBW egg mass. Egg masses with the same number of eggs per egg mass were glued 2 mm apart onto a 1 × 1.5 cm paper card. Two mm is the maximum distance that can be perceived by *Trichogramma* (Glas et al., 1981). The size of SBW egg masses averaged 17.4 ± 0.2 eggs/egg mass. The number of host eggs provided ensured that a host type would not be

completely depleted within the 2 h time frame of the assay. Females were removed after the 2 h exposure and host types were separated and reared individually at 25 °C. Twenty-four females from each source host were run in each assay and the assay was replicated 6 times: a total of 288 females were observed.

The preference of *T. minutum* for hosts reared from artificial diet or balsam fir was measured using the Chesson-Manly index, α (Chesson, 1983 cf. Manly et al., 1972). The index used the following formula for choice tests when resources are not replaced as they are depleted:

$$\alpha_i = \frac{\ln \frac{(n_i - r_i)}{n_i}}{\sum\limits_{j=1}^{m} \ln \frac{(n_j - r_j)}{n_j}}, \quad i = 1, \ldots m$$

(Chesson, 1983; cf., Manly et al., 1982), where n_i is the total number of eggs in the egg mass type *i* and is not assumed to be constant, r_i is the number of eggs parasitised in the egg mass type *i*, and m is the number of types of egg masses available. Indices were calculated using (1) number of parasitised SBW eggs (melanized chorion), and (2) number of emerged adult wasps, on each host type presented to a female. Acceptance was based on data collected after egg hatch because host diet did not affect the developmental success of *T. minutum* in tests of host suitability (Song, 1993). α ranges in value from 0 to 1 with increasing preference. Preference for a host was lowest when no parasitism occurred on the host and highest when eggs were laid exclusively on one egg mass. When parasitism was the same on both hosts, no preference was displayed and $\alpha = 0.5$.

Choice host acceptance assays – Direct observations. Continuous observation of females presented with a choice between AD-SBW and BF-SBW hosts provided detailed information on acceptance behaviour. Single AD-SBW and BF-SBW egg masses, each with the same number of eggs per egg mass, were glued approximately 2 mm apart on filter paper (Whatman #1). The paper was then placed in a petri dish (3.5 cm diameter and 1 cm deep).

A single female wasp that had emerged from either AD-SBW or BF-SBW, was released into the arena at a standard point and observed until it had either accepted a host (end of first oviposition event) or rejected both hosts (contacted both hosts and did not return for 3 min), (adapted from a similar technique used by van Dijken et al. [1986]). A female was restarted in the

same arena if it had not inspected the host in 3 min. Females were never restarted more than 3 times: 30.6% of females were restarted at least once. A new arena was used for each female to prevent any change in behaviour due to contact with another parasitoid's trail (Salt, 1937).

The length and number of behavioural events were recorded using a multi-timer programme (J. M. Schmidt, University of Guelph, Guelph, Ontario). Based on earlier studies (Pak & de Jong, 1987), behavioural stages were categorised as: (1) touch: any touch with antenna or feet lasting <5 s; (2) examining: walking and drumming antennae on host; (3) drilling: ovipositor is pushed into the host; and (4) ovipositing: ovipositor is deep into host. A host was considered accepted when oviposition was observed. Previous studies of no-choice assays demonstrated that observation of oviposition, as described here, resulted in egg laying (Song, unpubl.). Data were summarized as: (1) the number of times each type of host was accepted; (2) the behavioural stage in which host rejection was observed; (3) the total time spent handling the hosts where oviposition occurred, (i.e. total time spent in 4 behavioural stages); and, (4) the number of times a female left and returned to each host. The more times the female left and returned to a host before she finally accepted (contact:acceptance ratio), the lower the preference was for the host (van Dijken et al., 1986; Pak et al., 1986).

Statistical analysis. To examine the effect of source and target host on host acceptance by *T. minutum*, log-linear analyses were used for the categorical data (i.e., number of egg masses parasitised) (Sokal & Rohlf, 1981). Analyses of covariance were performed on continuous data with number of SBW eggs/egg mass, batch of *T. minutum*, and SBW used as covariates (Sokal & Rohlf, 1981). A paired *t*-test was used to analyse differences in α, index of preference, in the choice assays. Log-linear models were also used to analyse the effect of source host, target host and behavioural stage on host rejection in the choice assays with direct observation. Data were $\log(x + 1)$-transformed to ensure homogeneity of variances when necessary.

Results

No-choice host acceptance assays. The total number of egg masses parasitised depended on the target host to which the *T. minutum* female was exposed. Regardless

of their source host, females parasitised significantly more AD-SBW than BF-SBW hosts ($G = 12.73, P = 0.0004, n = 465$): 70.5% (165/234) of AD-SBW hosts were parasitised versus 54.5% (126/231) of BF-SBW hosts. There was no significant interaction between source host, target host and parasitism ($G = 1.16, P = 0.281$).

When data for females that accepted hosts were analysed, no differences in the number of eggs laid per SBW egg mass were observed for any treatment. Once a wasp made the decision to accept a host for oviposition, the number of eggs it laid in the SBW egg mass was the same regardless of the source host from which it emerged (mean from AD-SBW=27.5 ± 1.4, mean from BF-SBW=29.5 ± 1.2, $F = 0.71, P = 0.40$, $n = 288$) or the target host it attacked (mean on AD-SBW=29.3 ± 1.2, mean on BF-SBW=27.9 ± 1.4, $F = 0.17, P = 0.40, n = 288$). There was no significant interaction between the effects of source and target hosts ($F = 2.39, P = 0.12$).

Choice host acceptance assays – Indirect observations. In choice tests, host acceptance was affected by the target host to which the female was exposed but not by the source host from which the female emerged. *T. minutum* preferred to oviposit in AD-SBW more than BF-SBW hosts, based on the number of parasitised eggs per SBW egg mass (paired $t = 5.19, P < 0.0001$, $n = 288$) and the number of emerged *T. minutum* progeny per SBW egg mass (paired $t = 3.17, P = 0.002$, $n = 288$) (Table 1). This preference was consistent for females emerged from either AD-SBW or BF-SBW, based on both the number of parasitised hosts (using a for BF-SBW or AD-SBW hosts: $t = 1.16$, $P = 0.25, n = 288$) and the number of emerged progeny (using a from BF-SBW or AD-SBW hosts: $t = 0.90, P = 0.37, n = 288$) (Table 1).

Choice host acceptance assays – Direct observations. Using the number of hosts accepted, host preference was the same for females emerged from AD-SBW egg masses as for those emerged from BF-SBW egg masses ($G = 0.58, P = 0.44, n = 288$, Table 1). Female *T. minutum* that had emerged from either type of source host, accepted significantly more of the AD-SBW egg masses for oviposition than the BF-SBW egg masses, ($G = 4.15, P = 0.042, n = 288$, Table 1).

The number of times a female wasp got on and then left a host before it finally returned to oviposit (contact:acceptance ratio) was higher for females that had emerged from BF-SBW egg masses than those that
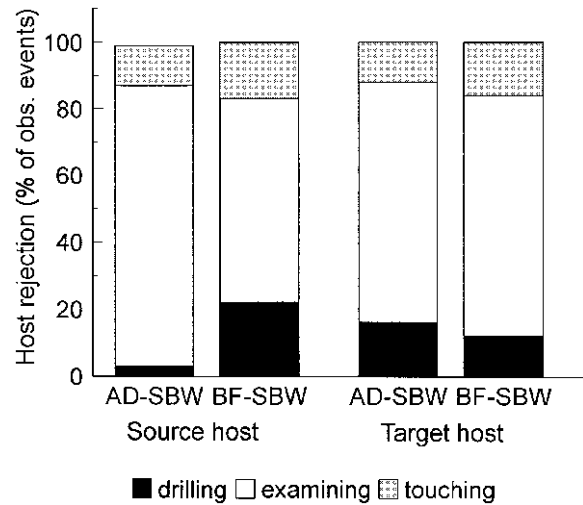

Figure 1. Effect of source and target host on percentage of observed rejection events that occurred during touching, examining or drilling on SBW hosts by *T. minutum* females. Rejection of hosts was significantly different between behavioural stages ($P < 0.0001$). Most rejection events occurred during examining.

had emerged from AD-SBW egg masses ($F = 4.20$, $P = 0.04, n = 90$, Table 1). The type of target host to which the female was exposed did not affect the number of times the wasp was on the host before it was accepted ($F = 0.068, P = 0.79, n = 90$, Table 1). There was no significant interaction between the effects of source and target host ($F = 2.28, P = 0.14, n = 90$).

The behavioural stage in which a host was rejected was not affected by the type of source host from which females had emerged ($G = 2.522, P > 0.25, n = 68$) or by the target host with which they were presented ($G = 0.280, P > 0.50, n = 68$). Rejection of hosts was significantly different between behavioural stages ($G = 45.86, P < 0.0001, n = 68$). The majority of hosts were rejected during the examining phase (Figure 1).

If the host was accepted for oviposition, the total time that the female wasp spent handling the host was not affected by the type of host that the female had been reared on (mean from AD-SBW=250.7 ± 12.1 s, mean from BF-SBW=267.1 ± 15.7 s, $F = 0.30$, $P = 0.59, n = 90$) or by the type of target host that it attacked (mean on AD-SBW=246.8 ± 12.9 s, mean on BF-SBW=274 ± 14.7 s, $F = 1.74, P = 0.19$, $n = 90$). There was no significant interaction between effects of source and target host ($F = 1.98, P = 0.16$, $n = 90$).

Table 1. Effect of source and target host on acceptance by *T. minutum* (TM) females given a choice of hosts and observed indirectly and directly

Treatment[1]	ASSAY			
	Choice-indirect observation		Choice-direct observation	
	α^2 for # of parasitised SBW eggs/egg mass[3]	α for # of emerged TM progeny/egg mass	% egg masses accepted	Contact: acceptance ratio
Source host				
AD-SBW	$0.38 \pm 0.05a^4$	$0.42 \pm 0.05a$	29.2a	$1.7 \pm 0.2a$
BF-SBW	$0.30 \pm 0.04a$	$0.36 \pm 0.05a$	33.3a	$2.9 \pm 0.7b$
Target host				
AD-SBW	$0.66 \pm 0.03a$	$0.61 \pm 0.03a$	36.8a	$3.4 \pm 0.2a$
BF-SBW	$0.34 \pm 0.03c$	$0.39 \pm 0.03c$	25.7b	$2.5 \pm 0.7a$

[1] Comparisons are made within each column between source host or target host.

[2] α ranges in value from 0 to 1 with increasing preference. Preference for a host was lowest when no parasitism occurred on the host and highest when eggs were laid exclusively on one egg mass. When parasitism was the same on both hosts, no preference was displayed and $\alpha = 0.5$.

[3] All means are reported $\pm$ standard error.

[4] Difference of one letter indicates significance at $P < 0.05$; difference of two letters indicates significance of at least $P < 0.01$.

Discussion

Most research examining the effect of the source host on host acceptance behaviour of *Trichogramma* addresses the effect of different host species (e.g., Taylor & Stern 1971; van Bergeijk et al., 1989; Kaiser et al., 1989; Bourchier et al., 1993). No studies have investigated the role of the host plant in the source host of *Trichogramma* and its effect on host acceptance behaviour. In some larval parasitoids, females which had experienced components of the host diet during development were attracted, as adults, to hosts fed on the same diet rather than to hosts fed on other types of diet (Monteith, 1958), or to the same host diet rather than to other types of diet (Vet, 1983; Vet & van Opzeeland, 1984). This phenomenon was not observed in our study: *T. minutum* females were not consistently attracted to hosts reared on the same diet as they had experienced during their development in the host.

Courtney et al., (1989) argue that insects possess the ability to rank hosts by quality and that the degree of host acceptance is based on a threshold that is affected by various factors such as genotype, experience and fecundity of the female. Both no-choice and choice assays suggest that AD-SBW hosts were judged as higher quality than BF-SBW hosts by females emerging from either type of host. There appears to be little effect of source host on this threshold. Females emerged from BF-SBW hosts may be more selective as demonstrated by their higher contact:acceptance ratio but there was no actual effect on oviposition rates. Differences in fecundity were not responsible for changes in contact:acceptance ratios: females from both host types had similar body sizes and egg loads (Song, 1993). Changes in female behaviour may have resulted from genetic selection or from experience with the host during development (Corbet, 1985).

The lower acceptability of BF-SBW versus AD-SBW hosts displayed by *T. minutum* females suggests that these hosts are less suitable for progeny development than AD-SBW hosts. Studies by Ruberson et al. (1985) of the egg parasitoid, *Edovum puttleri* Grissell, showed that a decrease in acceptance of hosts fed on resistant plants was accompanied by a decrease in longevity of parasitoids reared from the same host. Similarly, the size of the progeny of larval parasitoids, *Compsilura concinnata* Meigen, was reduced as levels of tannins added to the artificial diet of their gypsy moth hosts, *Lymantria dispar* L., were increased (Bourchier, 1991). In contrast, other studies by Song (1993) demonstrate that diet of SBW has no influence on probability of survival to adulthood, size or potential fecundity (egg load) of *T. minutum* offspring developed in either type of SBW host. *Trichogramma* does not appear to suffer from the possible presence of allelochemicals, such as terpenes (Mattson et al.,

1983), or from any difference in nutrient value of the host. It also does not benefit from hosts that were fed an optimal artificial diet supplemented with vitamins. Feeding spruce budworm on balsam fir versus artificial diet does decrease the success of spruce budworm egg hatch (McMorran, 1965) as well as pupal and egg mass weight (Song, 1993) but these effects were not transferred to the developing parasitoids.

An alternative explanation for lower acceptance on BF-SBW hosts versus AD-SBW hosts is that *T. minutum* may not recognize the egg masses of hosts reared on balsam fir as readily as those reared on artificial diet. Components of balsam fir in BF-SBW egg masses may act as a camouflage for hosts laid onto balsam fir needles. Response to AD-SBW hosts may be higher because these hosts are more distinct from their surroundings. *Trichogramma* are stimulated by the host and its products (e.g. Zaborski et al., 1987; Noldus, 1989); the host diet, as a component of the host, may alter the stimulatory nature of the host and affect the parasitoid's response.

The decision made by *T. minutum* to accept or reject is made externally, during the examining phase. Criteria that deter attack are probably assessed at this time. Females were never observed to reject hosts once oviposition had commenced; Pak & de Jong (1987) noted the same phenomenon. Although host diet did affect host colour, Song (1993) showed that colour did not affect acceptance. Similar realized fecundity and handling times per egg mass suggest that possible differences in host size do not affect acceptance. Host diet may affect volatile and contact kairomones which may repel parasitoids from egg masses of BF-SBW or attract parasitoids to AD-SBW.

Our results suggest that if *T. minutum* females do not reject the host during examining, both types of hosts are accepted completely. This effect differs from the results of other studies on *Trichogramma* comparing host acceptance where both host types were accepted for oviposition but clutch size, handling time or the contact: acceptance ratio differed depending on target host (e.g., Marston & Ertle, 1969; Pak et al., 1986; van Dijken et al., 1986). In this study, no differences in number of eggs per egg mass, handling time and contact:acceptance ratios between target hosts were observed. Although we could not measure clutch size per egg, these results suggest that clutch size may be the same on both host types.

In a natural environment, *T. minutum* are dependent on alternate hosts to propogate throughout the year (Houseweart et al., 1984). Although *T. minutum* are considered generalists, they appear not to be well-adapted to changes in host properties and this may be a factor contributing to their generally low rates of parasitism on spruce budworm in the field (Smith et al., 1990).

To date, laboratory tests of host acceptance by *T. minutum* on SBW eggs that aim to predict field performance have been conducted with AD-SBW eggs (Bourchier & Smith, 1996). Because SBW *in situ* would have fed on a natural diet such as balsam fir, this study predicts that host acceptance of SBW eggs would actually be lower in the field than predicted by these laboratory studies.

Acknowledgements

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