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Scope for genetic enhancement of the parasitisation potential of four native strains of *Trichogrammatoidea* sp. nr. *lutea* Girault (Hymenoptera: Trichogrammatidae) in Kenya

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Abstract

In response to emerging interest in commercial mass production of *Trichogramma* for *Helicoverpa armigera* biocontrol in eastern Africa, laboratory experiments were undertaken to assess the scope for genetic enhancement of the parasitisation potential of native strains of the local common trichogrammatid species, *Trichogrammatoidea* sp. nr. *lutea*. Four promising strains (ex-Kilifi – Kilifi District, ex-Kwa Chai – Kibwezi District, ex-Rarieda – Bondo District and ex-Ebuhayi, Kakamega District) were tested for cross-mating in reciprocal combinations with focus on fecundity and progeny female ratio. While all the crosses resulted in F1 progeny of both sexes, significant differences were observed between homogamic and reciprocal heterogamic crosses in fecundity, progeny production, proportion of female progeny and adult longevity. Among all the crosses, the cross between ex-Rarieda strain females and ex-Kilifi strain males resulted in progeny that was significantly superior in fecundity and progeny female ratio. Conversely, Kilifi strain females crossed to males from ex-Rarieda strain gave rise to progeny with relatively low fecundity and female ratio. There were significant differences between homogamic crosses and most reciprocal heterogamic crosses in the major biological attributes. Genotypic and phenotypic variance-covariance matrices generated for six life-history traits showed high positive correlations for most traits in both inbred ($P < 0.05$) and reciprocal heterogamic crosses ($P < 0.05$ and $P < 0.001$). Fecundity and number of female offspring were the most important factors in the heterogamic crosses. The results confirmed the scope for genetic enhancement through inter-strain crossing for improving the field impact potential of *T.* sp. nr. *lutea* being targeted for commercial mass production.

Keywords: *Biological control*, *Trichogrammatoidea* sp. nr. *lutea*, *cross-mating*, *genetic enhancement*

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Introduction

The importance of intra-specific variability among hymenopterous parasitoids in improving their biocontrol impact potential has been well recognised (Hopper et al. 1993). There is good scope for development of distinct strains in *Trichogramma*, because of the tendency in this genus for sibmating in isolated populations (Smith & Hubbes 1986a,b). Intra-specific genetic variability in trichogrammatid strains is an important consideration in selecting for and/or enhancing their adaptation and performance attributes (Pak & Van Lenteren 1986; Hassan 1988, 1990, 1994). Natural variability between populations (strains or ecotypes) has been linked to their effectiveness in the field (Kot 1968, 1979; Diehl & Bush 1984; Li Ying 1984). Hassan (1994) pointed out the need for selecting and utilising appropriate strains and to evolve methods for rearing them, towards ensuring success in the augmentative biocontrol with native trichogrammatid egg parasitoids.

The earliest report on intra-species differences in *Trichogramma* was by Flanders (1930), distinguishing 'yellow race' from 'grey race' in *T. minutum* Riley, while Harland and Atteck (1933) conducted the earliest breeding experiments in *Trichogramma*, among strains (races) of *T. minutum* in the West Indies. Partial or even complete reproductive isolation may occur between strains of the same species as a result of differences in ecological and nutrition factors (Huo et al. 1988). Ashley et al. (1974) carried out selection and hybridisation of *Trichogramma*, while Ram and Sharma (1977) demonstrated the importance of selective breeding for improving the fecundity and sex ratio of *T. fasciatum* (Perkins). Similar studies were conducted by Nargakatti and Nagaraja (1978) on laboratory reared and wild-type *T. confusum* Viggiani strains. Improving the life history traits and host acceptance among strains is possible with artificial selection, as suggested by Chassin and Bouletreau (1991) and Pavlik (1993). Wajnberg (1994) has comprehensively assessed the strategies to utilise genetic differences in biological attributes among trichogrammatids at intra-species level.

T. sp. nr. lutea Girault (Hymenoptera:Trichogrammatidae) are a common species occurring on *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) in Kenya, some what more abundantly in low (0–700 m a.s.l.) and mid-altitudes (701–1200 m a.s.l.), than high altitudes (above 1200 m a.s.l.) (Baya et al. 2002). Kalyebi et al. (2005) pointed out the variability in parasitism attributes and adaptation to temperature regimes among Kenyan strains of *T. sp. nr. lutea* assembled from the three distinct altitudes. The present study was undertaken to assess the potential for genetic enhancement among strains of this species through reciprocal cross-mating, with focus on commercially important attributes, namely fecundity, progeny production and progeny sex ratio.

Materials and methods

Native strains of trichogrammatids tested

The test strains of *T. sp. nr. lutea* originated from recoveries among eggs of *H. armigera* collected from tomato (*Lycopersicon esculentum* Mill.) in field surveys conducted during 2001–2003 in Kenya. The four strains chosen for the study had been collected from Kilifi, Kilifi District (low altitude), Kwa Chai, Kibwezi District (mid-altitude), Rarieda, Bondo District (mid-altitude), and Ebuhayi, Kakamega District (high altitude), each located at 400–600 km apart (Table I). The strains were

Table I. Details of origin of *Trichogrammatoidea* sp. nr *lutea* strains tested in crossing experiments.

Collection site	Collection code	Test code	Altitude (m a.s.l.)	Latitude	Longitude
Kilifi Institute, Kilifi District	Kil-A-2-Ha-3B	A	49	03°37' 25.4"S	39°50' 68.3"E
Kwa Chai, Kibwezi District	Ke-005B	B	846	02°23' 19.9"S	38°00' 21.1"E
Ebuhayi, Kakamega District	Ke-028B	C	1403	00°30' 29.0"S	34°65' 56.0"E
Rarieda, Bondo District	Ke-042B	D	1177	00°20' 53.0"S	34°34' 20.3"E

established from single isolated females, reared and maintained as isofemale lines on eggs of the factitious host, *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae) for 20–30 generations. Both rearing and the experiments were conducted on *C. cephalonica* eggs in 3 × 1-inch glass vials, at 25 ± 2°C, 70%, R.H. and at 12L:12D photoperiod.

Crossing procedure

The procedure for crossing the strains was the same as described for *Trichogramma* by Pinto et al. (1991). Individual host eggs were chosen when they turned black (around early pupal stage of the parasitoid) and were placed separately in individual glass vials (5 cm long; 1 cm diameter) and allowed to emerge singly. One-day-old virgin females and virgin males of each strain were transferred to glass tubes (7.5 cm long; 2.5 cm diameter) as single pairs and confined for mating, under reciprocal crossing plans in ten replications. Controls consisted of pairs from each strain (homogamic crosses). There were 10 replications. Ten percent (10%) honey fortified with gelatin, on strips on white paper was provided as diet to each adult pair, while about forty eggs of *C. cephalonica* glued on paper card strips (1 × 1 cm) were provided, so allowing access to abundant (*ad libitum*) number of eggs for parasitisation to each adult. The egg cards were withdrawn and replaced daily with fresh ones, while the adult diet was changed after every 2 days. The egg cards withdrawn were placed in glass vials and incubated at 25 ± 2°C, 70 ± 5%, R.H. for development and adult emergence.

Fecundity was measured as the number of progeny that was supported to adult emergence among host eggs oviposited each day. The counting of host eggs with one progeny each was non-restrictive, based on blackening of the host egg during the late larval stage of the parasitoid (Strand 1986). Daily fecundity (number of blackened eggs) by each female was determined for a limit of 15 days, by examining all the blackened eggs at 5 days after exposure for oviposition, under a microscope (×16). The total number of parasitised eggs from which progeny adults emerged, the total number of eggs from which progeny adults emerged (total number of eggs with exit holes), the total progeny adults produced and the number of female progeny produced daily were recorded for each pair in the 15 days. The life time of each parent (male and female) during the experiment was also recorded as the adult longevity. The life-time fecundity (pooled fecundity for 15 days) and effective fecundity (pooled fecundity for 5 days) per female parent were obtained from the daily fecundity data. Percent adult emergence was derived as a proportion of the eggs with emergence holes in the total number of eggs parasitised while the progeny sex ratio (proportion of females in progeny) was derived as the proportion of females in the total progeny produced.

Data analysis

The data on biological parameters observed among the heterogamic and homogamic crosses (longevity, parasitism, progeny emerged, number of progeny males and females, progeny sex ratio) were analysed by analysis of variance (ANOVA) using general linear model (GLM) procedure of SAS for PC (SAS Institute 1999–2000). Significant means were separated by Student–Newman–Keul's (SNK) test ($P=0.05$) (Sokal & Rolf 1995). Levene's method was used to test the homogeneity of variances for the group means within the reciprocal crosses. The variances were found to be homogenous for all parameters except the number of females (female longevity: $df=15$, $F=19.72$, $P<0.001$; fecundity: $df=15$, $F=2.95$, $p=0.001$; number of males: $df=15$, $F=3.72$, $P<0.001$; number of females: $df=15$, $F=1.35$, $P=0.1643$; percent females: $df=15$, $F=3.47$, $P<0.001$).

To calculate the genetic variance (V_g) of six life history traits, data was transformed as described by Liu and Smith (2000). Natural logarithms were used to transform adult female longevity; fecundity and the number of males; while square roots were used to transform the number of females and sex ratio of offspring, and arc sine for progeny emergence. Cross means of transformed data were then used to calculate the genetic variance for each of the six traits by equating estimated mean squares between the strains to their corresponding expected mean squares (in one-way ANOVA). The proportion of variance explained by genetic differences between isolines from different strains were calculated for the six life history traits. A relative trait value was obtained by dividing each observation by the grand mean (for the crosses) and the genetic variance and the index of genetic differentiation calculated as described above. The genetic correlation index (equal to the correlation between strain means) and phenotypic correlation coefficients were calculated from the cross means and statistically tested to find if they differed significantly from zero (t -test; Rosner 1990).

Results*Biological attributes*

Comparison between reproductive compatibilities in homogamic and heterogamic crosses showed that single crossing between all strains resulted in both male and female progeny. However, significant differences were observed between strains and crosses in fecundity, progeny emergence, progeny production and proportion of females in progeny

In the homogamic crosses, virgin females from ex-Rarieda strain (Ke-042B) registered higher fecundity than females in the other strains, with the lowest fecundity recorded in the ex-Ebuhayi strain (Ke-028B) (Figure 1a,b). The highest parasitoid emergence ($70.1 \pm 9.79\%$) and resultant adult progeny in the homogamic crosses was also recorded in the Rarieda strain, while the lowest (35.0 ± 4.65) was again recorded in the ex-Ebuhayi strain (mean = 52.4, $P=0.002$) (Figures 2 and 3a). In the reciprocal heterogamic crosses, the inter-strain mating between females from ex-Kilifi (Kil-A-2-Ha-3B) and males from ex-Rarieda strains resulted in the highest relative life-time fecundity ($41.9 \pm 2.58\%$, sum = 138) (mean = 21.9, $P<0.001$) and effective fecundity ($49.6 \pm 4.27\%$, sum = 74) (mean = 25.3, $P<0.001$), which was highly superior to all the other crosses (Figure 1a,b). Significant improvement in fecundity in inter-strain than intra-strain crosses was also evident in crosses involving virgin females

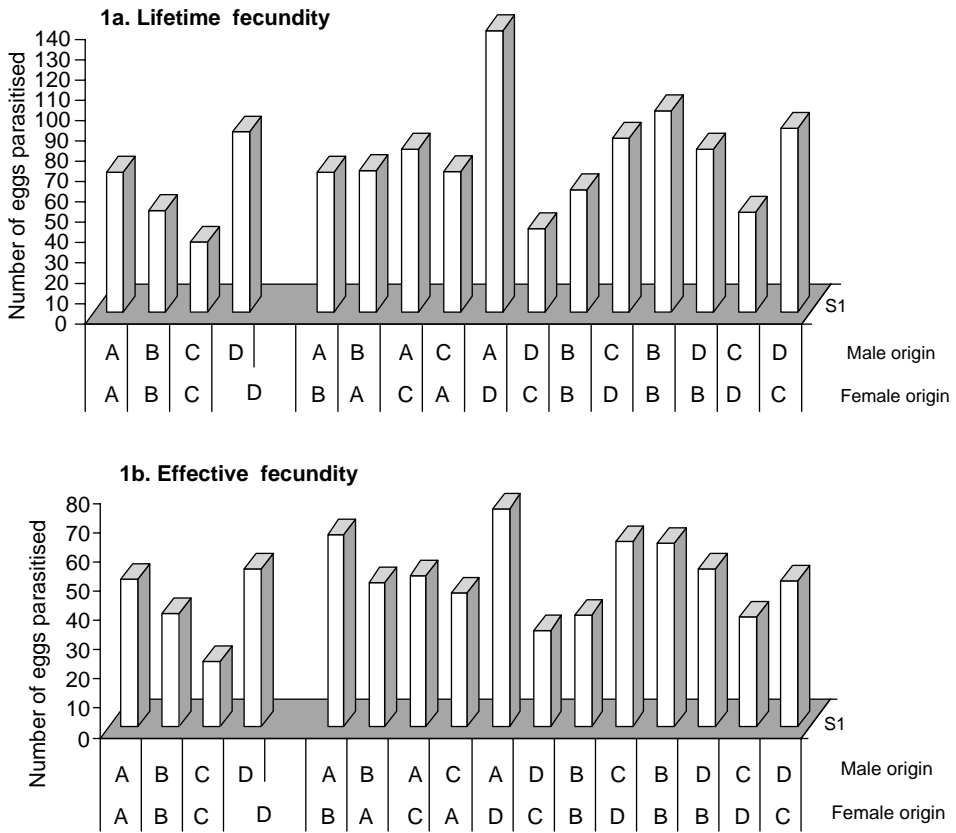


Figure 1. Relative life-time (15 days) (a) and effective (5 days) (b) fecundity (parasitism) in homogamic (parental) and heterogamic crosses in four Kenyan strains (A–D) of *Trichogrammatoides* sp. nr. *lutea*.

from ex-Ebuhayi strain with males from ex-Kilifi, ex-Kwa Chai (Ke-005B) and ex-Rarieda strains, and with virgin females from ex-Kwa Chai mated by males from ex-Kilifi, ex-Ebuhayi and ex-Rarieda strains (Figure 1a,b). The effective fecundity in the cross between males from Kilifi and females from ex-Kwa Chai strains was almost at

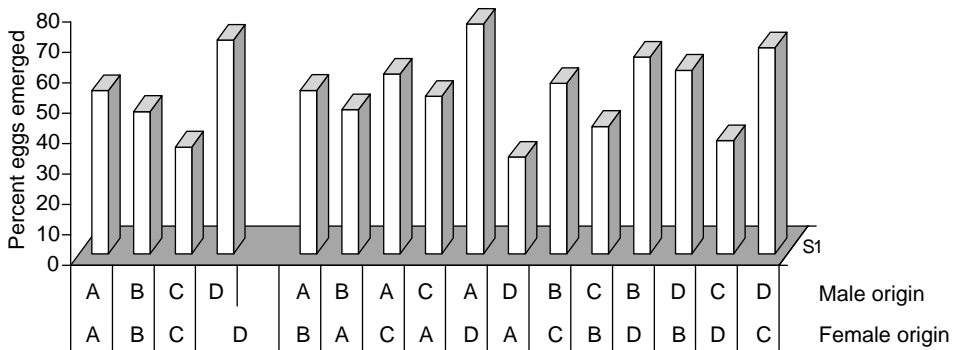


Figure 2. Relative survival (progeny emergence) per female in life-time in homogamic (parental) and heterogamic crosses in four Kenyan strains (A–D) of *Trichogrammatoides* sp. nr. *lutea*.

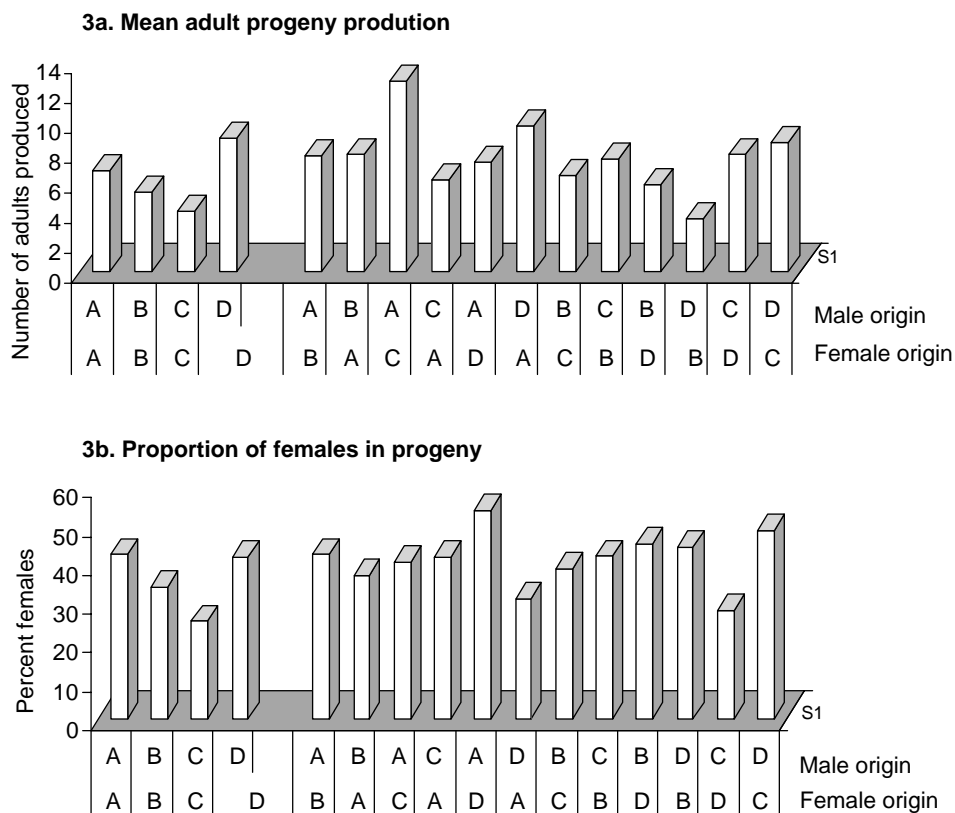


Figure 3. Figure 3. Relative daily number of progeny produced per female (a) and proportion of females in progeny (b) in homogamic (parental) and heterogamic crosses in four Kenyan strains (A–D) of *Trichogrammatoidea* sp. nr. *lutea*.

par (Figure 1b). Except for the one case involving females from ex-Rarieda strain and ex-Kilifi strain males, no other significant improvement in fecundity was achieved with inter-strain crosses with ex-Kilifi and ex-Rarieda strain females. Progeny survival (percent emergence from parasitised eggs) was highest (75.4 ± 3.22) (mean = 55.4, $P < 0.001$) in the cross between ex-Kilifi strain males and ex-Rarieda strain females but lowest (37.8 ± 4.76) in its reciprocal cross, just as in the fecundity (Figure 2). The resultant adult progeny and female sex ratio also showed a similar trend (Figure 3a,b). The minimum female progeny sex ratio value was obtained for the ex-Ebuhayi homogamic cross (sex ratio = 25.1 ± 3.55 ; mean = 40.0, $P < 0.001$), while the highest (42.2 ± 3.60) in the ex-Kilifi homogamic cross. The heterogamic crosses generally exhibited higher female sex-ratios (Figure 3b), the highest (53.5 ± 296 ; mean = 41.0, $P < 0.001$) being in the cross between ex-Kilifi strain males and ex-Rarieda females and the lowest (27.8 ± 3.85) being the ex-Ebuhayi strain males and ex-Rarieda strain females cross. There were also contrasting results in reproductive capabilities in the reciprocal heterogamic crosses between ex-Kilifi and ex-Kwa Chai strains, ex-Kilifi and ex-Ebuhayi strains, ex-Kwa Chai and ex-Ebuhayi strains, Kwa Chai and Rarieda strains; with variations changing in fecundity (life-time and effective), relative survival and progeny production. The variations in these crosses were not much for the progeny sex ratio.

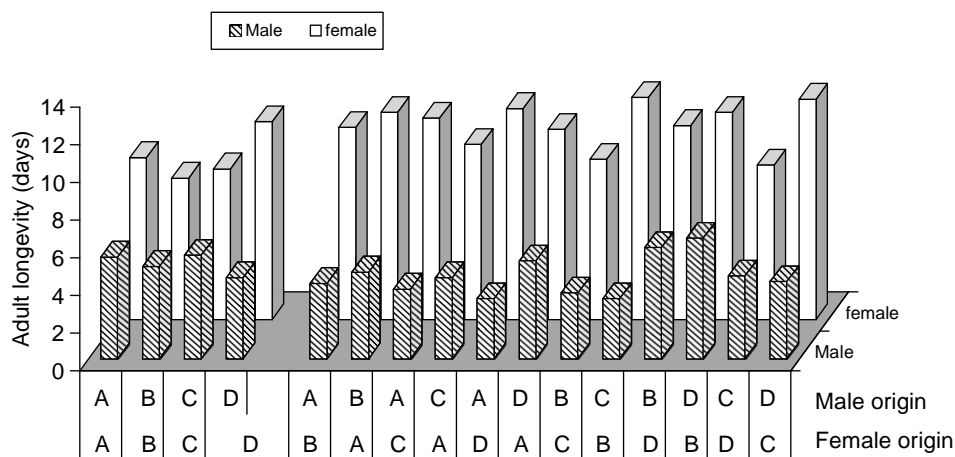


Figure 4. Average life span (days) of virgin males and females in homogamic (parental) and heterogamic crosses in four Kenyan strains (A–D) of *Trichogrammatodea* sp. nr. *lutea*.

Fecundity generally decreased as adults grew older, with females being more fecund in the first 5–6 days. However, the relative daily fecundity in the heterogamic crosses involving ex-Rarieda strain females and ex-Kilifi strain males, and that involving ex-Ebuhayi strain females and ex-Rarieda strain males remained consistently superior, with no significant differences between days. In the homogamic crosses, this trend was only observed in the ex-Rarieda strain.

Significant differences in adult longevity were also observed within the homogamic and heterogamic crosses. The male longevity in the heterogamic crosses was significantly lower (mean = 4.6 days, $P=0.05$) than female longevity (mean = 10.3 days, $P=0.05$) (Figure 4). Adult male longevity in the heterogamic crosses ranged from 3.4 ± 0.11 to 6.4 ± 0.31 days, while in the homogamic crosses, it ranged from 4.3 ± 0.21 to 5.5 ± 0.32 days. On the other hand, adult female longevity in the heterogamic crosses ranged from 8.2 ± 0.40 to 11.8 ± 0.35 days, whereas in the homogamic crosses it ranged from 7.5 ± 0.25 to 10.5 ± 0.31 days.

Genetic variation

Genetic variance and relative variance due to strain effect (intra-class correlation) varied among the four strains and their reciprocal crosses (Tables II and IIIa,b). Percent emergence had the highest genetic variance in both cases (1660.72 and 1343.17, respectively), followed by female progeny sex ratio (472.68 and 372.25, respectively). In the homogamic crosses, the next highest genetic variances were observed in fecundity followed by female longevity (Table IIa), while in the heterogamic crosses, the next highest was fecundity followed by female longevity and number of females. Broad-sense heritability (between strain proportion of variance) over the four inbred and twelve reciprocal crosses were generally medium in fecundity, though high in the female longevity. In the homogamic crosses, they were high for female longevity (1.17), moderate for number of females (0.68), fecundity (0.63), and number of males (0.58); but low for progeny sex ratio (0.43) and percent emergence (0.39) (Table IIa). In the heterogamic crosses, intra-class correlation was high for female longevity (0.95), moderate for percent emergence (0.76), number of

Table IIa. Genetic variance (V_g) of six life-history traits in four inbred populations of *Trichogrammatoidea* sp. nr. *lutea*.

	Life history trait	Relative trait value (Fitness component)
Longevity (days)	23.92	0.244
Fecundity (% parasitism)	29.28	0.538
Emergence (% eggs)	1660.72	0.554
No. of females	16.08	0.698
No. of males	5.17	0.765
Sex ratio (% females)	472.68	0.297
Mean	365.98	0.516

$V_g = (MS_p - MS_e)/10$, where MS_p and MS_e were mean squares for cross and error, respectively, and derived from the one-way ANOVA (GLM) and 10 = the number of replications.

Table IIb. Proportion of variance between populations (genetic differences) in six life-history traits and their relative values, for four inbred (Homogamic) and outcrossed (Heterogamic) populations of *Trichogrammatoidea* sp. nr. *lutea*.

	Life history trait		Relative trait value (Fitness component)	
	Homogamic	Heterogamic	Homogmic	Heterogamic
Longevity (days)	0.97	0.95	0.95	0.83
Fecundity (% parasitism)	0.63	0.65	0.65	0.50
Emergence (% eggs)	0.39	0.76	0.76	0.94
No. of females	0.68	0.50	0.50	0.52
No. of males	0.58	0.70	0.70	0.41
Sex ratio (% females)	0.43	0.30	0.30	0.38
Mean	0.61	0.60	0.60	0.60

males (0.70), fecundity (0.65) and number of females (0.50); while being low for progeny sex ratio (0.30) (Table IIb).

The genetic variances (V_g) of the relative trait values were low (0.244 to 0.765), while the indices of genetic differentiation were the same as in the life history traits in the homogamic crosses (Table IIa).

Phenotypic and genetic (genotypic) correlation indices

The phenotypic and genetic correlation indices for the life-history traits studied were generally positively correlated (Table IIIa,b). Significant correlations in the homogamic crosses were found only at $P < 0.05$ while most of those in the reciprocal crosses were significant at $P < 0.001$.

The following five out of fifteen possible phenotypic correlations in the homogamic crosses were significant: (1) fecundity and percent emergence; (2) fecundity and number of females; (3) fecundity and female sex ratio; (4) percent emergence and number of females; and (5) percent emergence and number of males (Table IIIa). The phenotypic and genetic correlation index coefficients in the relative trait values were exactly the same as those in life-history traits, with the same relationships showing significant positive correlations.

Table IIIa. Genotypic (below the diagonal) and phenotypic (above the diagonal/dashes) correlation coefficients of six life-history traits for four inbred strains of *Trichogrammatoidea* sp. nr. *lutea*.

	Life history trait					
	Female Longevity	Fecundity (Parasitism)	Emergence (% eggs)	No. of females	No. of males	Sex ratio (% females)
Longevity (days)	–	0.74	0.88	0.90	0.87	0.62
Fecundity parasitism)	0.74	–	0.96*	0.98*	0.90	0.98*
Emergence (% eggs)	0.88	0.98*	–	0.97*	0.99*	0.87
No. of females	0.90	0.96*	0.97*	–	0.99	0.90
No. of males	0.87	0.90	0.99*	0.93	–	0.87
Sex ratio (% emales)	0.62	0.98*	0.87	0.90	0.78	–

*The correlation coefficient differed significantly from zero at $P < 0.05$ (t -test; Rosner 1990).

Table IIIb. Genotypic (below the diagonal) and phenotypic (above the diagonal/dashes) correlation coefficients of six life-history traits 12 reciprocal crosses in four strains of *Trichogrammatoidea* sp. nr. *lutea*.

	Life history trait					
	Female Longevity	Fecundity (Parasitism)	Emergence (% eggs)	No. of females	No. of males	Sex ratio (% females)
Longevity (days)	–	0.34	0.49	0.46	0.38	0.62*
Fecundity (parasitism)	0.34	–	0.89***	0.97***	0.94***	0.85***
Emergence (% eggs)	0.49*	0.89***	–	0.91***	0.92***	0.95***
No. of females	0.46*	0.97***	0.91***	–	0.91***	0.90***
No. of males	0.38	0.94***	0.92***	0.91***	–	0.82***
Sex ratio (% females)	0.62*	0.85***	0.92***	0.91***	0.82***	–

*The correlation coefficient differed significantly from zero at $P < 0.05$ (t -test; Rosner 1990). *** The correlation coefficient differed significantly from zero at $P < 0.001$.

Unlike in the homogamic crosses, 11 out of the 15 possible phenotypic correlations in the heterogamic crosses were significant, the highest being in fecundity and number of females. The following four relationships were not significant: (i) female longevity and fecundity; (ii) female longevity and percent emergence; (iii) female longevity and progeny sex ratio; and (iv) fecundity and number of males (Table IIIb). The correlation coefficient between female longevity and progeny sex ratio was significant at $P < 0.05$, while the other coefficients were significant at $P < 0.001$. Out of the 15 possible genetic correlation indices, only two were not significant, namely: (i) fecundity and female longevity; and (ii) progeny sex ratio and female longevity. Genetic correlation index coefficients between female longevity and percent emergence, number of females and progeny sex ratio were lower and significant at $P < 0.05$.

Discussion

The study has shown that scope exists for genetically enhancing the parasitisation potential among native trichogrammatid strains through selective crossing among them.

The fecundity and related biological parameters were found to be significantly improved by suitable crosses and parentage selection, as when ex-Rarieda strain females were cross-mated with ex-Kilifi strain males and when ex-Kwa Chai strain

females were cross-mated with ex-Rarieda strain males. An improvement was also found when ex-Ebuhayi strain females were cross-mated with ex-Kilifi and Rarieda strains. However, there was only limited improvement in performance parameters when ex-Kilifi strain males were cross-mated with females from ex-Kwa Chai and ex-Ebuhayi strains. Cross-mating ex-Ebuhayi strain males with females from ex-Rarieda strain resulted in contrasting results. The reciprocal cross involving ex-Rarieda strain males and ex-Kilifi strain females did not result in any gain in their biological attributes. It is thereby established that the biological attributes are most significantly improved when females of ex-Rarieda strain are cross-mated with males from ex-Kilifi strain. On the other hand, the biological attributes of the intra-strain (homogamic) crosses were also better in the ex-Rarieda strain, followed by those of the ex-Kilifi and ex-Ebuhayi strains. However, cross-mating these strains resulted in improving the biological parameters, though some crosses were better than the reciprocals. It is therefore evident from the present study that a quantum jump in fecundity potential and other biological parameters could be gained by selective crossing of the native trichogrammatid strains.

Although a better strain could be pointed out, improvement in performance could be achieved by appropriate choice of males and females from the four strains and eventually reciprocally cross-mated for a choice to be made. The performance of the subsequent progenies is being studied and the interbred adults with better biological parameters from such crosses will be used to establish lines that could compete for improved impact in field release trials.

While there is a good chance in exploiting this advantage in commercial *Trichogramma* production, the fact that reciprocal cross-mating of males and females from different strains could bring about contrasting results could be investigated further. In the case of the reciprocal cross between males and females of ex-Kilifi and ex-Rarieda strain, both male and female progeny were produced in crosses made in both directions. Nagaraja (1978) speculated that insemination reaction could be the main cause of variation in F1 progeny and percentage of females in reciprocal crossing as an indicator of partial reproductive isolation across five strains of *Trichogrammatoidea bactrae* Nagaraja assembled from different habitats. He thought this could be an indication of various levels of genetic isolation. An attempt to study the mating behavior and insemination would enable better understanding of these contrasting responses in the reciprocal crosses. Although Kilifi and Rarieda are about 1020 km apart, while Kilifi and Ebuhayi are about 925 km apart, these two regions experience more or less similar hot and humid weather conditions, though Kilifi is in low altitude and Rarieda in mid-altitude. Kilifi and Kwa Chai are more closely situated (about 395 km apart) and in closer altitudes (low and mid), but Kwa Chai experiences hot dry weather (semi-arid). Similarly, Rarieda is closer to Ebuhayi (about 100 km apart), but the latter is on high altitude and experiences cool and wet conditions. Our speculation is that there could be possible genetic differences among the strains because of long-term adaptation to the geographic and agro-climatic differences between the locations from which the strains were collected. Nevertheless, the range in progeny sex ratio values being similar in homogamic and heterogamic crosses, suggests the absence of reproductive barriers between strains, and they were obviously compatible. This follows the principles described by Pinto et al. (2003), where compatible cultures produce relatively high levels of female progeny (20% or greater) in both directions; incompatible cultures produce 0–5% females in both directions

while partially compatible cultures produce at least 14% females in one direction only. The production of female offspring in both directions in all crosses in this study, with females above 20%, indicates that the four strains are reproductively compatible. The importance of such studies, besides adaptability to climatic conditions, was underscored by Pak and Van Lenteren (1986) and the importance of crossing compatibility emphasised by Stouthamer et al. (1996, 2000). In this study, it would be expected that viable mating might occur between these strains when mixed in the field. This differs from the observations of Pinto et al. (1991) where among several crosses between *T. minutum* lines from east of the Rocky Mountains and coastal California indicated some to be reproductively incompatible.

The observation that females lived longer than males is in agreement with the findings by Manickavasagan et al. (1994) on *T. minutum*; however, this trend differs from that of Stinner et al. (1974) where *T. pretiosum* males lived longer than females. Most of the female progeny in the homogamic crosses were produced in the first 5 days while in the heterogamic crosses, progeny production was spread out in a longer period. However, normal sex ratio (70% females) was obtained in intra-strain crosses unlike in the inter-strain crosses. Manickavasagan et al. (1994) postulated that a parasitoid that delivers over 50% of its progeny within the first day of emergence is more suitable in ecological zones with extreme weather conditions, while that with a greater fecundity spread out is suitable for moderate conditions. Sorati et al. (1996) found differences amongst strains of *Trichogramma* nr. *brassica* for all traits apart from fecundity, suggesting heritable variation. It is recommended that the adult female behaviour and sex allocation factors be studied in these four strains.

Quantitative genetic analysis with strains showed significant variation in the life-history traits. Percent emergence and female progeny sex ratio showed very high levels of genetic variance in homogamic crosses, followed by life-time fecundity and female longevity. Intra-class (relative variance due to strain effect) was higher in female longevity, followed by life-time fecundity and number of females. Liu and Smith (2000) reported high levels of genetic variance and intra-class correlations in life-time fecundity and number of females for *T. minutum* and pointed out that these high values suggest a strong genetic component and could be improved through selection. Little research has been conducted in this area. It is known that traits with low genetic variability are highly affected by environmental factors and are difficult to improve through selection. The genetic variations in the fitness components were low but not as low as observed by Liu and Smith (2000), while the intra-class correlation values were the same as in the life history traits in the homogamic crosses. As Liu and Smith (2000) suggested, we could therefore use the fitness components like the life-history traits in genetic selection in the present case also.

Most of the life-history traits and fitness components tested were positively correlated with each other; hence selection for one could also help improve the other. High positive genotypic and phenotypic correlations were found in life history traits and their respective fitness components, between female longevity and progeny sex ratio, percent emergence and number of females and progeny sex ratio in both homogamic and heterogamic crosses. These findings are in contrast to the results from studies by Liu and Smith (2000) on *T. minutum*. Perhaps it is due to differences in the gene pools of the strains/species being compared. No significant genotypic and phenotypic correlations were also found in the homogamic crosses between female longevity and fecundity, percent emergence, number of females and males. However,

significant ($P < 0.05$) correlations were found between fecundity and percent emergence, percent emergence and number of females, contrary to the studies by Liu and Smith (2000). In the heterogamic crosses, significant correlations were not observed by Liu and Smith (2000) between female longevity and progeny sex ratio ($P < 0.05$); fecundity and percent emergence, percent females and number of females ($P < 0.001$). Correlations which were not significant in our study but significant in Liu and Smith's (2000) studies were: female longevity and fecundity, percent emergence and sex ratio. Chassin and Bouletreau (1991) reported no significant correlation between fecundity and progeny sex ratio in *T. brassicae* Bezdenko and *Trichogramma cacoeciae* Marchal though not stated whether genotypic or phenotypic. The role played by the environment in the six life history traits studied was not clear since there was no major difference between the genotypic and phenotypic correlations as suggested by Liu and Smith (2000).

Our study has shown that strain and progeny selection can still be based on phenotype. These results have pointed to the importance of strain/population crossing studies in native trichogrammatid strains from different geographical origins before selecting an effective one for field release and the potential for quantum jump in fecundity for selecting appropriate parents between strains demonstrated. To utilise this knowledge in benefiting commercial mass production, there is need for follow up studies on the nature of inheritance of these traits in subsequent generations.

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