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Influence of environmental conditions and parasitoid quality on field performance of *Trichogramma minutum*

R. S. Bourchier[1] & S. M. Smith[2]
[1]*Canadian Forest Service, Sault Ste. Marie, P.O. Box 490, Sault Ste. Marie, Ontario, Canada P6A 5M7*
[2]*Faculty of Forestry, University of Toronto, Toronto, Ontario, Canada M5S 3B3*

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Abstract

The effects of weather conditions and two parasitoid quality attributes, realized fecundity and host acceptance, were assessed on the field efficacy of mass-released *Trichogramma minutum.* Temperature was the most important single variable, explaining up to 75% of the variation in field parasitism. There were significant positive relationships between both the sum of the maximum temperatures and the number of degree-hours above a 15 °C threshold, accumulated in the three days following the release, and parasitism in the field. There was a significant negative relationship between the mean relative humidity and the odds of parasitism in the field. Quality parameters based on parasitoid biology were not effective for predicting field efficacy if poor weather conditions persisted after a release. If weather conditions were 'good' (i.e. accumulated maximum temperatures above 62 °C, in the 3 days following the release), then parameters such as release rate and fecundity in the lab were useful predictors of field performance. There was no relationship between host acceptance measured in the lab and field parasitism. Given the importance of field temperatures for field performance, selection for cold tolerance of *T. minutum* would be desirable.

Introduction

There are a number of factors that will influence the success of an inundative release program using an egg parasitoid such as *Trichogramma minutum* Riley. Two critical factors are the environmental conditions into which parasitoids are released and the biological attributes of the parasitoids being released. The influence of environmental conditions on insect biology has been well recognized (Wellington & Trimble, 1984). For *Trichogramma* spp. the influence of environmental factors has been most intensively studied in the laboratory. Researchers have been interested in the influence of temperature on parasitoid attributes, such as longevity, fecundity, emergence, parasitoid sex ratio and host acceptance (Pak & Oatman, 1982; Russo & Voegelé, 1982; Calvin et al., 1984; Pak & van Heiningen, 1985; Smith & Hubbes, 1986; Cabello & Vargas, 1988; Gross, 1988; Gou, 1988; Pavlik, 1992, Bourchier et al., 1993). These laboratory experiments are valuable in that they allow us to understand the results of field programs, however, few studies have examined the activity of parasitoids under actual field conditions. In the boreal forest of northern countries like Canada, where optimal weather conditions may be limited (e.g. temperatures tend to be low even during the summer), it is essential to determine under what specific environmental conditions releases are worth doing, and if done, what is their probability of success.

Biological attributes (e.g. parasitoid quality; see Bigler, 1994) directly influence the ability of a parasitoid to follow the sequence of events required for successful parasitism, (Doutt, 1959; Vinson & Iwantsch, 1980). Bigler et al. (1988) conducted one of the few experiments linking quality attributes to field efficacy. Using *Trichogramma brassicae*, they demonstrated that parasitoids which walked slowly were also poor at parasitizing hosts in the field. Cerutti & Bigler (1991) examined other biological attributes of *T. brassicae* and developed an index for predicting its field efficacy in corn. Similar information to predict field efficacy in forests, where the spatial and environmental conditions are very different from agricultural crops is required.

In this study we examined the effect of weather and two quality parameters (realized fecundity and host acceptance) on field performance of *Trichogramma minutum*. Our first objective was to quantify the effects of environmental factors on parasitoid efficacy and to identify the trade-offs between releasing parasitoids under poor conditions or delaying the release. Our second objective was to assess the utility of using the 'parasitoid quality' measures (Bigler, 1989) of realized fecundity and host acceptance to predict field performance for *Trichogramma minutum*.

Materials and methods

Parasitoid material. Five parasitoid lines of *T. minutum* were used for field releases, providing a range of parasitoid qualities (based on realized fecundity; Bigler, 1994) to test the sensitivity of the laboratory assays for predicting field efficacy. Fecundity estimates for lines 1–4 were obtained in 1992, prior to field release experiments, after a minimum of 45 generations of laboratory rearing; the fecundity estimate for line 5 comes from Bourchier et al. (1994). Line 1 originated from spruce budworm (SBW), *Choristoneura fumiferana* (Clemens) egg masses collected in Quetico Provincial Park, Ontario, Canada, (48 °7′N, 91 °1′W) during July, 1988. This line was maintained in a mass production facility (CIBA-Biologicals, Guelph, Ontario) on the Mediterranean flour moth (MFM), *Ephestia kuehniella* Zell., for approximately 100 generations (mean fecundity on MFM eggs during rearing, 88.4 ± 8.9 eggs per female). Lines 2–4 were collected from SBW egg masses near Dryden, Ontario (49°5′ N, 92°5′ W) during, 1990 (line 2), 1988 (line 3), and, 1991 (line 4); lines were reared in the laboratory for between 40 and 75 generations on MFM eggs. Line 2 had high fecundity attacking MFM eggs (190.7 ± 14.1 eggs/female), Line 3 had low fecundity (79.6 ± 5.9 eggs/female), and Line 4 had an average fecundity (135.1 ± 10.7 eggs/female). Line 5 was collected from SBW egg masses at the same time and location as Line 4, but was reared in the laboratory on SBW eggs rather than MFM eggs, for approximately 24 generations (mean realized fecundity when tested on MFM eggs, was a maximum of 74.7 ± 5.3 wasps emerged per female, see Bourchier et al., 1994). Parasitoids collected in 1988 and 1990 were all identified as *T. minutum* Riley by J. Pinto and G. Platner (University California, Riverside) and voucher specimens of both years have been deposited with the Royal Ontario Museum, Toronto, Ontario, Canada.

Field efficacy. Nineteen separate release trials were conducted during the summer of 1992 in a white spruce (*Picea glauca* (Moench) Voss) plantation near Vermilion Bay, Canada (49°6′ N, 93°6′ W). Trees in the stand were planted in the late 1970's and had a mean height of 5.9 ± 0.1 m (mean ± SE).

Release design. The experimental design was such that two parasitoid lines were tested on each release date, pairs were: 1) Line 1, half of which were provided with honey as newly-emerged adults in the release vials and half of which were unfed; 2) Lines 2 and 3; or 3) Lines 4 and 5. One of these three pairs was released for each trial (total, 19 trials), such that pair 1 was replicated 4 times, pair 2 was replicated 8 times and pair 3 was replicated 7 times. This replication over the summer resulted in parasitoids of differing qualities being released under a range of environmental conditions. All parasitoids excluding the fed portion of Line 1 were released without food.

Thirty release stations were established in the plantation at the start of the summer. Stations were located 25 m apart, and consisted of a central release tree and eight trees closest to the central tree (mean distance from the central tree ± SE; 2.2 ± 0.1 m). Parasitoids were released in either parasitized SBW or MFM eggs glued to white cards. Release cards were placed in an open glass vial (95×25 mm) which was then set inside a 10-cm square plastic flower pot. The pot was tied 60 cm above the ground to a bamboo stake and the stake sprayed with Stickum^R to prevent predation by ants. The stake was placed in the ground at the base of the central release tree.

During each trial, parasitoids were released at four stations (two stations for each parasitoid line tested) while three stations were left as controls. The four release stations were randomly selected from the 30 possible stations set up at the beginning of the summer. Parasitoids were not released at the control stations in order to monitor background populations of *T. minutum*, either native or from previous releases.

Release rates. Release rates were estimated by measuring the emergence of sub-samples of material placed at each station. The estimate for parasitoids emerging from SBW egg masses was based on the mean emergence of female parasitoids from between 25 and 30 egg masses. Mean emergence per egg mass was then multiplied by the number of parasitized budworm egg masses placed at each station to obtain the station estimate. The estimate for parasitoids emerging from MFM eggs was based on the mean female emergence from ten cards (0.5 × 1.0 cm) that had been cut from each of the larger release cards placed at the stations. For tests involving environmental variables, release rates and parasitism were summed for all treatment stations (i.e. four stations) to avoid pseudo-replicating under specific environmental conditions (mean release rate ± SE; 10111 ± 1578 females per release date). For regressions involving host acceptance and realized fecundity, release rates and parasitism were summed for the stations where the same treatment was released on the same date (e.g. the number of parasitoids from a given line released at 2 stations; mean release rate ± SE; 5828 ± 1263 females per treatment). Release rates were log-transformed when used in regression models to linearize the relationship between release rates and parasitism.

Assessment of efficacy. Field performance of the parasitoids was assessed by counting the number of sentinel SBW egg masses that were attacked (based on the presence/absence of black eggs) at each station. Sentinel egg masses consisted of SBW egg masses laid on balsam fir foliage which were placed in the field on the morning of the release day (Smith et al., 1986; Wallace & Smith, 1995 for photos). A total of 28 egg masses were placed at each treatment station for each release; 16 sentinels attached to the eight trees surrounding the release tree and 12 sentinels on the central release tree. Sentinel egg masses were attached to rope pulleys, as in Wallace & Smith (1995), using one pulley on each surrounding tree (two sentinels per pulley: one at the top and one 1 m above ground), and four pulleys for each central release tree (three sentinels per pulley: one at the top, one in the middle, and one 1 m above ground). Each of the four pulleys on the central tree was placed in one of the cardinal directions. Control trees only had pulleys on the central tree for a total of 12 egg masses. Sentinel egg masses were collected three days after the release and placed in gel caps to assess parasitism (number of black SBW eggs) and emergence.

Environmental conditions. Temperature, relative humidity, rainfall, wind speed and wind direction were measured in the release plots for the entire summer, using a Campbell CR21× data logger connected to a 207 combined temperature and RH probe, a TB3 rain bucket, and a RM Young wind monitor probe. Measurements were taken each minute and mean or total values were calculated each hour. Weather data for the three days after each release were used to match environmental conditions with the periods when sentinel egg masses were in the field.

Parasitoid quality. Parasitoid quality was assessed by measuring the biological parameters of host acceptance and realized fecundity (Bourchier et al., 1993). For both parameters, a sub-sample of 40 female parasitoids from each of the two parasitoid lines was selected prior to release. Females were unfed (except for fed individuals from pair 1) and between three and six h old at the time of both tests.

Host acceptance assay. Female parasitoids were placed individually in 60 × 15 mm glass vials with a single SBW egg mass. Their behaviour was checked every 5 min during a 2-h observational period and they were scored as being either on or off the egg mass. The proportion of time spent on the egg mass was calculated by dividing the total number of times the female was observed on the egg mass during the 2-h assay by 25 (the maximum number of times that a female could be observed on the egg mass in two hours). Bourchier et al. (1993) demonstrated that host acceptance, measured using this type of assay, could be used to predict the realized fecundity of females in vials. The assay allows prediction of realized fecundity at the time of oviposition, rather than waiting for parasitoids to emerge.

Realized fecundity. A single female parasitoid was placed in a 60 × 15 mm glass vial with a SBW egg mass containing 15–20 eggs. Egg masses were laid on a balsam fir needle that was glued to a 20 × 10 mm paper card and inserted into the vial. The number of black eggs and the lifetime realized fecundity of the female parasitoids (the number of progeny that survived to emerge as adults) was counted after all emerged parasitoids had died. Parental females dying in the first 24 h were omitted from the analysis.

Statistical analysis. Temperature effects were assessed using maximum temperatures and degree hours. Maximum temperatures were summed for the 3 days following the release. Accumulated degree-hours for a release were calculated by summing the number of degrees above a threshold of 15 °C (DH15) for each hour of the 3-day period following the release. This threshold was selected because Forsse et al. (1992) showed that *Trichogramma* do not fly below this temperature; thereby limiting their ability to disperse and parasitize host eggs.

Relative humidity and wind speed were assessed by computing mean values over the 3-day period following the release. Wind speed was also assessed by summing the wind speeds measured for each hour over the 3 days following the release to calculate a total accumulated wind speed as a measure of wind activity. Total rainfall was summed over the 3-day period following the release. Field parasitism was expressed as an odds ratio calculated by taking the log of the ratio between the number of sentinel egg masses parasitized and the number of sentinel egg masses not parasitized (Crawley, 1993). Total maximum temperatures, accumulated degree-hours, mean relative humidity, total rainfall, mean wind speed and total accumulated wind speed were related to this odds ratio using simple linear regressions and a stepwise multiple-regression procedure in the MGLH module of Systat. Because the release rate of parasitoids could not be held constant, its importance as a predictor of field efficacy under the differing environmental conditions was tested by adding it as a second variable to each of the simple regressions and including it in the multiple-regression procedure.

Host acceptance and realized fecundity for each line were tested to see if they were useful predictors of field efficacy. The mean number of eggs parasitized and progeny emerged, or the mean % of time spent on an egg mass during the host acceptance assay were compared to odds ratios of parasitism, for each parasitoid line in the field.

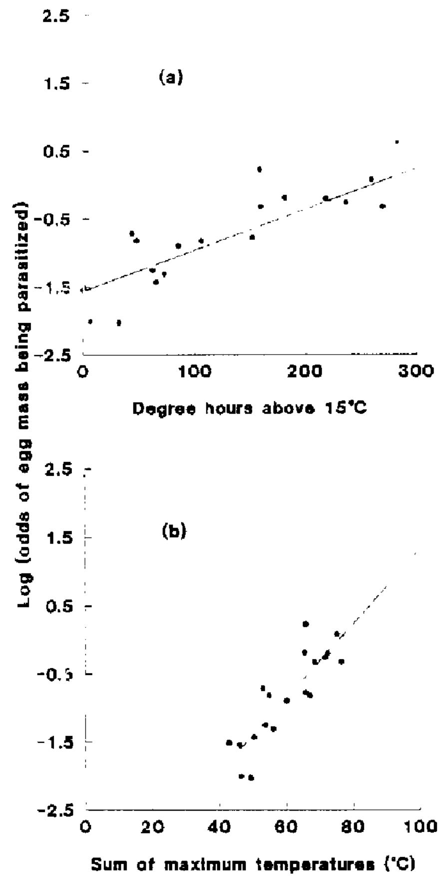

Figure 1. Temperature measurements and odds of parasitism in the field: (a) Relationship between the number of hours above 15 °C in the 3 days following a release and the log (odds of parasitism) of spruce budworm egg masses in the field ($Y = -1.56 + 0.006X$; $R^2 = 0.71$; $P < 0.001$; $N = 19$); (b) Relationship between the sum of the maximum temperatures for the 3 days following a release and the log (odds of parasitism) of spruce budworm egg masses in the field ($Y = -4.1 + 0.054X$; $R^2 = 0.75$; $P < 0.001$; $N = 19$).

Results

SBW sentinel egg masses placed at control trees were not attacked in 15 of the 19 field trials. There were negligible background levels of parasitism by *Trichogramma* in four trials; parasitism was 1.3% of the available egg masses at the control trees.

Environmental conditions. Temperature and relative humidity had significant effects on the odds of parasitism of sentinel egg masses in the field (Table 1). There were significant positive relationships between both the sum of the maximum temperatures and the number of degree-hours accumulated above a 15 °C threshold in the 3 days following the release and parasitism in the field (Table 1; Figure 1a, b). There was a significant negative relationship between the odds of parasitism in the field and the mean relative humidity during the 3 days following the release (Table 1; Figure 2). Given the relationship with relative humidity, it was not surprising that there was also a significant negative relationship between total rainfall and the odds of parasitism (Table 1). A comparison of total rainfall vs. mean relative humidity on a per day basis indicated that rainfall did not occur below a mean r.h. of 85%.

Table 1 Relationships between environmental variables and the odds of parasitism when *Trichogramma minutum* was released in the boreal forest

Independent variables	Equation	P-value	R^2
Degree hours (DH)	$Y^a = -1.562 + 0.006$ DH	<0.001	0.71
Maximum temperature (MT)	$Y = -4.101 + 0.054$ MT	<0.001	0.75
Relative humidity (RH)	$Y = 5.96 - 0.078$ RH	<0.001	0.54
Total rainfall (RAIN)	$Y = -0.595 - 0.018$ RAIN	0.011	0.33
Log (release rate) (RR)	NS	NS	
Degree hours + RR	$Y = -3.18 + 0.006$ DH $+ 0.49$ RR	<0.001	0.76
Maximum temperature + RR	$Y = -5.38 + 0.053$ MT $+ 0.35$ RR	<0.001	0.77
Relative humidity + RR	$Y = 5.227 - 0.076$ RH $+ 0.49$ RR	<0.001	0.54
Mean wind speed (WS)	NS	NS	
Total wind speed (TWS)	NS	NS	
MT + RH (stepwise)[b]	$Y = -0.61 + 0.04$ MT $- 0.03$ RH	<0.001	0.80

[a] Y = odds ratio for parasitism in the field; log(number of available egg masses parasitized/number of available egg masses not parasitized); sample size for all regressions was 19.
[b] This regression is the best-fit model using a stepwise regression procedure. The factors tested for the model were MT, RH, RR, RAIN and WS

Table 2. Relationships between realized fecundity on spruce budworm egg masses and the odds of parasitism when *Trichogramma minutum* was released in the boreal forest under 'good'[a] weather conditions

Independent variables	Equation	P-value	R^2
Realized fecundity in the lab: # of host eggs parasitized (BEGGS)	$Y^b = -1.716 + 0.145$ BEGGS[c]	0.003	0.60
Realized fecundity in the lab: # of wasps ex from black eggs (WASP)	$Y = -1.183 + 0.04$ WASP	0.012	0.49
Log(release rate)(RR). for stations where fecundity estimates were available	$Y = -4.259 + 1.104$ RR	0.006	0.41
BEGGS + RR	$Y = -1.961 + 0.137$ BEGGS $+ 0.089$ RR	0.016	0.60
WASP + RR	$Y = -1.821 + 0.034$ WASP $+ 0.215$ RR	0.048	0.49

[a] Only trials where the median value for the sum of the maximum temperatures, for the 3 days following each release was above 62°C and stations within these trials for which lab fecundity estimates were available were used thus n = 12.
[b] Y = odds ratio for parasitism in the field: log(number of available egg masses parasitized/number of available egg masses not parasitized).
[c] This regression is the best-fit model using a stepwise regression procedure The components tested for the model were BEGGS, RR and host acceptance.

There were no relationships between the odds of parasitism and wind speed, accumulated wind speed and the release rate of females. Adding the release rate into the temperature and RH regressions as a second predictor improved the fit marginally, but release-rate coefficients for all regressions were non-significant (Table 1). The best-fit model using the stepwise regression procedure testing the variables, maximum temperature, relative humidity, rainfall, wind speed and release rate was the model that included maximum temperature and relative humidity (Table 1). The fit of the multiple-regression model ($R^2 = 0.80$) was slightly better than the simple regression involving maximum temperature (Table 1).

Parasitoid quality. There was no relationship between the parasitoid quality parameters (realized fecundity and host acceptance) and the odds of parasitism when data under all weather conditions were included. To remove the effects of 'poor' weather, we selected those trials for which the sum of the maximum temperatures for the 3 days following each release was above the median value (i.e. above 62 °C).

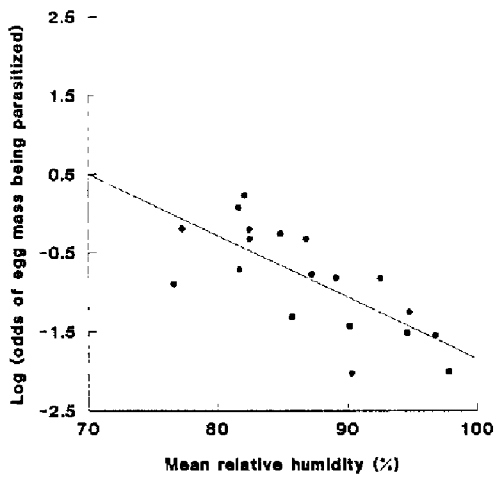

Figure 2. Relationship between the mean relative humidity for the 3 days following a release and the log (odds of parasitism) of spruce budworm egg masses in the field ($Y = 5.96 - 0.078X$; $R^2 = 0.54$; $P < 0.001$; $N = 19$).

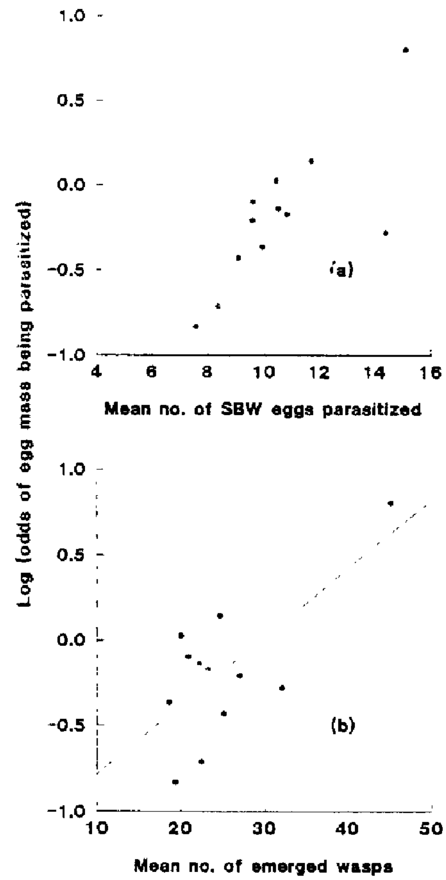

Figure 3. Fecundity measurements in the lab and odds of parasitism in the field: (a) Relationship between the number of spruce budworm eggs parasitized in the laboratory and the log (odds of parasitism) of spruce budworm egg masses in the field ($Y = -1.72 + 0.145X$; $R^2 = 0.60$; $P = 0.003$; $N = 12$); (b) Relationship between the number of wasps emerging from parasitized spruce budworm eggs in the laboratory and the log (odds of parasitism) of spruce budworm egg masses in the field ($Y = -1.18 + 0.04X$; $R^2 = 0.49$; $P = 0.012$; $N = 12$).

Considering only these 'good' weather trials, there was no relationship between the amount of time spent on the egg mass during the lab host-acceptance assay and the odds of parasitism in the field. There was however, a significant positive relationship between the number of SBW eggs parasitized in the vials and odds of parasitism in the field (Figure 3a; Table 2). There was also a positive linear relationship between the mean number of wasps emerging from a SBW egg mass in the laboratory and the odds of parasitism in the field (Figure 3b; Table 2). The odds of parasitism also increased with release rate, however the R^2 for this regression was lower than for those involving black eggs or wasp emergence (Table 2). Adding release rate as a predictor to the fecundity regressions did not improve the fit of either the black eggs or wasp emergence models (see R^2; Table 2). The best-fit model using the stepwise regression procedure testing the variables black host eggs, release rate and host acceptance was the simple regression model for black eggs (Table 2).

Discussion

In our field trials, temperature and relative humidity were the only environmental variables that influenced the odds of parasitism in a predictable way. These field results are not surprising because other researchers have found that temperature influences the activity of *Trichogramma* spp. in the lab (Biever, 1972; Boldt, 1974; Kot, 1979; Forsse et al., 1992) and that free water reduces parasitoid survival (Gross, 1988). Our experiments with *T. minutum* are the first to quantify these effects under field conditions and provide insight into the efficacy of inundative releases using hymenopterous parasitoids.

Temperature, expressed as either the sum of the maximum temperatures for the 3 days following the release or as the number of degree hours above 15 °C, was a good predictor of the odds of parasitism. These relationships support field observations of poor success with releases made during inclement weather (Parker et al., 1971; Remund & Bigler, 1986; Smith et al., 1986, 1990). Releases conducted below the median of the sum of the maximum temperatures of 62 °C, resulted in a mean parasitism of 5.8% (n = 10), whereas for releases above the median, the mean parasitism was 36.7% (n = 9). From an applied perspective, any reductions in release rates that may result from holding parasitoids for a few days to avoid 'poor' conditions, can now be compared to the loss in field efficacy, if parasitoids are actually released under those conditions. Given that mean temperatures for over half of the releases between 20 June and 31 August, 1992 were below 15 °C, a cold tolerant strain of *T. minutum* would be desirable for use in the boreal forest.

Bigler et al. (1988) demonstrated a positive relationship between walking speed and parasitism by *T. brassicae* in the field. Our observation of reduced parasitism during low temperature periods in the field (Figure 1) combined with previous associations of low temperatures and poor activity (Biever, 1972; Boldt, 1974; Forsse et al., 1992), suggest that walking speed may also be a good predictor of field efficacy for *T. minutum*.

Higher humidity was associated with reduced odds of parasitism in the field (Figure 2). Mean humidities above 85% represent periods of rainfall, and this impedes the movement of small parasitoids such as *Trichogramma*, either in flight or on leaf surfaces (Kot, 1979; Keller et al., 1985). Reduced activity results in reduced parasitism (Boldt, 1974; Keller et al., 1985; Gross, 1988) and this suggests that parasitoids should not be released if significant rainfall is forecast in the 3 days following release.

Fecundity is one of the most commonly cited indicators of parasitoid quality because it is an easy parameter to measure (Bigler, 1994). Screening for quality control usually takes place at rearing facilities and the majority of fecundity tests are conducted in vials (Cerutti & Bigler, 1991; Bourchier et al., 1993) or at best, in slightly larger arenas (Thorpe & Dively, 1985). Our observed relationship between realized fecundity in vials and the number of egg masses parasitized in the field (Figure 3a, b) confirms the usefulness of fecundity, as a quality measure for *Trichogramma* rearing facilities. We observed a better fit between black eggs and egg masses parasitized in the field ($R^2 = 0.60$) than between emerged parasitoids and egg masses parasitized in the field ($R^2 = 0.49$) because the latter had the added variance resulting from: 1) multiple parasitoids emerging from a single black egg; and 2) additional mortality of parasitoids occurring between the pupal and adult stage of the parasitoid (Marston & Ertle, 1973; Bourchier et al., 1993). The relationship between black eggs and egg masses parasitized in the field, relates a measure of host suitability for pupation (i.e. as indicated by black eggs) with field efficacy, whereas the relationship between emerged parasitoids and egg masses parasitized in the field, relates a measure of host suitability for adult emergence to field efficacy.

The prediction of field performance of *T. minutum* is a two-tiered process. Although temperature is correlated with a number of other weather conditions, our data indicate that 75% of the variation in parasitism can be explained by temperature alone. Both the release rate of parasitoids and their quality is irrelevant if poor weather conditions, as indicated by low temperatures, persist after a release. If weather conditions are 'good' (accumulated maximum temperatures are above 62 °C in the 3 days following the release) then biological parameters, such as release rate and fecundity in the lab are useful predictors of field performance. The move to standardize biological parameters for other lines of mass-reared parasitoids (Bigler, 1994) will also be useful for *T. minutum* rearing programs. It appears however that prediction of the field performance of *T. minutum* depends first on environmental factors, and that for ultimate success with this parasitoid, we should examine selection for cold tolerance.

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