

## Influence of plant structural complexity on the foraging success of *Trichogramma minutum*: a comparison of search on artificial and foliage models

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### Abstract

The influence of structural complexity on the foraging success for host eggs (*Ephestia kuehniella* Zeller) by *Trichogramma minutum* Riley was investigated in the laboratory. Naive females were released into arenas with structurally different paper models or foliage (simple: trembling aspen *Populus tremuloides* Michx., complex: balsam fir *Abies balsamea* L.). Observations of individual females were made every 15 min and searching success was measured by the number of host egg clusters found and the amount of time taken to find them, within a period of 196 min. Females found significantly more egg clusters and were quicker at finding them on the sample paper and foliage surfaces than on the most complex paper or foliage surfaces. Older females (2–3 days) were more successful and searched quicker than younger (< 24 h) females on all paper surfaces. The timed observations suggested that wasps which spent more time walking had a significantly decreased probability of finding an egg mass and were significantly slower at finding them. Females that spent more time on paper surfaces had an increased probability of finding an egg mass. The significance of searching differences is discussed in relation to the potential effects of plant surfaces on *Trichogramma* movements and to the physiological readiness of the wasp.

### Introduction

Inundative releases of the parasitoid *Trichogramma minutum* Riley (Hymenoptera, Trichogrammatidae) are being considered for use against the spruce budworm, *Choristoneura funiferana* (Clemens) (Lepidoptera, Tortricidae), in Canada. To date, this approach has required the release of large numbers of parasitoids in forests (several million wasps/ha) to achieve high levels of egg parasitism, relative to agriculture (200 000–600 000 wasps/ha) (Smith, 1996). Aspects of the environment that might influence search include the volume and complexity of foliage. The forest is a complex environment which may make parasitoids unable to successfully locate host eggs. Thus, in order to improve the efficacy of releases, it is first necessary to understand the way in which *Trichogramma* searches for host eggs.

*Trichogramma* can be influenced by a number of environmental factors while foraging for hosts, includ-

ing host-related chemical products (e.g., frass, body scales, sex pheromones), odours from host eggs and attributes of the host plant (tritrophic level interactions) (Noldus, 1989). In terms of the host plant, *Trichogramma* has been shown to respond to plant-derived chemicals (Norlund et al., 1985), and to physical attributes, such as foliar pubescence (Treacy et al., 1986) or changes in leaf surface area (Smith, 1996). Physical factors have received less attention than chemical ones.

The physical aspect of plant growth has two components, biomass and architectural arrangement of biomass in space (structural complexity); the latter is a result of plant branching or connectivity patterns (Kuppers, 1989; Andow & Prokrym, 1990). Studies in aquatic systems, involving the effect of the physical environment on foraging have clearly demonstrated that increasing the complexity of the environment results in reduced foraging success of predators (e.g.,

Russo, 1987). Very little is known about the role of habitat complexity in host-parasitoid interactions.

The natural forest environment is composed of a heterogeneous mixture of plant architectures which changes both temporally and spatially; this may influence the foraging success of *T. minutum*. Some authors have examined the effect of plant community composition on searching success of *Trichogramma* through field studies (Kemp & Simmons, 1978; Thorpe, 1985). Although some studies have suggested plant structural effects (Thorpe, 1985; Smith, 1988) this has rarely been examined under controlled laboratory conditions. Where this has been studied with wasps searching on paper surfaces, increased structural complexity has been shown to reduce the searching efficiency of *T. nubilale* Ertle and Davis (Andow & Prokrym, 1990).

The purpose of this study was to further work by Andow & Prokrym (1990), by examining the response of searching by *Trichogramma* using models of foliage. Examining behavioural outcomes of the parasitoid to complexity in a highly artificial system and then comparing observations on foliage could lead to improved behavioural predictions under natural conditions. Specifically, we examined the following questions: (1) do structurally different paper surfaces influence searching success; (2) do individual females of *T. minutum* differ in their searching at different ages; (3) is searching success influenced by structurally different plant foliage; and (4) do any other plant attributes alter foraging success? A series of experiments were designed to address these questions by comparing behavioural outcomes between artificial surfaces and foliage models, in the laboratory.

## Materials and methods

### *Parasitoid material*

*Trichogramma minutum* used in this study originated from parasitized egg masses of *C. fumiferana* collected in the summer of 1990 from five regions of northern Ontario. Prior to all experiments, the parasitoid colony was maintained on a factitious host, *Ephesia kuehniella* Zeller (Mediterranean flour moth) in 25 × 95 mm glass vials at L16:D8 and 15 °C for 12 generations. Subsequent generations (13–26) used in our experiments were reared at 15 or 25 °C (L16:D8) depending on the starting time of the experiment.

### *Experimental design*

Behavioural assays of all experiments were carried out in inverted 30 dram (75 × 45 mm) clear, plastic, snap cap vials with a Whatman No. 1 filter paper placed in the cap. Each artificial surface (one per vial) was glued in an upright position, perpendicular to the filter paper lining so that it did not contact the sides of the vial. This ensured that the female would have to either walk onto the surface from the filter paper or fly to it in order to find host eggs. A small cluster (20–30) of fresh host eggs (*E. kuehniella*) was glued with white glue to the upper right hand corner of each artificial surface. Experiments were conducted in a room under fluorescent lighting (807 lux) at 24 (± 2 °C) and between the hours of 0830–1500 h.

In all experiments, female parasitoids were mated by males upon emergence and were naive with respect to contact with host eggs. Because a difference in response was suspected for parasitoids of different ages, responses of younger (< 24 h) and older (2–3 days) females were tested separately in Experiment 1. Only older (2–3 days), honey-fed females were used in subsequent experiments (Experiments 2–4), because they demonstrated a better searching response than younger (< 24 h) females. Food (1:1 = honey:water) was provided to the older females because deprivation has been shown to influence the searching behaviour of *Trichogramma* (Keller et al., 1985). Preliminary studies suggested that the searching success of younger female *T. minutum* was similar whether they were provided with honey or not, thus they were not provided with honey.

Individual females (one per vial) were monitored by direct observation (for 10s) every 10–15 min. This 15-min-period was the time it took to observe and record types of behaviour for 60–70 female wasps in sequential order. The experiment started when the first female was lightly tapped into the centre of the cap and was terminated after she had been observed for either 196 min or was seen making direct contact with the egg cluster (a successful find), whichever occurred first. This 196-min-period was long enough to ensure a number of successful finds and, for Experiment 1, to discern the behavioural sequence prior to locating the egg mass.

*Experiment 1. Effect of artificial complexity.* Three types of paper surfaces of increasing complexity were used to compare the response of older (2–3 days) and younger (< 24 h) female *T. minutum*. The surfaces were created by folding and cutting white, waxed paper

sections of 20 × 50 mm. The complexity consisted of simple (receiving no cuts), intermediate (8 equal cuts, 1 section = 6.2 mm), and complex (28 equal cuts, 1 section = 1.8 mm). Sections of the complex surface were cut approximately to the width of a balsam fir (*Abies balsamea* L.) needle.

At each observation, the position of the parasitoid in the vial (on the paper surface vs. elsewhere) and her activity (walking vs. stationary) were recorded. These two parameters were measured because the success of a female on a particular surface complexity could be accounted for by either her position in the vial or her activity level. Parasitoids finding the egg cluster within the first observational period were eliminated from that data set because only the influence of position and activity on search success were to be examined.

The response of 20 *T. minutum* females on each complexity type was tested during each experimental trial (60 per trial). This was replicated four times for each age class.

*Experiment 2. Effect of foliage colour.* The response of 70 older female wasps to the colour of green foliage was examined on two different types of surfaces (35 females per surface). The first surface was the same as the simple (uncut) white waxed paper surface from Experiment 1. The second surface was of the same simple structure but made of green LETRASET tint (PANTONE 370-A). This material had a similar texture as the waxed paper.

*Experiment 3. Effect of simplified foliage.* The effect of plant attributes such as odour and texture were examined by comparing the searching of *Trichogramma* on two tree species. The attributes of plant surface area and structural complexity were held constant by providing real foliage arranged on the simple wax paper surface from Experiment 1. The paper was cut slightly smaller (15 × 40 mm) to accommodate the entire length of a balsam fir needle. A flat balsam fir surface was created by removing individual needles from a small branch then cutting and glueing them side by side to one side of the paper section. A flat trembling aspen (*Populus tremuloides* Michx.) surface was created by cutting and glueing an individual leaf to one side of an entire paper section. The aspen leaf was then cut in strips of needle width to create a surface similar in texture as the fir needles. The searching success of 30 older females was monitored on each surface type.

*Experiment 4. Effect of natural foliage.* Two tree species having structurally different foliage surfaces were compared: leaves of trembling aspen and branches of balsam fir. In the vial arenas, a small cork stopper was glued to the filter paper in the cap to support a segment of upright foliage. Foliage (50 × 35 mm) was positioned so as not to contact any side of the arena. A small cluster of fresh *E. kuehniella* eggs was glued onto the upper right hand section of each foliage surface.

Sixty older females were compared in these arenas, 30 females on each foliage type. Because surface area could not be held constant, a LI-COR 3000 portable area meter was used to measure leaf and needle surface area after the experiment was completed. The experiment was repeated on a second day.

### Statistical analyses

The number of egg clusters found among treatments and between age classes were compared statistically using 2 × 2 contingency tables (Chi-square analysis) adjusted for continuity (PROC FREQ; SAS, 1988). On the natural foliage (Experiment 4), logistic regression was further used to determine if structural complexity had a significant effect on the probability of the parasitoid finding host eggs, taking into account potential differences in plant surface areas. Differences in mean surface area between the two tree species were analysed using the t-test procedure (PROC TTEST; SAS, 1988).

The logrank test (PROC LIFETEST; SAS, 1988) was used to determine estimates of the mean times taken by *Trichogramma* to find egg clusters on natural foliage and paper models. This test is a non-parametric method for testing the null hypothesis that treatment groups are samples from the same population with respect to the time taken for host location. It takes right-censored data into account; in our experiment, this arises from a maximum observational time of 196 min.

Two separate approaches were used to analyze the influence of all variables: treatment, age and the two behavioural responses (position in the vial and activity level) on searching success, in Experiment 1. Logistic regression analysis (PROC CATMOD; SAS, 1988) tested whether the variables significantly influenced the probability of *T. minutum* finding egg clusters. Proportional hazards regression analysis (PROC LIFEREG; SAS, 1988) was used to test whether the variables sig-

nificantly influenced the time taken to find host eggs by *T. minutum*.

## Results

*Experiment 1. Effect of artificial complexity.* *Trichogramma minutum* females found significantly more egg clusters on the simple surface than on the complex surface during the 196-min assay, for both younger and older females (Table 1). Older females were more successful than younger females on the simple and complex surfaces ( $\chi^2 > 20$ ,  $df = 1$ ,  $P < 0.0001$ ), but not on the intermediate surface ( $\chi^2 = 1.61$ ,  $df = 1$ ,  $P = 0.205$ ).

Results of the logrank test revealed significantly different search times among complexity types for both younger ( $\chi^2 = 16.6$ ,  $df = 2$ ,  $P = 0.0002$ ) and older ( $\chi^2 = 37.43$ ,  $df = 2$ ,  $P < 0.0001$ ) females (Table 1). Overall, wasps found egg masses quicker on simple surfaces than on either the intermediate or complex surfaces and older females were faster than younger ones.

The results of the logistic regression analysis revealed that an increase in the proportion of time a female spent walking decreased the probability of her finding an egg mass (Table 2). Also, the more time a female spent on the surface, the more likely she was to find host eggs. Results of the proportional hazards test showed that those females who spent more time walking had significantly longer searching times (Table 2), i.e. females who walked more took more time to find host eggs. Parasitoids that spent proportionately more time on the treatment surface had quicker search times than those that spent their time elsewhere in the arena.

The effect of the surface complexity and age variables on foraging success, using both logistic regression and proportional hazards analyses, were similar to results of the chi-square and logrank tests, respectively. Thus, we have not tabulated the latter tests here.

*Experiment 2. Effect of foliage colour.* Female *T. minutum* found host eggs equally on white and green simple surfaces ( $\chi^2 = 0.16$ ,  $df = 1$ ,  $P = 0.69$ ) (Table 3). Likewise, searching times taken to find the egg cluster did not significantly differ between the treatments ( $\chi^2 = 0.15$ ,  $df = 1$ ,  $P = 0.70$ ). These results were comparable to the results of older females searching on the simple surface of Experiment 1; about 89% of the hosts were found and mean times were similar (see Table 1).

*Experiment 3. Effect of simplified foliage.* An equal number of host egg masses were found by female *T. minutum* on the flat surfaces of balsam fir and trembling aspen (Table 3). Likewise, searching times did not significantly differ ( $\chi^2 = 0.15$ ,  $df = 1$ ,  $P = 0.70$ ). On the simplified foliage of this experiment, only 60% of the hosts were found and females took longer to find them than those on paper surfaces.

*Experiment 4. Effect of natural foliage.* Results of the logistic regression analysis showed that surface area was not a significant factor that affected searching success ( $\chi^2 = 1.68$ ,  $df = 1$ ,  $P = 0.19$ ) because the mean surface area of each plant species was the same ( $T = 1.59$ ,  $P = 0.11$ ) (Table 3). Significantly more egg clusters were found by female *T. minutum* on the aspen leaves than on the balsam fir needles ( $\chi^2 = 11.68$ ,  $df = 1$ ,  $P = 0.0006$ ). Similarly, females were significantly faster at finding egg masses on aspen leaves than balsam fir ( $\chi^2 = 13.21$ ,  $df = 1$ ,  $P = 0.0003$ ). The outcome of foraging on aspen by *T. minutum* in this experiment, showed similar results to Experiment 3 were females searched on simplified aspen.

## Discussion

Our study shows that host searching by females of *Trichogramma minutum* is affected by the structural complexity of the surroundings. Both the time taken to find egg clusters and the number found were significantly different according to the complexity of the surface on which females searched. Female *Trichogramma* took less time to search for host eggs on continuous surfaces and they found more egg masses on these surfaces than on divided ones. Our work concurs with that of Andow & Prokrym (1990) using a different parasitoid species and greater surface complexity.

The improved searching response of older *T. minutum* may be partly due to their reduced tendency to disperse and greater need to oviposit. In addition to many other factors, the initiation of search depends upon the internal readiness of the wasp (Bell, 1990); wasps may not show positive search movements until a pre-ovipositional period has passed (Vinson, 1984). The fact that younger wasps are more sensitive to light and show a suppressed host-seeking response than older ones supports this (Smits, 1982). Host rejection also may occur more often for younger females because they have less of a drive to oviposit than older females (24–48 h old) (Kaiser et al., 1989). Time spent moving

Table 1. Effect of paper surface complexity on the searching success of younger (< 24 h) and older (2–3 days) females of *T. minutum* in a 196-minute period. Data from four replicates were pooled prior to analysis for each surface type

Surface Type	Younger females <sup>2</sup>			Older females		
	n	Total <sup>1</sup> # egg clusters found	Mean time <sup>3</sup> (min) (±SE)	n	Total <sup>1</sup> # egg clusters found	Mean time <sup>3</sup> (min) (±SE)
Simple	80	44 <sup>a</sup>	134.9 (±7.8)	80	71 <sup>a</sup>	69.4 (±7.0)
Intermediate	80	33 <sup>ab</sup>	156.4 (±6.9)	80	42 <sup>b</sup>	127.9 (±8.4)
Complex	80	21 <sup>b</sup>	173.2 (±5.5)	80	53 <sup>b</sup>	120.6 (±7.7)

<sup>1</sup> Treatment totals followed by different letters within each age class are significantly different at  $\alpha = 0.05$  ( $\chi^2$ -statistic).

<sup>2</sup> Comparisons were made between the two parasitoid ages within the same complexity level for both total # egg clusters and mean times. All values were significantly different except those associated with the intermediate surface ( $\alpha = 0.05$ ).

<sup>3</sup> Results of the logrank test show a significant difference in mean time taken to find host eggs, between the three surface complexities ( $\alpha = 0.05$ ). The estimates of the means were biased because of censored observations (see PROC LIFETEST; SAS 1988).

Table 2. Effect of the proportion of observations that a female spent 1) walking or 2) on the paper surface on searching success. Estimates were taken from a model which also included the independent variables, complexity and age

Analysis	Explanatory <sup>1</sup> Variable ( $x_i$ )	Estimate ( $\beta_i$ )	Standard error se( $\beta_i$ )	$\chi^2$ -statistic	P
Probability of finding an egg cluster (logistic regression)	arcsine (walking)	-2.48	0.335	54.85	< 0.0001
	arcsine (surface)	1.16	0.471	6.10	0.0135
Proportion of time taken to find an egg cluster (proportional hazards regression)	arcsine (walking)	1.13	0.154	53.25	0.0001
	arcsine (surface)	-0.44	0.191	5.33	0.0209

<sup>1</sup> Variables were transformed using the arcsin transformation because untransformed proportions are not normally distributed.

Table 3. Influence of various surface types on the foraging success of older (2–3 days) *T. minutum* females

Treatment	n	Total <sup>1</sup> egg clusters found (min)(±SE)	Mean time <sup>3</sup> taken to find host eggs	Surface area (cm <sup>2</sup> )(±SE)	
Experiment 2	white paper	35	32 <sup>a</sup>	59.1 (±9.2) <sup>a</sup>	–
	green paper	35	31 <sup>a</sup>	63.3 (±9.4) <sup>a</sup>	–
Experiment 3	simplified aspen	30	18 <sup>a</sup>	113.6 (±12.4) <sup>a</sup>	–
	simplified fir	30	18 <sup>a</sup>	140.5 (±11.4) <sup>a</sup>	–
Experiment 4	natural aspen	60 <sup>2</sup>	33 <sup>a</sup>	142.3 (±7.9) <sup>a</sup>	17.90 (±0.51) <sup>a</sup>
	natural fir	60	15 <sup>b</sup>	179.6 (±5.1) <sup>b</sup>	19.52 (±0.88) <sup>a</sup>

<sup>1</sup> Within an experiment, values followed by different letters are significantly different,  $\alpha = 0.05$ .

<sup>2</sup> Data were pooled from two repetitions.

<sup>3</sup> Estimates of the means are biased, because of censored observations (see PROC LIFETEST; SAS 1988).

and the rate of movement vary greatly with the age of the female; younger females (0–8 h old) are relatively inactive, and only start to move continuously after 24–36 h (Marston & Ertle, 1973). Even before dispersal behaviour begins, many females may spend considerable time preening (Noldus et al., 1991b; Forsse et al., 1992), up to several hours after emergence or after release onto test surfaces (personal observations). Given that our experiments were only about 3.3 h long, younger females may have spent a large part of their time in such activities and not in searching. Because of these reasons, many researchers have used female *Trichogramma* greater than 24 h old (Kaiser et al., 1989; Noldus et al., 1991a).

The more time wasps spent on the 'host plant' paper surface, the more likely they were to find an egg cluster and less time they spent searching. This was as predicted because the eggs were located on the surface; females being elsewhere in the vial would not increase their likelihood of finding the egg mass. *Trichogramma* wasps do not perceive egg masses (either visually or chemically) until they pass within millimetres of them (Kaiser et al., 1989; Bruins et al., 1994).

Interestingly, for this experiment, the more time female wasps spent walking, the longer they took to search and the less likely they were to find egg masses. It is possible that this result was an artifact of our experimental design in that individuals were observed and their activity recorded only every 15 min. In some cases, this would mean that females may have contacted the egg mass several times before we actually observed the event. In other cases, our design would suggest that stationary behaviour leads to successful host finding when females immediately locate hosts eggs after a long period of inactivity (preening). It is also possible that the results truly reflect the behaviour of female wasps in that during the experiments, some were more motivated by factors other than host searching, e.g., dispersal. We observed many females on the side or upper portions of the vial, generally moving in an upward direction, apparently uninterested in searching for host eggs. More detailed studies, continuously following individual females until they find hosts, would determine whether these results have a biological or experimental basis.

On continuous surfaces such as the simple paper on aspen foliage, *Trichogramma* tended to move more rapidly and in straight lines than on broken surfaces. Encountering a large number of edges during host searching on broken surfaces may have redirected or slowed the parasitoid such that previously searched

areas were re-examined. This behaviour is often seen in movements after encountering kairomonal patch edges (Morrison & Lewis, 1981). On continuous surfaces, a greater area can be searched and there would be less overlap of search paths.

Overlap of previously searched areas by wasps while on complex surfaces can be demonstrated in another way. When moving randomly on a surface, *Trichogramma* effectively searches a 1 cm band (Noldus et al., 1991a), or at least orients toward host eggs from approximately 5 mm (Pak & Oatman, 1992; Bruins et al., 1994). Searching small areas, such as the projections of the complex paper surface (width = 1.8 mm) or balsam fir needles (width = 1.5 mm), would physically limit the wasp's potential surface coverage. As a consequence, it would take more time to examine the same amount of area on a complex surface as on a simple surface. By minimizing the overlap of search paths, searching time would be minimized and the subsequent encounter with hosts would be increased.

Considering the response to plant edges in a different way, wasps may be redirected at the edge to follow the margin of the leaf, as demonstrated in predators (Carter et al., 1984). Because the host egg cluster was positioned close to the paper edge on all surface types, the eggs would be discovered easily if searching along edges was a true foraging strategy employed by *T. minutum*. Studies by Noldus et al., (1991a, b) reported that upon reaching a leaf margin or edge of a platform, the wasps spent a large percentage of time walking in that zone. In our study, the simple surface had an available search margin (i.e., perimeter) of about 90 mm, whereas the complex surface had about 11 times as much margin. The increase in the available margin on the complex surface may have resulted in parasitoids spending more time searching this surface before the host eggs were found.

The sequence of experiments we describe was aimed at controlling those attributes of plant foliage other than structural complexity and to examine changes in search response of *Trichogramma* on artificial and natural surfaces. The foraging response of females did not appear to be influenced by colour of foliage. Female *T. minutum* were equally attracted to green and white surfaces. In Experiment 3, volatile or contact kairomonal compounds may have potentially differed between the two tree species but the foraging response of *T. minutum* did not appear to be affected. It has been suggested that host plant species can be differentially attractive to *Trichogramma*

(Rabb & Bradley, 1968), however, these differences are not conclusive and the behavioural mechanism is unknown (Noldus, 1989). Keller (1985) suggested that visual characteristics (e.g., certain wavelengths of reflected light) would unlikely influence female *Trichogramma* because the wasp is polyphagous and visual characteristics of plants associated with the host can vary substantially. In addition, generalist wasps may innately respond to chemical compounds that are common to most terrestrial plants but not to specific visual cues. Differential attractiveness (visual or chemical) or arrestment to species-specific rather than general plant chemicals is perhaps not selected for in generalist parasitoids.

The reduced searching success we observed between different foliage surfaces (Experiments 3 & 4) and artificial surfaces (Experiments 1 & 2) suggests that *T. minutum* responds to the presence of plant leaf chemicals. The kairomones associated with foliage in our study could have potentially resulted in the arrestment of female wasps similar to that observed by Keller (1987) for *T. exiguum* on maize and pigweed. This orthokinesis is a common component of odour-induced arrestment and is also part of the response of *Trichogramma* to contract kairomones (Shu & Jones, 1988). Additionally, physical irregularities in the aspen models, especially the simplified model, may have influenced rapid and straight line movements of these small wasps compared to those on the smooth paper.

The reduction in searching efficiency due to foliage complexity alone should be considered when extrapolating behavioural responses of *Trichogramma* on artificial surfaces (e.g., paper) in the laboratory to responses in field studies. The present study has demonstrated that plant structural complexity has a significant effect on a parasitoid's encounter rate while searching for hosts irrespective of other plant attributes (e.g., colour, surface area). This means that habitat structure will influence the searching success of *T. minutum* upon release, and that it should be considered when determining application rates for applied use.

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