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R. S. Bouchier ^{ab}; S. M. Smith ^a; J. E. Corrigan ^c; J. E. Laing ^c

^a Faculty of Forestry, University of Toronto, Toronto, Ontario, Canada ^b Forest Pest Management Institute, Sault Ste Marie, Ontario, Canada ^c Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada

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Effect of Host Switching on Performance of Mass-reared *Trichogramma minutum*

R. S. BOURCHIER,¹ S. M. SMITH,¹ J. E. CORRIGAN² AND J. E. LAING²

¹Faculty of Forestry, University of Toronto, Toronto, Ontario, Canada M5A 3B3; ²Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

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The effect of host switching on parasitism by *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae) (TM) was examined for parasitoids attacking a factitious host, the Mediterranean flour moth, *Ephestia kuehniella* Zell. (Lepidoptera: Pyralidae) (MFM), and a natural host, the eastern spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) (SBW). Parasitoids that were switched from rearing on the natural host to rearing on the factitious host had lower realized fecundities on both MFM and SBW eggs than a control line that was maintained continuously on the natural rearing host, SBW eggs. Conversely, *T. minutum* reared on the factitious host and switched to rearing on the natural host showed greater realized fecundities. This increase in realized fecundity was lost in the first generation after switching parasitoids back to the factitious rearing host. *T. minutum* that were maintained on the natural rearing host (SBW eggs) showed more variation in realized fecundity and host acceptance of both MFM and SBW eggs, than parasitoids that were reared on MFM eggs.

Keywords: *Trichogramma minutum*, *Choristoneura fumiferana*, *Ephestia kuehniella*, biological control, inundative release, parasitoid

INTRODUCTION

Trichogramma minutum Riley (Hymenoptera: Trichogrammatidae) is a polyphagous egg parasitoid that is commonly found attacking the spruce budworm, *Choristoneura fumiferana* (Clemens) (SBW) (Smith *et al.*, 1990). Budworm eggs are available only during the summer months; to maintain a continuous population, *T. minutum* must be capable of attacking a variety of different hosts eggs (listed in Houseweart *et al.* (1984)). Host switching is thus a fundamental part of this parasitoid's biology. A lack of alternative hosts has been suggested to be one reason for the large amount of variation in parasitism rates by *T. minutum* on SBW eggs (Miller, 1963; Neilson, 1963).

Host switching is also a fundamental component of mass-rearing programmes for *T. minutum*.

Correspondence to R.S. Bouchier, Forest Pest Management Institute, PO Box 490, Sault Ste Marie, Ontario, Canada P6A 5M7.

Because of the ease of rearing large numbers of host insects, parasitoids are often mass reared on a relatively small factitious host egg, such as the Mediterranean flour moth, *Ephestia kuehniella* Zell. (MFM) and then released to attack a larger target host, such as the spruce budworm. MFM eggs generally support the development of a single parasitoid whereas SBW eggs can support two or more parasitoids. A serious concern associated with the use of factitious hosts is the quality of parasitoids being produced (Bigler, 1989). Bigler *et al.* (1982) found a significant decline in the rate of parasitism by *T. brassicae* Bezdenko (called *T. evanescens* Westwood in Bigler's papers) attacking the European corn borer, *Ostrinia nubilalis* Hb. (Lepidoptera: Pyralidae) after five generations of rearing on the factitious host, *E. kuehniella*. To ensure the quality of *T. brassicae*, parasitoids are now maintained on the natural host *O. nubilalis* in relatively low numbers under semi-field conditions; when large numbers of parasitoids are required, parasitoid rearing is switched to the factitious host for up to five generations before the field release (Bigler, 1986).

In this paper, we report experiments to assess the effect of switching between target and rearing hosts on the realized fecundity and host acceptance behaviour of *T. minutum*. Our objective was to assess the utility of using a host-switching rearing system similar to Bigler's (1986), to improve the quality of mass-produced *T. minutum*.

MATERIALS AND METHODS

T. minutum were reared at 25°C and 16-h light:8-h dark photoperiod on either spruce budworm or Mediterranean flour moth eggs.

Parasitoid Colonies

The MFM line of *T. minutum* (MFM-tm) was reared from spruce budworm eggs collected from Vermilion Bay, Ontario, Canada (UTM: VF7222) in July 1990. This line had been maintained in the laboratory on MFM eggs for approximately 100 generations. The SBW line of *T. minutum* (SBW-tm) was also collected from spruce budworm eggs from the same site at Vermilion Bay, but in July 1991. This line had been maintained on laboratory reared SBW eggs for 8 months (approx. 24 generations). The material collected in 1990 was identified as *T. minutum* by John Pinto (Riverside), and voucher specimens of both the 1990 and 1991 collections have been deposited at the Department of Entomology, Royal Ontario Museum, Toronto, Ontario, Canada.

There were two separate experiments involving the MFM-tm and SBW-tm lines:

Experiment 1: SBW to MFM. The effect of switching *Trichogramma*, which started on SBW eggs, to four generations of rearing on MFM eggs was compared to a control line that was reared continuously on SBW eggs for five generations.

Experiment 2: MFM to SBW. The effect of switching *Trichogramma*, which started on MFM eggs, to SBW eggs for two generations and then back to MFM eggs for two generations was compared to a control line that was reared continuously on MFM for five generations.

At each generation, the realized fecundity and host acceptance were measured for 40 female wasps from each line attacking either SBW or MFM eggs. The treatment and control lines were given host eggs that were the same age.

Realized fecundity (the number of progeny, produced by a female wasp, which survive to emerge as adults) was estimated by placing a single female parasitoid in a 60 × 15 mm glass vial with either a SBW egg mass or approximately 80 irradiated MFM eggs. MFM eggs were irradiated to prevent cannibalism of MFM eggs by MFM larvae emerging from non-parasitized eggs. SBW egg masses (containing 15–20 eggs) were presented to the wasp on a fir needle glued to a 20 × 10 mm paper card that was inserted into the vial. MFM eggs were glued directly to the card which was inserted in the vial. The number of SBW and MFM eggs presented to the parasitoids was chosen to ensure parasitoids would not be host limited; *T. minutum* generally lay a single egg in MFM eggs whereas they usually lay two or more eggs in SBW eggs (Marston

& Ertle, 1973; Bourchier *et al.*, 1993). Females dying in the first 24 h after being placed in the vial were omitted from the analysis. Sixteen days after exposure to female wasps, the emerged adult parasitoids were counted. Parasitoids were not exposed to honey or water during the experimental period.

Host acceptance was assessed by calculating the percentage of the female wasps, alive after 24 h, that did not lay eggs that developed to adult wasps in the available hosts.

Statistical Analysis

Mean realized fecundities and standard errors were calculated for parasitoids that produced at least one progeny and survived for 24 h after being placed in the vial. Means of realized fecundity and the percentage host acceptance were plotted for each successive generation to compare trends between switched and control lines of *T. minutum*.

To assess the experiment-long effects of the rearing treatments: (1) mean realized fecundities when attacking SBW or MFM eggs were compared between generation 1 and generation 5 for each treatment line using *t*-tests (Sokal & Rohlf, 1981); and (2) the number of parasitoids that accepted host eggs was compared between generation 1 and generation 5 for each treatment line using a *G* test (Sokal & Rohlf, 1981).

RESULTS

Experiment 1: SBW to MFM. Parasitoids that had been switched to rearing on MFM eggs from SBW eggs had lower realized fecundities when exposed subsequently to either MFM or SBW eggs (Figure 1(a) and (b)) than parasitoids that were reared constantly on SBW eggs (control lines). *T. minutum* that were reared constantly on SBW eggs had more variation in mean realized fecundity on both target hosts than parasitoids that were switched to MFM eggs; the mean realized fecundity of *T. minutum* reared on MFM eggs remained relatively constant on both hosts for the four generations after the switch of rearing hosts (Figure 1(a) and (b); generations 2–5).

The realized fecundity of parasitoid lines switched from SBW to MFM host eggs declined between generations 1 and 5 when attacking MFM eggs, whereas the realized fecundity of the control line increased between generations 1 and 5 attacking both MFM and SBW eggs (Table 1).

Host acceptance by parasitoids increased with the number of generations after host switching irrespective of the rearing host (Figure 2). The relative frequency of SBW eggs parasitized by *T. minutum* increased significantly between generations 1 and 5 for both the switched and control line of parasitoids that originated on SBW eggs ($G = 15.5$, $P < 0.001$; $G = 8.17$, $P = 0.004$ respectively; Figure 2(a)). Host acceptance of MFM eggs increased between generations 1 and 5 for parasitoids that were switched to rearing on MFM eggs ($G = 18.4$, $P < 0.001$; Figure 2(b)). Host acceptance of MFM eggs by the control line initially increased, but by generation 5, host acceptance was not significantly different from generation 1.

Experiment 2: MFM to SBW. The realized fecundity for parasitoids that had been switched from MFM eggs to rearing on SBW eggs increased when attacking both MFM and SBW eggs in comparison with parasitoids that had been maintained on MFM eggs (control line; Figure 3(a) and (b)). There was a generation delay before fecundity increased on the larger host (SBW eggs, Figure 3(a)) whereas parasitoids attacking MFM eggs showed an immediate increase in realized fecundity (Figure 3(b)). The increase in fecundity on both target hosts disappeared as soon as *T. minutum* were switched back to being reared on MFM eggs (Figure 3(a) and (b); at generation 4).

The realized fecundity of parasitoids that had their rearing host switched from MFM to SBW eggs and the control line that was reared constantly on MFM eggs did not change between generations 1 and 5 (Table 1).

Host acceptance by parasitoids that originated from MFM eggs, including both those that had their rearing host switched to SBW eggs and the control line, did not change on either MFM or SBW eggs between generations 1 and 5 (Figure 4(a) and (b)).

TABLE 1. Realized fecundity at generations 1 and 5 for *T. minutum* from four rearing treatments attacking SBW and MFM eggs

Rearing treatment	Mean realized fecundity \pm SE on:			
	SBW eggs		MFM eggs	
	Initial	At generation 5	Initial	At generation 5
1. SBW-tm switched to MFM eggs for five generations	22.3 \pm 4.7 (12) ^a	15.9 \pm 2.6 (23)	49.9 \pm 4.4 (23)	25.4 \pm 2.0** (30)
2. SBW-tm given SBW eggs for five generations (Control 1)		40.0 \pm 4.6* (24)		74.7 \pm 5.3** (16)
3. MFM-tm switched to SBW eggs for two generations then switched to MFM eggs for three generations	24.5 \pm 3.3 (21)	19.7 \pm 2.3 (23)	44.6 \pm 3.3 (31)	39.6 \pm 2.8 (34)
4. MFM-tm reared on MFM eggs, five generations (Control 2)		19.2 \pm 1.2 (30)		40.2 \pm 2.4 (39)

^aNumber in parentheses is sample size.

*, **Initial realized fecundity is significantly different from realized fecundity at generation 5, $P < 0.05$ and $P < 0.001$ respectively.

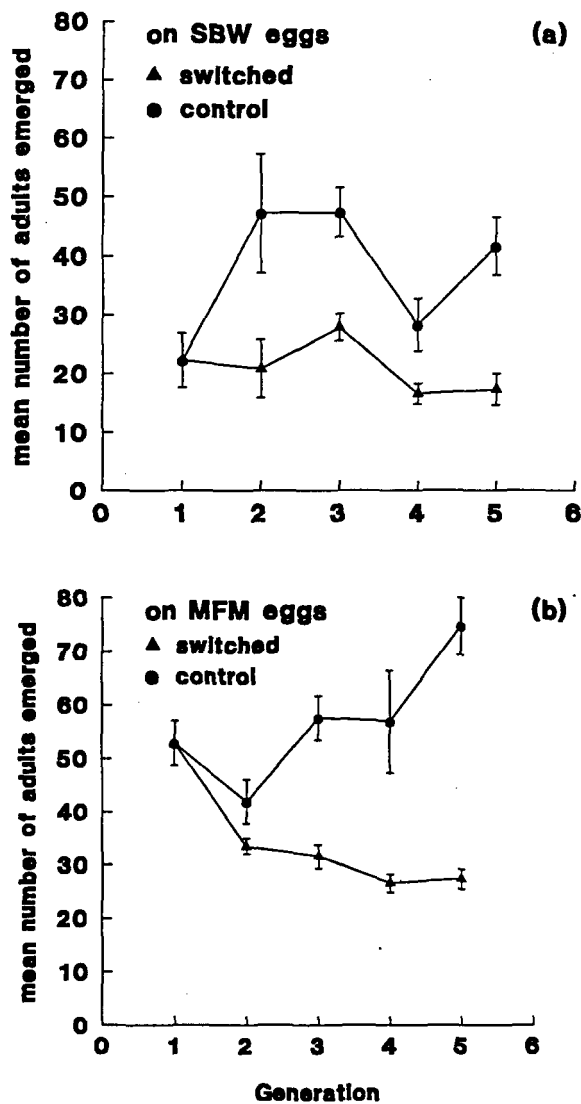


FIGURE 1. Comparison of mean realized fecundity and SE when attacking (a) SBW eggs and (b) MFM eggs for parasitoids that (1) started on SBW eggs and were switched for four generations to rearing on MFM eggs (\blacktriangle) or (2) parasitoids that were left on SBW eggs for five generations (control lines, \bullet). See Table 1 for range of sample sizes.

DISCUSSION

Host acceptance and realized fecundity for *T. brassicae* reared continuously on a factitious host have been shown to decline when the parasitoid is exposed to the target host, in the field (Bigler *et al.*, 1982, Bergeijk *et al.*, 1989). To compensate, *T. brassicae* are transferred from a larger target host, *O. nubilalis*, to a smaller factitious host (MFM) for mass rearing, for no more than five generations before field releases against the target host (Bigler, 1986). This situation is analogous to experiment 1, switching the SBW-tn line to rearing on MFM eggs and then testing them against SBW eggs at generation 5 (Figure 1(a)). As in the *T. brassicae* system (Bergeijk

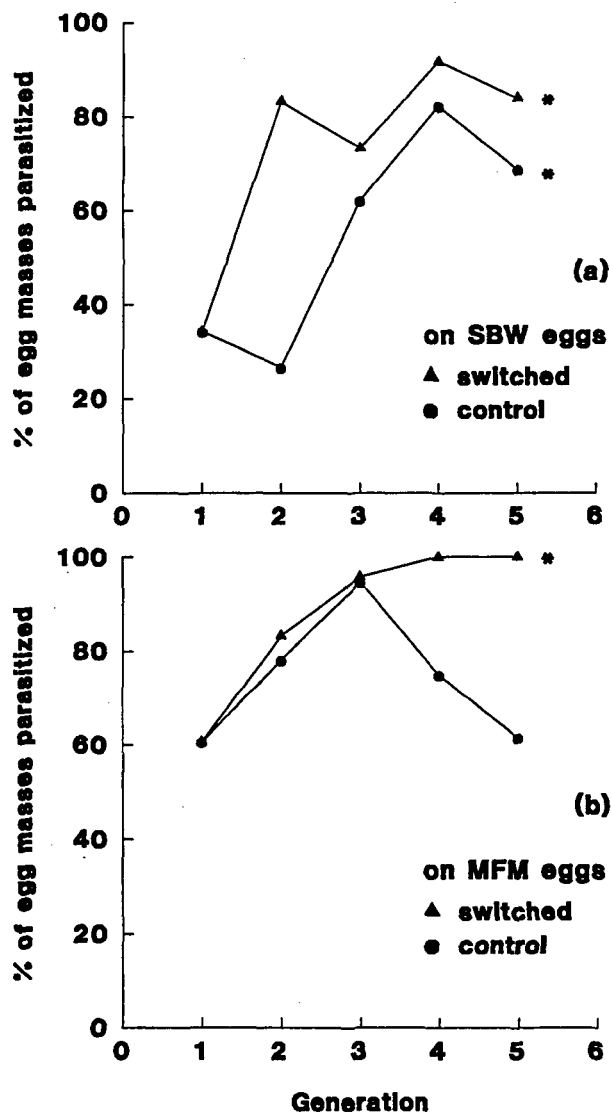


FIGURE 2. Comparison of the percentage of (a) SBW eggs and (b) MFM eggs accepted by parasitoids that (1) started on SBW eggs and were switched for four generations to rearing on MFM eggs (\blacktriangle) or (2) parasitoids that were left on SBW eggs for five generations (control lines, \bullet). (* indicates rearing line where host acceptance at generation 5 was significantly different from host acceptance at generation 1; G statistic, Sokal & Rohlf (1981, $P < 0.05$).

et al., 1989), there was no effect on host acceptance of the target host at generation 5 for parasitoids which had been switched to the factitious rearing host (Figure 2(a), comparison of host acceptance by treatment relative to the control line). There was, however, a significant reduction in the realized fecundity of the parasitoids reared on the factitious host, when attacking the target host eggs (SBW; Figure 1(a); switched line at generations 1 and 5 versus control at generations 1 and 5).

Bigler *et al.* (1982) also examined the effect of host switching on the fecundity and walking speed of parasitoids that had been reared on a factitious host (MFM) for 110 generations.

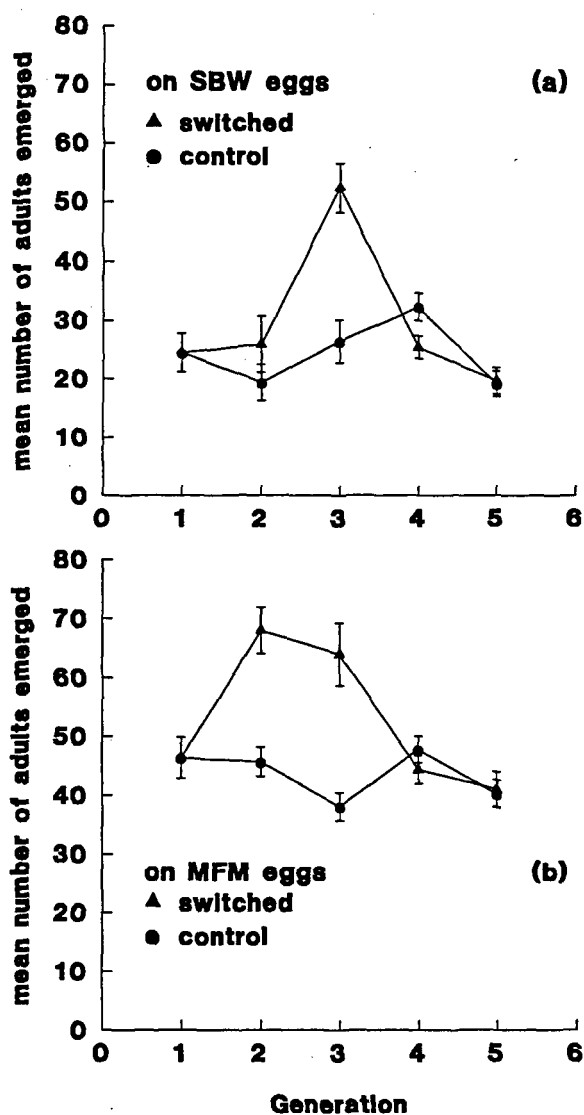


FIGURE 3. Comparison of the mean realized fecundity and SE on (a) SBW eggs and (b) MFM eggs for parasitoids that (1) started on MFM eggs and were switched for two generations to rearing on SBW eggs and then switched back for two generations to MFM eggs (▲) or (2) parasitoids that were left on MFM eggs for five generations (control lines, ●). See Table 1 for range of sample sizes.

Parasitoids were switched to rearing on the target host (*O. nubilalis*) for 12 generations and then were returned to rearing on the factitious host. This situation is analogous to our experiment 2 where we switched MFM-tm to SBW eggs for two generations and then returned them to rearing on the factitious host for two generations. Bigler *et al.* (1982) found that the realized fecundity of parasitoids attacking *O. nubilalis* increased when they were reared on *O. nubilalis* and that realized fecundity on *O. nubilalis* declined, with the return to the factitious host rearing. Similarly, with *T. minutum* in experiment 2, parasitoid fecundity on the SBW eggs was improved within two generations of the switch to rearing on SBW eggs; however, this improvement in

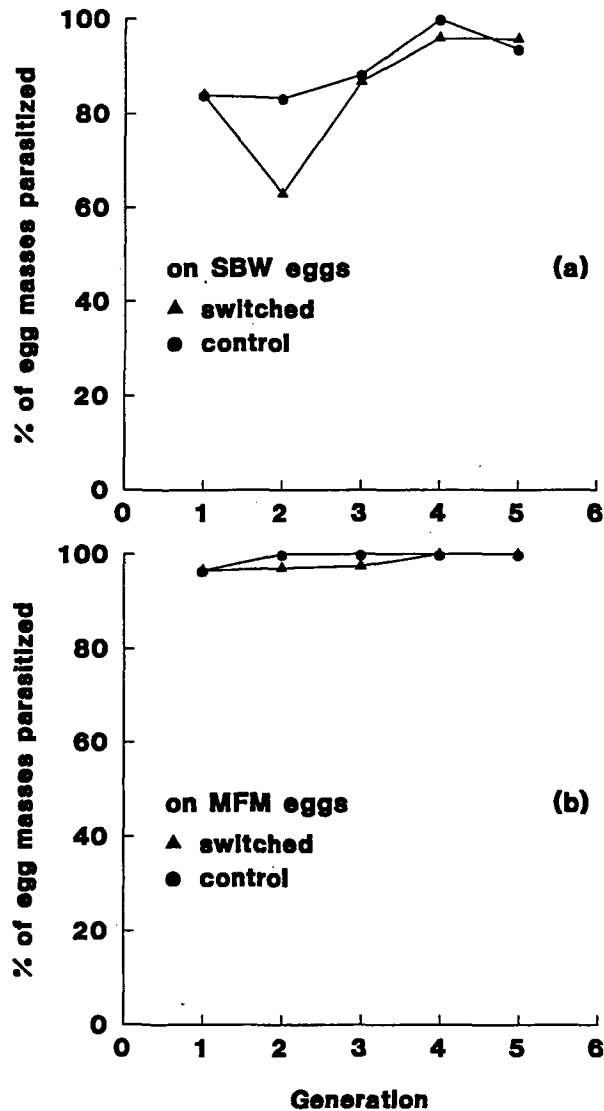


FIGURE 4. Comparison of percentage of (a) SBW eggs and (b) MFM eggs accepted by parasitoids that (1) started on MFM eggs and were switched for two generations to rearing on SBW eggs and then switched back for two generations to MFM eggs (\blacktriangle) or (2) parasitoids that were left on MFM eggs for five generations (control lines, \bullet). (Host acceptance at generation 5 was not significantly different from host acceptance at generation 1 for either host species; G statistic, Sokal & Rohlf (1981, $P > 0.05$.)

fecundity disappeared immediately when parasitoids were returned to rearing on the factitious host (MFM). It is not possible to maintain the improvements in realized fecundity for *T. minutum* associated host switching to larger rearing hosts because of the close relationship between parasitoid size and host egg size (Marston & Ertle, 1973; Southard *et al.*, 1982; Bourchier *et al.*, 1993).

Bigler *et al.* (1982) found that by using host switching it was possible to maintain parasitoid walking speed which was later shown to be an important characteristic of parasitoid quality for *T. brassicae* (Bigler *et al.*, 1988). The improved performance by parasitoids as a result of the host

switching may result from the selection for movement that occurs during the *O. nubilalis* rearing under semi-field conditions, rather than an increased affinity for the target host. Walking speed has not been assessed as a quality criteria for *T. minutum*; if it is a good predictor of *T. minutum* quality, then selection for movement during rearing and or host switching may become a useful mass-rearing technique for *T. minutum*. There is currently no benefit of host switching for *T. minutum* rearing on the basis of changes in realized fecundity or host acceptance by the parasitoids.

Host switching from SBW eggs is a fundamental characteristic of natural populations of *T. minutum* (Houseweart *et al.*, 1984). Parasitoids that have been in long-term mass-rearing programmes often experience inadvertent selection (Hopper *et al.*, 1993). In *Trichogramma* rearing programmes, there may be selection for large, fast laying individuals, that are effective attacking a relatively homogeneous substrate, MFM eggs. The ability to respond to host eggs of different sizes, shapes or qualities may be lost in these rearing programmes. Parasitoids that originate from SBW eggs may be better equipped to deal with variable host eggs because of the inherent variation in size and shape of SBW egg masses. These parasitoids had higher fecundities, but with more variation on both MFM and SBW eggs than parasitoids reared on MFM eggs (Figure 1(a) and (b)). In a worst-case scenario, parasitoids from SBW will always perform as well as parasitoids from MFM, but there will also be cases where SBW-tm will perform far better because of their ability to take advantage of variable host eggs. Selection for host-switching capability or for variation in the response to host eggs may result in higher realized fecundities in the field, because, to be effective, parasitoids, such as *T. minutum*, must function in a variable environment.

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