Biocontrol Science and Technology (2000) 10, 3–13

Measurement and Selection of Parasitoid Quality for Mass-Reared *Trichogramma minutum* Riley Used in Inundative Release

FU-HUA LIU AND S. M. SMITH

Faculty of Forestry, University of Toronto, 33 Willcocks St, Toronto, Ontario, Canada M5S 3B3

(*Received for publication 9 October 1998; revised manuscript accepted 27 August 1999*)

Parasitoid quality, subject to both genetic and environmental influences, is critical to the success of any biological control program, however, its measurement and improvement is poorly understood. In this study, a classic genetic approach is taken to develop two indices, namely a character index and a fitness index, for the measurement and selection of high quality parasitoids used in inundative release. Six life-history traits and corresponding fitness components in 33 inbred strains of Trichogramma minutum *were used to generate both genotypic and phenotypic variance–covariance matrices that then allowed for the construction of the indices. Most traits and their fitness components were positively correlated, both phenotypically and genotypically, with lifetime fecundity and the number of female offspring appearing to have an important influence. Selection of the top three strains showed that parasitoid quality could be improved by 36% using the character index and possibly up to 150% using the fitness index. The two indices were linearly correlated suggesting that either could be used to measure quality. The character index is recommended because it requires information on only three life-history traits (fecundity, number of female offspring, and number of male offspring) and has highly correlated responses of fitness components. Our work demonstrates that the best quality* T. minutum *will be obtained by using the character index to select for inbred strains which have high fecundity and number of female offspring.*

Keywords: Trichogramma minutum, *quantitative genetics, parasitoid quality, character index, fitness index*

INTRODUCTION

Parasitoid quality has been widely recognized as a key factor in the success of any biological control program (Bigler, 1994). Considerable effort has been made to develop techniques for maintaining parasitoid quality during mass-production and inundative release based only on phenotypic measurements (Greenberg, 1991; Cerutti & Bigler, 1995; Smith, 1996).

Correspondence to Fu-Hua Liu. Tel: +1 416 978-0879; E-mail: liu.fuhua@utoronto.ca

ISSN 0958-3157 (print)/ISSN 1360-0478 (online)/00/010003-11

Because quality has a genetic base as well as an environmental influence, a better technique, which can measure the phenotype and quantify the genetic contribution, would be more informative. Quantitative genetics, used classically in breeding studies, can achieve this, but has not yet been applied to a parasitoid system.

While parasitoid quality is defined as the performance of a parasitoid in its intended role after release into the field, it is not clear which biological trait or traits are the best to make this prediction (Bigler, 1994; Smith, 1996). Some researchers have suggested female body size as a useful predictor but this is still controversial (Bigler, 1994). Bigler *et al*. (1991) proposed that a few simple life-history traits, such as the number of parasitized eggs or deformed individuals, parasitoid emergence, sex ratio, longevity, and activity, be used to estimate quality during commercial production. A few other studies have attempted to combine several traits into a single quality index to predict field performance (Greenberg, 1991; Cerutti & Bigler, 1995). To date, an organism's fitness has not been used as a measure of its quality even though Falconer (1989) considered that fitness directly reflected the possible field performance of an organism.

Fitness is defined as the probability of an organism to survive and reproduce and is highly correlated with life-history traits (Charlesworth, 1984). In fact, a single life-history trait or character itself can sometimes be considered as a measure of fitness and can be expressed as a simple character index (Hughes, 1995). However, fitness is usually best estimated by measuring a number of specific fitness components (traits), then using these components to derive a genetic variance–covariance matrix and finally, condensing this information into a single fitness index (Lin, 1978; Nordskog, 1978). When very low or zero, such an index predicts poor parasitoid quality (poor survival or reproduction). This type of fitness index can provide a better measure of quality than current indices because both independent and correlative contributions of all measured fitness components are taken into account. Nordskog (1978) and other applied geneticists have termed such character and fitness indices as performance indices.

Performance indices can be used to select for desirable traits and genetically improve organisms (Young, 1961). While genetic improvement can be achieved in classic breeding programs by focusing on either individuals, families or strains, the index approach is the most efficient (Finney, 1962) because it makes use of the basic genotypic and phenotypic variation within a species to achieve the best selection criteria.

Phenotypic variation has been well documented between and within many parasitoid species, such as *Trichogramma*, but very little is known about their genetic variation (Wajnberg, 1994; Smith, 1996). Our study attempts to measure the genetic variation and correlation found in selected biological traits of the egg parasitoid, *T. minutum* Riley, to derive and compare performance indices which can then be used to selectively improve the quality of parasitoids for inundative release.

MATERIALS AND METHODS

Parasitoid Material

Thirty-three inbred strains of *T. minutum* were established from parasitized spruce budworm, *Choristoneura fumiferana* (Clemens), eggs. The strains were collected in northwestern Ontario, Canada (approx. 45–50°N; 62–96°W) during 1988, 1990 and 1992 (Table 1). The number of initial egg masses for each strain varied and no known gene flow or overlap in generations occurred during the rearing process. Factitious host eggs of the Mediterranean flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), were used for rearing and all experimentation. At the time of the experiment, strains 1–15 had been cultured for 140 generations, strains 21–35 for 94 generations; and strains 36, 37, and 44, for 43 generations. Each strain had a similar population size (approximately 2000–5000 individuals) in each generation.

TABLE 1. Strain al means for six life-history traits and performance indices in 33 inbred strains of *T. minutum* Riley reared at 25 C, RH = 75% and L:D = 16:8

	Life-history trait							Index[a]		
Strain	No.[b] eggs	Longevity (days)	Fecundity (parasitism)	Emergence (adult %)	No. females	No. males	Sex ratio (female %)	I_a	I'_a	I_b
1	2	3.4	62.4	85.0	26.1	25.8	49.1	7.2	6.9	0.04
2	5	4.0	66.5	84.4	30.6	25.3	54.6	7.2	7.7	0.02
3	3	6.8	80.5	80.5	37.5	25.7	60.7	8.3	9.2	0.22
4	1	5.7	64.0	85.4	24.7	29.0	46.1	7.7	6.8	0.27
5	—	7.9	80.1	83.4	32.7	33.1	51.3	9.2	8.6	0.48
6	2	5.2	73.5	84.5	33.5	27.8	53.8	7.9	8.3	0.18
7	—	6.5	79.9	80.4	31.6	30.5	51.6	9.1	8.4	0.38
8	3	6.0	66.1	82.2	30.9	23.0	56.2	6.9	7.7	0.11
9	1	4.2	64.5	76.8	28.2	21.4	56.7	6.9	7.3	−0.04
10	5	5.6	52.9	81.9	19.4	20.8	45.9	6.3	5.6	0.14
11	1	9.6	108.0	78.4	51.4	34.0	61.8	10.9	12.2	0.68
12	1	5.1	78.5	79.7	35.7	26.4	57.8	8.3	8.9	0.15
13	3	7.8	89.6	85.9	41.8	35.4	54.0	9.7	10.1	0.52
14	3	6.3	71.1	81.6	30.1	26.9	55.1	7.9	7.9	0.20
15	1	7.0	77.5	82.7	33.0	30.5	52.5	8.7	8.5	0.37
16	6	7.2	84.6	80.9	36.9	30.1	56.2	9.1	9.3	0.38
17	1	5.2	86.6	81.4	36.4	32.7	52.0	9.7	9.3	0.36
18	1	6.9	97.4	89.8	45.5	35.1	58.4	10.2	10.9	0.47
19	1	8.2	83.3	83.4	34.7	33.8	51.8	9.5	8.9	0.52
20	1	7.4	103.3	82.6	45.8	38.6	53.7	11.2	11.2	0.65
21	1	6.6	57.7	84.5	24.4	24.1	49.6	6.6	6.5	0.19
22	2	6.6	64.6	80.3	27.5	24.8	51.9	7.2	7.2	0.21
23	5	6.1	73.6	79.2	26.0	31.0	49.3	8.9	7.5	0.32
24	5	6.9	74.9	84.2	29.6	32.2	48.6	8.8	7.9	0.41
25	5	5.6	72.6	81.9	30.6	28.8	52.3	8.2	7.9	0.23
26	5	11.0	84.5	85.4	34.3	38.3	48.6	9.9	9.0	0.80
27	5	4.8	62.9	81.2	26.3	23.6	52.2	7.0	7.0	0.07
28	10	5.8	79.9	83.4	35.9	31.1	50.9	8.7	8.9	0.36
29	27	6.2	86.1	81.8	41.7	27.8	58.4	8.7	9.9	0.29
30	69	4.9	58.9	81.3	22.5	25.2	45.5	7.0	6.3	0.17
31	1	7.0	85.2	80.9	30.8	37.4	47.1	10.4	8.6	0.55
32	1	5.6	75.3	83.9	30.4	31.5	49.7	8.8	8.0	0.31
33	5	9.0	117.0	79.2	40.8	52.9	44.3	14.5	11.3	1.08
Grand means		6.4	77.8	82.4	32.9	30.1	52.1	8.7	8.5	0.34
$Pr(< W)$[c]		0.28	0.18	0.87	0.61	0.01	0.79	—	—	—

[a] Two indices (I_a, I'_a) were character indices [$I_a = -1.15$ longevity (L) + 12.23 fecundity (F) + 3.17 emergence (E) − 10.00 no. females (Fem) + 7.90 no. males (M) + 31.80 sex ratio (S) and $I'_a = 5.32F + 10.57\ Fem + 1.64S$]; the third ($I_b$) was fitness component index ($I_b = 0.41L + 0.84F + 0.11E - 1.02S$).

[b] The number of original egg masses used to establish each strain.

[c] Probability that the trait means of the 33 strains were normally distributed (Shapiro–Wilk test).

Experimental Design

The following six life-history traits were selected to measure because of their importance in overall fitness and their practical value for assessing parasitoid quality in commercial production: longevity, lifetime fecundity, emergence, number of females, number of males, and sex ratio of the offspring. Twenty virgin females and 20 virgin males were taken randomly from each of the 33 strains and allowed to mate in a single pair within each strain. Each of the mating pairs was placed in a glass vial (3.5 × 1.2 cm), fed a 50 : 50 honey : water solution, supplied with an egg card containing about 200 host eggs and reared at 25°C, 65% relative humidity (RH) and a photoperiod of 16 L : 8 D. The egg card was replaced every two days until the female died.

For each strain, five vials (one mating pair/vial) were placed in a Petri dish and considered as a group for selection by strain. This provided a completely random design with 132 groups in total (four dishes/strain for 33 strains) and allowed variance and covariance to be estimated by strainal mean. Fecundity (the number of parasitized host eggs per female, alternatively termed parasitism) and adult female longevity were recorded every two days. After emergence of the offspring, the number of females, the number of males, and sex ratio of the offspring (percentage of females per brood) were determined.

Data Analyses

All data analyses were performed using either SAS Version 6.03 (1988) or SAS/IML Version 6 (1990). The 33 strainal means were calculated for each trait and their normality was tested using a Shapiro–Wilk statistic (Table 1). Bartlett's method was used to test the homogeneity of variance for the group means within the 33 strains. Because the variances were not homogeneous, natural logarithms were used to transform adult female longevity ($df = 32$, $\chi^2 = 29.04$, $P > 0.10$), fecundity ($df = 32$, $\chi^2 = 38.11$, $P > 0.50$), and the number of males ($df = 32$, $\chi^2 = 20.37$, $P > 0.05$), square roots were used to transform the number of females ($df = 32$, $\chi^2 = 37.44$, $P > 0.25$) and sex ratio of the offspring ($df = 32$, $\chi^2 = 23.85$, $P > 0.10$), and arcsine was used to transform emergence ($df = 32$, $\chi^2 = 21.17$, $P > 0.10$). The normality was not tested for each strain because analysis of variance is robust for homogeneous variance or critical α values (Anderson & McLean, 1974).

The strainal means (transformed data) were used to calculate the genetic variance (V_g) for each trait by equating estimated mean squares between the 33 strains to their corresponding expected mean squares (in a one-way ANOVA). The broad-sense heritability (h^2 = variability) for each of the six traits was then estimated to measure the genetic variability of that trait. The fitness component of a trait was calculated by dividing each observation by the grand mean (for the 33 strains; shown by trait in Table 1). The Shapiro–Wilk statistic was again applied to test the normality of these fitness components. The genetic variance and heritability were then calculated for each fitness component as described previously.

The strainal means were also used to calculate the genetic covariance for each pair of traits (Kempthorne, 1957) in order to derive the genotypic correlation coefficients. These were then examined to determine whether they differed significantly from zero (T-test; Rosner, 1990).

Character and fitness component indices were constructed on the strainal means and their genetic variance and covariance according to the least-square regression method (Smith, 1936; Hazel, 1943). Both indices required the economic weight of each trait to be estimated. Economic weights for the character index were derived from principle component analysis (PCA) (Jacquard, 1974) using the correlation coefficient matrix calculated above. These weights were 0.09 for adult female longevity, 11.29 for fecundity, 0.01 for emergence, 5.39 for the number of females, 1.91 for the number of males, and 0.03 for the sex ratio of the offspring. For the fitness component index, the economic weights for each trait were not calculated, but instead considered equal [1, 1, 1, 1, 1, 1] as there was no evidence to rank one fitness component over another. Because little information was available on the true cost/benefit of any particular trait in commercial production, these economic weights should actually be considered pseudo-economic weights (Rouvier, 1969).

The relative importance of each trait in both indices was examined in the same way; by estimating the correlation coefficient (R^2_{IH}) between the aggregate breeding value (H) and the index (I) (Lin, 1978). Nordskog (1978) showed that R^2_{IH} is equal to the heritability of the index when the index is considered to be a performance index, as in this case. This meant that the indices could be used to measure parasitoid quality because they functioned as heritable traits. The character and fitness component indices were then compared to each other by regressing the latter on the former to determine whether they were linearly related and thus, whether a single index could be used to measure parasitoid quality.

The quantitative approach of Falconer (1989) was used to determine whether the indices

could be used to improve parasitoid quality. The three best strains of parasitoids were selected with both indices. The realized response for each index was then calculated from the difference between the grand means and the newly selected mean of the three strains divided by the grand mean for each trait. The expected response was estimated by multiplying the difference between the grand mean and selected mean for each trait with the heritability (h^2) for that trait (Lin, 1978). Improvement in a trait was considered to be a percentage of the realized response divided by the grand mean. Standard errors of the strainal means before and after selection were then estimated as described by Pesek and Baker (1970) to justify whether the difference between expected and realized responses was due to a random error. Finally, the correlated response (CR) for each trait was calculated by multiplying the difference between the selected and grand means for that trait with its heritability and genetic correlation coefficient (Falconer, 1989). This was then divided by the grand mean to obtain the percentage correlated improvement for each trait.

RESULTS

Genetic Variation

The 33 strains varied in their mean values for the six selected traits (Table 1). Fecundity had the highest genetic variance ($V_g = 11.42$), followed by the number of males, and the number of females (Table 2). Because of the calculation process, the genetic variance of the sex ratio was so low that it was in fact negative; in quantitative terms, this can be considered zero. Genetic variabilities of the group means over the 33 strains, as measured by the broad-sense heritabilities (h^2), was classified as high, moderate, and low (Table 2). Those traits with high variability were female longevity (0.81), life-time fecundity (0.79), and the number of female offspring (0.83). Such traits have a high degree of genetic determination and can be improved through selection. The number of male offspring (0.66) was of moderate variability, implying that this trait was more influenced by environmental factors than the previous three. The sex ratio of the offspring (-0.27, which was considered zero) had the lowest variability followed by emergence (0.34), suggesting that these two traits were highly affected by environmental factors and would be difficult to improve through selection.

Fitness components were normally distributed ($n = 132$) for five of the six traits; female longevity ($P = 0.275$), fecundity ($P = 0.183$), the number of female offspring ($P = 0.595$), emergence ($P = 0.870$), and the sex ratio of the offspring ($P = 0.787$). Only the number of male offspring was not normally distributed ($P = 0.010$). This suggested that a fitness component index could be constructed through regression analysis on all the fitness components (Smith, 1936; Hazel, 1943).

The genetic variance and heritability of the fitness components were very low ($V_g \approx 0$ to

TABLE 2. Genetic variances (V_g)[a] and broad-sense heritabilities (h^2) of six life-history traits and corresponding fitness components in 33 inbred strains of *T. minutum*

	Life-history trait		Fitness component	
	Genetic variance	Heritability	Genetic variance	Heritability
Longevity (days)	2.13	0.81	0.010	0.040
Fecundity (parasitism)	11.42	0.79	0.006	0.039
Emergence (adult %)	0.95	0.34	0.000	0.000
No. of females	4.89	0.83	0.008	0.041
No. of males	5.06	0.66	0.006	0.034
Sex ratio (female %)	0(−0.53)	0(−0.27)	0.001	0.032
Mean	3.99	0.67	0.005	0.031

[a] $V_g = (MS_s - MS_e)/4$, where MS_s and MS_e were mean squares for strain and error, respectively, and derived from the one-way ANOVA table in Appendix 1, and 4 = the number of replications.

0.01, $h^2 \approx 0$ to 0.04) (Table 3). The number of female offspring had the highest heritability ($h^2 = 0.041$), followed by adult female longevity ($h^2 = 0.040$) and fecundity ($h^2 = 0.039$), indicating that these three fitness components could be improved through selection easier than those with lower heritabilities.

Phenotypic and Genotypic Correlations

In general, the six life-history traits studied in *T. minutum* were both phenotypically and genetically correlated (Table 3). Of the 15 possible phenotypic relationships, only three were not significantly correlated: (1) adult female longevity and sex ratio of the offspring; (2) fecundity and emergence; and (3) emergence and the number of females. This was the same for the 15 possible genotypic relationships, with the addition of the number of males and the sex ratio of the offspring, which were also not correlated. Both had a single common negative correlation coefficient (e.g. emergence and sex ratio of the offspring), but in addition, the phenotypic correlation between the number of males and sex ratio of the offspring was also negative. The 10 positively correlated genotypic coefficients suggest that selection for one trait will automatically improve the other while the sole negative correlation between emergence and sex ratio of the offspring suggests that improving either of these traits will reduce the other.

All genotypic correlation coefficients for the fitness components were lower than their corresponding life-history coefficients, except for one (the number of males and sex ratio) (Table 3). This suggests that the relationship between the fitness components was weaker than that between their corresponding life-history traits. Six of the 15 phenotypic correlation coefficients among the fitness components were almost double that of their corresponding genotypic correlation coefficients (Table 3). This indicates that the adaptability of such traits is affected synergistically by both genetic and environmental factors with the environment playing an important role. There was a single negative correlation coefficient for fitness components in each of the genotypic (longevity and sex ratio) and phenotypic (number of males and sex ratio of the offspring) analyses (Table 3).

Measurement of Parasitoid Quality

The character index (I_a) derived from the regression analysis included all six life-history traits such that: $I_a = -1.15$ longevity (L) + 12.23 fecundity (F) + 3.17 emergence (E) − 10.00 no. of female offspring (Fem) + 7.90 no. of male offspring (M) + 31.80 sex ratio (S). Values for each strain were divided by 100 and are shown in Table 1. According to this index, strain 33 was the best, followed, respectively, by strains 20, 11, 31, and 18.

The correlation coefficient (R^2_{IH}) between this I_a and the aggregate breeding value (H) was 0.84. When both fecundity and the number of female offspring were removed from the equation, the (R^2_{IH}) decreased to 0.75. Removal of any other traits (one or two simultaneously) from the equation retained (R^2_{IH}) at 0.83. This suggests that fecundity and the number of female offspring both play an important role in the character index and must be included whenever it is used to measure parasitoid quality. In fact, similar values for the index could be obtained using $I'_a = 5.32F + 10.57Fem + 1.64S$, wherein ($R^2_{IH}$) was 0.83 (Table 1). This means that measuring fecundity, the number of female offspring, and the number of male offspring is sufficient to evaluate parasitoid performance.

When all six fitness components were incorporated into a fitness component index ($I_b = 1.45L + 2.11F + 16.90Fem - 15.38M - 0.88E - 37.13S$), the correlation coefficient was very poor ($R^2_{IH} = 0.26$). R^2_{IH} was increased when either the number of male offspring, the number of female offspring, or the sex ratio of the offspring were removed from the equation. R^2_{IH} was the highest (0.85) when both the number of female and male offspring were simultaneously removed, suggesting that these components both lowered the efficiency of this index. Thus, the fitness component index that best measured parasitoid quality included adult female longevity, fecundity, emergence, and sex ratio of the offspring ($I_b = 0.41L + 0.84F + 0.11E - 1.02S$).

TABLE 3. Genotypic (below the diagonal) and phenotypic (above the diagonal) correlation coefficients of six life-history traits and their corresponding fitness components for 33 inbred strains of *T. minutum*

	Life-history trait						Fitness component					
	Longevity	Fecundity	Emergence	No. females	No. males	Sex ratio	Longevity	Fecundity	Emergence	No. females	No. males	Sex ratio
Longevity	—	0.65***	0.17***	0.52***	0.68***	−0.08	—	0.648***	0.003	0.526***	0.657***	0.016
Fecundity	0.60***[a]	—	0.00	0.90***	0.85***	0.17***	0.333***	—	0.000	0.901***	0.854***	0.263***
Emergence	0.44***	0.09	—	0.07	0.21***	−0.16***	0.000	0.000	—	0.049	0.101	0.000
No. females	0.52***	0.95***	−0.03	—	0.58***	0.55***	0.281***	0.710***	0.000	—	0.584***	0.599***
No. males	0.68***	0.86***	0.43***	0.67***	—	−0.34***	0.328***	0.483***	0.000	0.339***	—	−0.240***
Sex ratio	−0.06	0.40***	−0.56***	0.65***	−0.11	—	−0.403***	0.010	0.000	0.281***	0.775***	—

[a] The correlation coefficient differed significantly from zero at $\alpha < 0.05$ (*T*-test; Rosner, 1990).

Strains 33, 26, 11, 20, and 31 were ranked the best as identified by I_b; similar to those determined by either I_a or I'_a except for strain 26. This suggests that the character index may be linearly associated with the fitness component index. Regressing I_a on I_b showed $I_b = -0.83 + 0.13\ I_a$ wherein both the intercept ($T = -9.6$, $P = 0.0001$) and slope ($T = 13.8$, $P = 0.0001$) were significantly different from zero. This confirms that I_a was indeed linearly associated with I_b and that either index could measure parasitoid quality.

Selection for Parasitoid Quality

According to the simplest character index (I'_a), the best three strains in decreasing order were Strains 11, 20, and 33 (Table 1). The realized response achieved when these strains were selected differed from the expected response; this difference is due to random error because the difference was less than two standard errors of the strainal means before and after selection (Table 4). Four traits were improved positively through selection with I'_a; adult female longevity (35.9%), fecundity (40.6%), the number of female offspring (38.9%), and the number of male offspring (38.9%) (Table 4). Selection by this index improved the sex ratio of the offspring by only 2.3% whereas it reduced emergence by 2.8%. Improvement in CR of the fitness components for these traits was 35.0% for adult female longevity, 40.0% for fecundity, −15.2% for emergence, 39.7% for the number of male offspring, 33.6% for the number of female offspring, and 1.6% for the sex ratio of the offspring (Table 4).

The fitness component index (I_b) showed that strains 11, 26, and 33 had the greatest parasitoid quality in decreasing order (Table 1). Selection with this index improved adult female longevity by 55.3%, fecundity by 33.3%, the number of female offspring by 28.0%, the number of male offspring by 38.4%, and the sex ratio of the offspring by 1.4%, while it reduced emergence 1.7% (Table 4). A large part of these responses may not be real, however, because the difference between the two (expected and realized) was beyond two standard errors of the strainal means (Table 4). This large amount of error was not unexpected

TABLE 4. Responses of six life-history traits and their fitness components as well as indices when the top three strains [selection intensity = 9% (3/33 strains)] were selected using the simplest character index (I'_a) or the fitness component index (I_b) for 33 inbred strains of *T. minutum*

Statistic	Strain selected	Longevity (days)	Fecundity (parasitism)	Emergence (adult %)	No. females	No. males	Sex ratio (female %)	Index (I'_a)
Selection by character index (I'_a)								
	11	9.6	108.0	78.4	51.4	34.0	61.8	12.2
	20	7.4	103.3	82.6	45.8	38.6	53.7	11.2
	33	9.0	117.0	79.2	40.8	52.9	44.3	11.3
Expected response	—	2.8	24.5	0.1	7.6	6.5	1.3	—
Realized response	—	2.3	31.6	−2.3	13.1	11.7	1.2	3.1
Improvement (%)	—	35.9	40.6	−2.8	39.8	38.9	2.3	36.1
2 SE[a]	—	1.6	14.0	2.4	6.8	6.0	4.1	—
Correlated response[b]	—	35.0	40.0	−15.2	39.7	33.6	1.6	—
Selection by fitness component index (I_b)								(I_b)
	11	1.500	1.399	0.957	1.559	1.129	1.190	0.7
	26	1.781	1.087	1.042	1.040	1.271	0.936	0.8
	33	1.406	1.511	0.967	1.239	1.753	0.853	1.1
Expected response	—	0.038	0.029	−0.003	—	—	−0.007	—
Realized response	—	0.556	0.333	−0.017	0.280	0.384	−0.015	0.5
Improvement (%)	—	55.271	33.260	−1.655	27.985	38.388	1.439	154.9
2 SE[a]	—	0.302	0.224	0.038	0.256	0.247	0.098	—
Correlated response[b]	—	54.211	32.602	−1.704	28.173	38.642	−1.023	—

[a] 2 SE was two standard errors estimated using a formula developed by Pesek & Baker (1970).
[b] Correlated response of selecting with each index.

because the genetic variance for the fitness component analysis was also low (Table 2). If we take a conservative approach, this error could be estimated as the difference in improvement (%) between the two indices for each life-history trait. This ranged from approximately 0 to 20% depending on the trait, with longevity being the largest. The improvement in the correlated response of the six life-history traits was 54.2% for adult female longevity, 32.6% for fecundity, −1.7% for emergence, 28.2% for the number of female offspring, 38.6% for the number of male offspring, and −1.0% for the sex ratio of the offspring.

When the fitness component index was used to select the top three strains, parasitoid quality was improved by 154.9% (Table 4). This was almost four times that achieved when the top three strains were selected using the simplest character index (36%). As above, a large part of this improvement in the fitness component index may be erroneous because of the low genetic variation for the fitness components and thus, the character index may be the most predictable (Table 2).

DISCUSSION

Our quantitative analysis suggests that there is significant genetic variation in a number of life-history traits for *T. minutum*. The average genetic variability (heritability) for six traits among the 33 strains studied here was 66.7%. In particular, we found lifetime fecundity and the number of female offspring to both have high levels of genetic variance and heritability suggesting that these traits have a strong genetic component and can be improved through selection. Very little previous research has examined this genetic aspect in *Trichogramma*, or other parasitoids in general (Antolin, 1992; Liu, 1998). Using four *RAPD*-DNA and two specific DNA markers, Sappal *et al.* (1994) found the average variability for 15 strains of *T. minutum* at the molecular level was 24%. Unfortunately, this molecular approach cannot be compared directly to our quantitative study.

Genetic variation in the fitness components of the life-history traits, as opposed to the actual traits themselves, in *T. minutum* was very low (mean = 0.005). This is not unexpected as fitness components are highly dependent on a given set of environmental conditions (Merrell, 1981). Because our experimental conditions were relatively stable (e.g. in terms of temperature, host conditions, length of time in culture, and population size/interactions), the fitness-related genes we measured may not have been fully expressed and therefore, we were unable to detect much variation. The fitness components we derived, however, were generally continuous, meaning that a fitness index could be constructed to predict parasitoid quality and allow for improved selection.

We found that most of the six life-history traits and their respective fitness components we examined for *T. minutum* were correlated. Chassain and Boulètreau (1991) reported that fecundity in *T. brassicae* Bezdenko and *T. cacoeciae* Marchal was not significantly correlated with the sex ratio of their progeny, however, they did not distinguish between phenotypic or genotypic correlation. The positive genotypic correlation between fecundity and sex ratio of the offspring that we estimated is similar to Antolin's (1992) findings on the same traits in *Muscidifurax raptor* Gir. & Sand. Many of the traits we examined were positively correlated which means that selection for one will improve the other. However, comparison between genotypic correlations and their corresponding phenotypic correlations (especially for fitness components) suggests that the environment plays an important role in at least six of these relationships, including fecundity and the number of female offspring. This means that selecting on the basis of a given phenotype does not always improve the corresponding genotype of such traits and thus, an index is needed to integrate all of these life-history traits and fitness component values to improve parasitoid quality.

Our approach develops two performance indices which predict parasitoid quality in *T. minutum* with a relatively high degree of accuracy ($R^2 = 0.83$–0.85). Both indices incorporate a genetic component and can be calculated by estimating as few as three to four

variables based on commonly measured life-history traits. A few other indices have been proposed to measure parasitoid quality in *Trichogramma* species focusing on phenotypic relationships such as female body size and parasitoid quality (Greenberg, 1991; Bigler, 1994). In contrast, we emphasize the genetic basis of quality which allows more reliable predictions about field performance. Because of this genetic approach, our indices can be used to improve the quality of parasitoids without collecting data from field trials on individual traits. This general approach can be used to examine other traits that might be important to quality, such as walking speed and flight or host-searching ability, or applied to other parasitoid species with little modification.

Both indices were suitable for predicting parasitoid quality because they were linearly related to each other (Hughes, 1995). If they had not been positively correlated, then the fitness component index would have been preferred over the character index because it represents possible future fitness in a broader sense and therefore can best reflect field performance. In fact, our work suggests that the character index is the better choice here because it requires fewer life-history traits to be measured (fecundity, number of female offspring, and number of male offspring) with effectively the same accuracy and has highly correlated responses of fitness components. Thus, we recommend its use when trying to improve the quality of mass-reared *T. minutum*.

Our work suggests that the best quality of parasitoids will be obtained by selecting and rearing those of high fecundity and number of female offspring in inbred strains. While such inbreeding has often been associated with inbreeding depression or the reduction in fecundity, longevity and environmental adaptability for diploid organisms (Falconer, 1989) and some haplodiploid species, such as the honeybee (Brückler, 1978), recent studies suggest that it is unlikely to be a problem in *Trichogramma* species (Sorati *et al.*, 1996; Liu, 1998). Similarly, this approach can only achieve those genetic responses predetermined by the original base population from which the strains are selected. Thus, as expected, the widest possible genetic pool is recommended as a starting point for selection of any given trait and if improvement beyond this is required, then selective crossings must be considered.

APPENDIX 1. One-way analysis of variance for six lifehistory traits in *T. minutum* and their corresponding fitness components

			Character				Fitness component			
Trait	Source	df	*SS*	*MS*	*F*	*pr* > *F*	*SS*	*MS*	*F*	*pr* > *F*
Longevity	Strain	32	288.63	9.02	18.05	0.0001	8.96	0.28	1.17	0.3506
	Error	99	49.46	0.50			23.76	0.24		
	Total	131	338.09				32.72			
Fecundity	Strain	32	1558.90	48.72	16.05	0.0001	5.50	0.17	1.16	0.3509
	Error	99	300.53	3.04			14.63	0.15		
	Total	131	1859.44				20.13			
Emergence	Strain	32	180.61	5.64	3.06	0.0001	45.72	1.43	1.00	0.3957
	Error	99	182.57	1.84			141.43	1.43		
	Total	131	363.18				187.15			
No. females	Strain	32	657.97	20.56	20.53	0.0001	7.01	0.22	1.17	0.3506
	Error	99	99.16	1.00			18.52	0.19		
	Total	131	757.13				25.53			
No. males	Strain	32	731.09	22.85	8.76	0.0001	6.22	0.19	1.14	0.3511
	Error	99	258.06	2.61			16.88	0.17		
	Total	131	989.16				23.10			
Sex ratio	Strain	32	12.79	0.40	0.16	0.8835	1.10	0.03	1.13	0.3527
	Error	99	249.46	2.52			2.99	0.03		
	Total	131	262.25				4.09			

ACKNOWLEDGEMENTS

We thank Dr K. Ritland for his valuable suggestions and comments on an earlier draft of the manuscript. This work was supported by NSERC and the Premier's Council Technology Fund through CIBA-Geigy Canada.

REFERENCES

Anderson, V.L. & McLean, R.A. (1974) *Design of Experiments: A Realistic Approach*. Marcel Dekker, New York.

Antolin, M.F. (1992) Sex ratio variation in a parasitic wasp. I. Reaction norms. *Evolution* **A46,** 1496–1510.

Bigler, F. (1994) Quality control in *Trichogramma* population, in *Biological Control with Egg Parasitoids* (Wajnberg, E. & Hassan, S.A., Eds). Biddles, Guildford & King's Lynn, pp. 93–112.

Bigler, F., Cerutti, F. & Laing, J. (1991) First draft of criteria for quality control (product control) of *Trichogramma*, in *Proceedings of Fifth Workshop of the IOBC Global Working Group—Quality Control of Mass Reared Arthropods* (Bigler, F. & Wageningen, N.L., Eds) pp. 200–201.

Brückner, D. (1978) Why are there inbreeding effects in haplo-diploid system? *Evolution* **32,** 456–458.

Cerutti, F. & Bigler, F. (1995) Quality assessment of Trichogramma brassicae in the laboratory. *Entomologia Experimentalis et Applicata* **75,** 19–26.

Chassain, C. & Boulètreau, M. (1991) Genetic variability in quantitative traits of host exploitation in *Trichogramma. Genetica* **83,** 195–202.

Charlesworth, B. (1984) The evolutionary genetics of life histories, in *Evolutionary Ecology* (Shorrocks, B., Ed.). Blackwell, Oxford, pp. 117–133.

Falconer, D.S. (1989) *Introduction to Quantitative Genetics*, 3rd edn. Longman Scientific & Technical, John Wiley & Sons, New York.

Finney, D.J. (1962) Genetic gains under three methods of selection. *Genetic Research* **3,** 417–423.

Greenberg, S.M. (1991) Evaluation techniques for *Trichogramma* quality, in *Proceedings of Fifth Workshop of the IOBC Global Working Group—Quality Control of Mass Reared Arthropods* (Bigler, F., Ed.). Swiss Federal Research Station for Agronomy, Reckenholz, pp. 138–145.

Hazel, L.N. (1943) The genetic basis for constructing selection indices. *Genetics* **42**, 421–432.

Hughes, K.A. (1995) The evolutionary genetics of male lifehistory characters in *Drosophila melanogaster. Evolution* **49,** 521–537.

Jacquard, A. (1974) The genetic structure of populations, in *Biomathematics*, Vol. 5. Springer-Verlag, Berlin, pp. 420–493.

Kempthorne, O. (1957) *An Introduction to Statistical Genetics*. John Wiley, New York; Chapman & Hall, London.

Lin, C.Y. (1978) Index selection for genetic improvement of quantitative characters. *Theoretical and Applied Genetics* **52,** 49–56.

Liu, F. (1998) *Quantitative Genetics of Male-Haploid Organisms Used for Biological Control*. PhD dissertation, University of Toronto, Canada.

Merrell, D.J. (1981) *Ecological Genetics*. University of Minnesota Press, Minneapolis.

Nordskog, A.W. (1978) Some statistical properties of an index of multiple traits. *Theoretical and Applied Genetics* **52,** 91–94.

Pesek, J. & Baker, R.J. (1970) An application of index selection to the improvement of self-pollinated species. *Canadian Journal of Plant Science* **50,** 267–276.

Rosner, B. (1990) *Fundamentals of Biostatistics*. PWS-Kent Publishing Company, Boston.

Rouvier, R. (1969) Ponderation des valeurs genotypiques dans la selection par index sur plusieurs caractères. *Biometrics* **25,** 295–307.

Sappal, N.P. (1994) Some Characteristics of the Genome Structure of Trichogramma. MScF Thesis, Faculty of Forestry, University of Toronto, pp. 51–74.

SAS 6.03 version (1988) *SAS/STAT User's Guide*. SAS Institute, Cary, USA.

SAS/IML software (1990) *Version 6*, 1st edn. SAS Institute, Cary, USA.

Smith, H.F. (1936) A discrimination function for plant selection. *Annual Eugenics (London)* **7,** 240–250.

Smith, S.M. (1996) Biological control with *Trichogramma*: advances, successes, and potential of their use in biological control. *Annual Review of Entomology*, **41,** 375–406.

Sorati, M., Newman, M. & Hoffman, A.A. (1996) Inbreeding and incompatibility in *Trichogramma* nr. *brassicae*: evidence and implications for quality control. *Entomologia Experimentalis et Applicata* **78,** 283–290.

Wajnberg, E. (1994) Intra-population genetic variation in *Trichogramma*, in *Biological Control with Egg Parasitoids* (Wajnberg, E. & Hassan, S.A., Eds) Biddles Ltd, Guildford & King's Lynn, pp. 245–272.

Young, S.S.Y. (1961) A further examination of the relative efficiency of three methods of selection for genetic gains under less restricted conditions. *Genetics Research* **2,** 106–121.