

Fitness enhancement by crosses between two populations of *Trissolcus vassilievi* (Hymenoptera: Scelionidae)

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Abstract

Trissolcus vassilievi (Mayr) (Hymenoptera: Scelionidae) is one of the most important egg parasitoids of the common sunn pest (CSP), *Eurygaster integriceps* Puton (Hemiptera: Scutelleridae) in Iran. In this study, the fitness of two populations of *T. vassilievi* was studied on two populations of hosts in terms of life history parameters. Two populations of *T. vassilievi* were selected: 1/ Tabriz (as a temperate area), and 2/ Varamin (as a subtropical area), as well as for CSP. Moreover, regarding that outcrossing between populations can produce progeny with superior characteristics, the progeny of reciprocal crosses between original populations also were examined on a single host. The crosses between the two populations caused 13.9-18.5% higher net fecundity than maternal populations which suggests fecundity to be a function of maternal phenotype. The intrinsic rate of increase showed minor differences among treatments which varied between 0.291 ± 0.003 to 0.305 ± 0.003 . The partial advantage of the Varamin wasps over the Tabriz ones and the crosses over the original populations was obvious. Such differences may be used to obtain more efficient parasitoids in augmentation programs.

Key Words: intrinsic rate of increase, life expectancy, net reproduction rate, parasitoid wasp, reciprocal crosses.

Introduction

The biological fitness of a living organism is the relative ability of an organism to survive and pass on its genes to the next generation (Krebs and Davies, 1993). This is possible through birth (transferring more proportion of genes to the next generation) in the shortest possible time (high speed of gene transcription) and the ability of progeny to survive (persistence of the genes). Therefore, the developmental rate, the mortality rate at all stages of life, and the fecundity are relevant features of fitness and the ability of a living organism to compete with other species. These characteristics can be examined as life tables and stable population growth models (Lotka 1907a, b, Portilla et al. 2014). So far, several studies have investigated the stable population

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growth parameters in egg parasitoids of common sunn pest (CSP), *Eurygaster integriceps* Puton (Hem., Scutelleridae), and related stinky bugs. These are dominantly on *Trissolcus* spp. and *Telenomus* spp. (Hymenoptera: Scelionidae) (Asgari and Kharrazi Pakdel 1998; Laumann *et al.* 2008; Amir-Maafi and Parker, 2011, Nozad-Bonab *et al.* 2014, Bazavar *et al.* 2015, Benamolaei *et al.* 2015 a, b, Abdi *et al.*, 2017, Teimouri *et al.* 2019), and *Ooencyrtus* spp. (Hymenoptera: Encyrtidae) (Ahmadpour *et al.* 2013, Mele *et al.* 2024).

There is little information about intra- and inter-specific variation of survival value and reproductive potential of egg parasitoids of CSP, and it is limited to few studies. In the 1970s, several species of CSP's egg-parasitoids, collected from different regions of the world, were transferred to the former Soviet Union and compared with native species, especially *Trissolcus grandis* (Thomson), in laboratory and field conditions. The overall result of this study showed that native species had superiority and it was due to the adaptation of native species to climatic and seasonal conditions (Nouri *et al.*, 2011). Awan *et al.* (1990) compared three geographical populations of *T. basalis* (Wollaston) collected from France, Italy, and Spain regarding biological and behavioral characteristics. The emergence rate of adult wasps from *Nezara viridula* (L.) eggs was significantly higher in the French population than in the Italian and Spanish ones. The development of immature stages of the Italian population was significantly longer than the other two populations. Taghadosi *et al.* (1993) and Nozad Bonab *et al.* (2014) observed differences among populations of *T. grandis* of Tehran-Alborz-Qazvin and East Azarbaijan provinces respectively. A comparison of biostatistics of Scelionidae by Amir-Maafi (2010) during 2004-2006 in different provinces of Iran revealed significant differences between species and populations of the wasps. Fecundity, oviposition period, and gross and net reproductive rates differed between species or populations. The net fecundity of *T. vassilievi* (Mayr) from Lorestan and Tehran was 240.8 and 227.5 eggs respectively, which was 2.5 times as much as the other populations. The highest intrinsic rate of increase of *T. grandis*, *T. semistriatus* (Nees), and *T. vassilievi* was recorded for Golestan, West Azarbaijan, and Tehran provinces, respectively.

It can be seen from the above reports that inter-specific and intra-specific differences in the parasitism rate and population growth rate of the parasitoid wasps are sometimes very considerable. Therefore, in this study, we attempted to study the differences between two populations of *T. vassilievi* with temperate (Tabriz) and subtropical (Varamin) origins simultaneously. On the other hand, since the parasitoid spends all immature stages within the host body, it can be affected by the host's quality, so the host population was also included as a second variable. Finally, the hypothesis was tested to find if crosses between populations could

enhance the fitness of populations. Therefore, crosses as Tabriz-female×Varamin-male (T×V) and Varamin-female×Tabriz-male (V×T) were conducted to evaluate the possibility of obtaining populations with superior or intermediate characteristics.

MATERIAL AND METHODS

Cultures of *Eurygaster integriceps* Puton

Adult bugs were collected on several occasions at the end of the winter from mountains around Tabriz and Varamin before leaving the resting sites. Collectings of specimens were continued in wheat fields during post diapause phase. The collected insects were transferred to a greenhouse unit of the Department of Plant Protection, Faculty of Agriculture, University of Tabriz. Transparent rectangular cubic plastic containers (20×30×9cm) equipped with a mesh cap for ventilation were used for the rearing of both populations. Dry wheat grain was used as a foodstuff and soaked cotton balls as a water source. The paper strips folded fan-like to be served as an oviposition substrate. These insects were exposed to 25±2 °C, 40±10% RH, and 16: 8 h L: D photoperiod (Iranipour *et al.* 2015).

Cultures of *Trissolcus vassilievi* (Mayr)

In this study, two populations of *T. vassilievi*, namely original populations, one from Tabriz (1360 AMSL, 46°E, 38°N) and the other from Varamin (918 AMSL, 51°E, 35°N) were examined. To collect egg parasitoids, host egg traps (yellow cardboards, 5×15 cm, folded twice to construct a Δ-shaped structure) were used (Safavi, 1973). The traps were tied to wheat ears and removed after one week, then the parasitized eggs were transferred to glass vials (1.5×10 cm) and kept in a growth chamber (Iran Khodsaz Co., IKH.RH model) under constant conditions (26±1 °C, 50±5% RH and 16:8 h L:D photoperiod). The emerged wasps were identified by the identification key of Kozlov and Kononova (1983). After rearing for one generation, males and females of the second generation from the same population were randomly coupled and each pair was transferred to a similar vial supplied by host eggs of either population. Small drops of honey were used to feed the wasps.

Fecundity-life table studies

Ten clutches of 24-hour-old CSP eggs (14 eggs per clutch) from each population were exposed to 48-hour-old mated *T. vassilievi* females of second-generation of each population. After 24 hours, females were removed and the host eggs were kept as a life table cohort in so-called growth chambers to determine their fate. The experiment was conducted as a factorial experiment in a completely randomized design framework, with two factors including wasp

and host populations respectively; each one in two levels which are represented as TT, TV, VT, and VV (original populations); the first letter delineates the parasitoid origin, and the second one host origin (T=Tabriz, V=Varamin). Twenty pairs of wasps of the third generation from each population were coupled as random and five clutches of 24-hour-old CSP eggs were daily offered up to death. The fate of host eggs was followed by daily checks, and the date of emergence was recorded separately for males and females.

In the next step, the progeny of the third generation of the two populations reciprocally crossed to the other population. Thus, two kinds of the cross were present, Tabriz females×Varamin males (T×V) and Varamin female×Tabriz males (V×T). Considering the non-significant effect of the host, the outcrossed wasps were studied only on CSP eggs of Varamin in the same manner described for inbred populations.

Measures of stable population growth parameters

The method described by Carey (1993) was used to calculate life table parameters and entropy (Eq.1).

$$H = \frac{\sum_{x=0}^{\omega} e_{x^*} d_x}{e_0} \quad \text{Eq.1}$$

The entropy values less than, equal to and greater than 0.5 represent the survivorship curves of type I (convex), type II (straight line), and type III (concave), respectively. Stable population growth parameters, including gross reproduction rate (GRR), net reproduction rate (R_0), mean generation time (T), doubling time (DT), intrinsic rate of increase (r_m) finite rate of increase (λ), intrinsic birth rate (b), and intrinsic death rate (d) were estimated. The r_m -value was calculated by solving the Lotka equation using iterative calculations of the Newton-Raphson method as follows:

$$\sum_{x=0}^{\omega} e^{-r_m x} l_x m_x = 1 \quad \text{Eq.2}$$

To determine the standard error of the above statistics, we used bootstrap methods in 1000 replicates (Meyer *et al.*, 1986). Estimation of the parameters was carried out by a program in Excel (Iranipour, 2018).

Statistical analyses

Statistical analysis was performed using SPSS software. Since the host-effect was non-significant in all parameters, this factor was excluded from analysis and comparison between main populations and crossed populations was done by One Way ANOVA. The means were compared by Tukey's test at 0.05 significance level. Bootstrap estimates of r_m and the other stable population growth parameters also were compared among main populations and crosses.

Pairwise comparisons between those treatments were done by the random pairing of estimates, and the differences of randomly paired values were ranked from smallest to largest value; then the smallest and the largest 25 samples were excluded and 950 median values were considered as 95% confidence interval (CI). If 95% CI included zero no significant difference between the two treatments was interpreted.

RESULTS

Life history parameters of *T. vassilievi*

In life table studies, two populations of *T. vassilievi* were compared on two host populations (Table 1), and due to the insignificant effect of the host and their interactions, the host effect was excluded from the analysis. The wasps from the crosses on the Varamin host were compared with their parental populations only on the Varamin host.

Table 1. Analysis of variance of life history components of two populations of *T. vassilievi* on two populations of sunn pest eggs.

Parameter	Wasp		Host		Wasp × Host	
	F	P	F	P	F	P
Female longevity	14.61	<0.001	1.74	0.191	0.42	0.519
Male longevity	3.43	0.068	0.00	1.000	0.01	0.939
Oviposition period	29.41	<0.001	0.31	0.580	0.17	0.678
Post-oviposition period	36.66	<0.001	1.54	0.219	0.31	0.578
Total fecundity	24.16	<0.001	1.80	0.183	1.58	0.212
Average daily fecundity	0.00	0.949	2.37	0.128	0.84	0.364
Sex ratio	0.04	0.847	0.01	0.932	0.22	0.641

* df for all treatments=1,76.

Analysis of variance showed that there was a significant difference in the longevity of both females and males when crosses were included as well (Tabriz population, Varamin population, T×V, and V×T crosses; $F_{3,76}=3.62$, $P=0.017$ for female longevity, and $F_{3,76}=3.12$, $P=0.031$ for male longevity). The highest longevity of females and males was observed in Tabriz and Varamin wasps, respectively (Table 2).

Table 2. Reproductive parameters of two *T. vassilievi* populations on two CSP populations and crosses as T×V and V×T.

Treatments	TT	VT	TV	VV	T×V	V×T
Female longevity (d)	31.80±1.19A	28.25±1.14B	31.05±1.15Aa	26.05±0.86Bb	29.90±1.50ab	28.10± 1.23ab
Male longevity (d)	19.60±0.49A	20.75±0.55A	19.55±0.41Aab	20.80±0.95Aa	18.30±0.32b	18.75±0.32ab
Oviposition period (d)	18.50±0.41A	20.60±0.37B	18.45±0.39Ab	20.25±0.23Ba	18.40±0.48b	18.60±0.53b
Post oviposition period (d)	13.30±1.08A	7.65± 1.15B	12.60±1.02Aa	5.80±0.84Bb	11.50±1.39a	9.50±1.01ab
Life time fecundity	216.90±5.36A	249.30±5.07B	230.55±6.02Ac	249.75±4.30Bb	280.40±2.77a	269.50±4.80a
Daily egg	11.80±0.34A	12.13±0.23A	12.63±0.49Ab	12.34±0.20Ab	15.46±0.47a	14.67±0.43a
Sex ratio	0.82±0.03A	0.82±0.02A	0.82±0.02Aa	0.82±0.02Aa	0.78±0.05a	0.86±0.01a

* Means bearing the same letter in a row are not significantly different (Tukey's HSD, $\alpha=0.05$). Capital letters are for comparison between original populations and lower cases are for comparison between original populations and reciprocal crosses reared on the Varamin host.

Female wasps from the crosses showed intermediate longevity of the two populations so their differences were not significant with either population. However, the male progeny of crosses had a shorter lifespan than their parents (Table 2). Females lack a pre-oviposition period. The mean oviposition period of *T. vassilievi* females was significantly higher in the Varamin population than in Tabriz and cross populations ($F_{3,76}=4.36$, $P=0.007$). The total fecundity of *T. vassilievi* females was significantly higher in cross populations than parental populations ($F_{3,76}=22.38$, $P<0.001$). Females of crosses laid 8–29% more eggs than both populations. The highest fecundity was observed in T×V. Almost in all cases, maximum oviposition occurred on the first day of life and declined to zero with a non-linear trend in less than three weeks (Fig.1). The highest fecundity was obtained in T×V, and V×T crosses respectively, followed by original populations (Table 2). The age-specific sex ratio (proportion of females) declined at senescence (Fig.2).

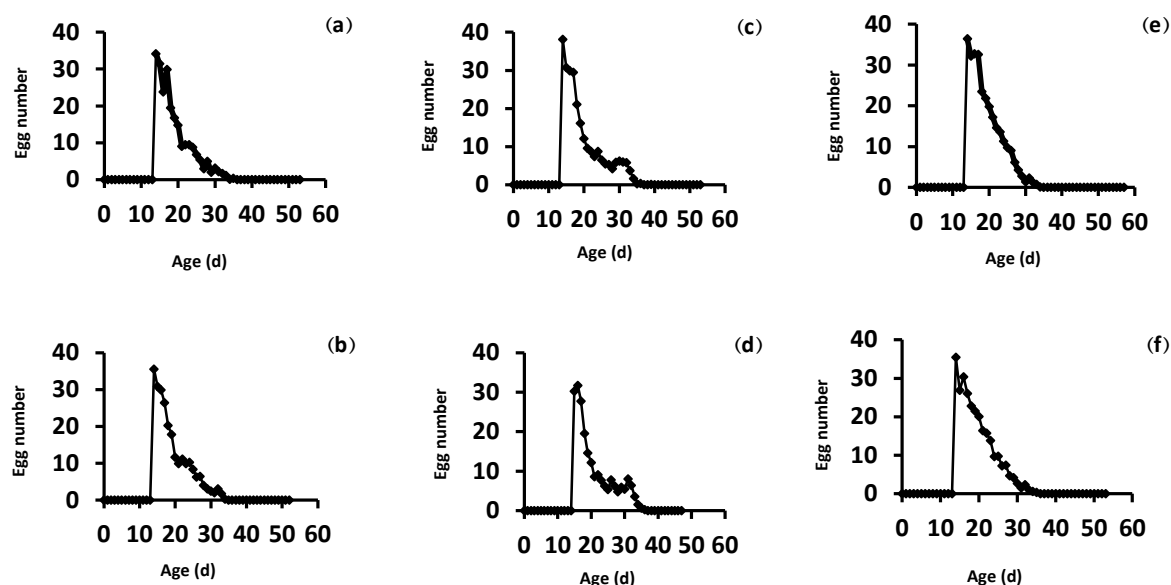


Figure 1. The trend of Oviposition of two *T. vassilievi* populations on two CSP populations and their reciprocal crosses, a) TT, b) TV, c) VT, d) VV, e) T×V, and f) V×T.

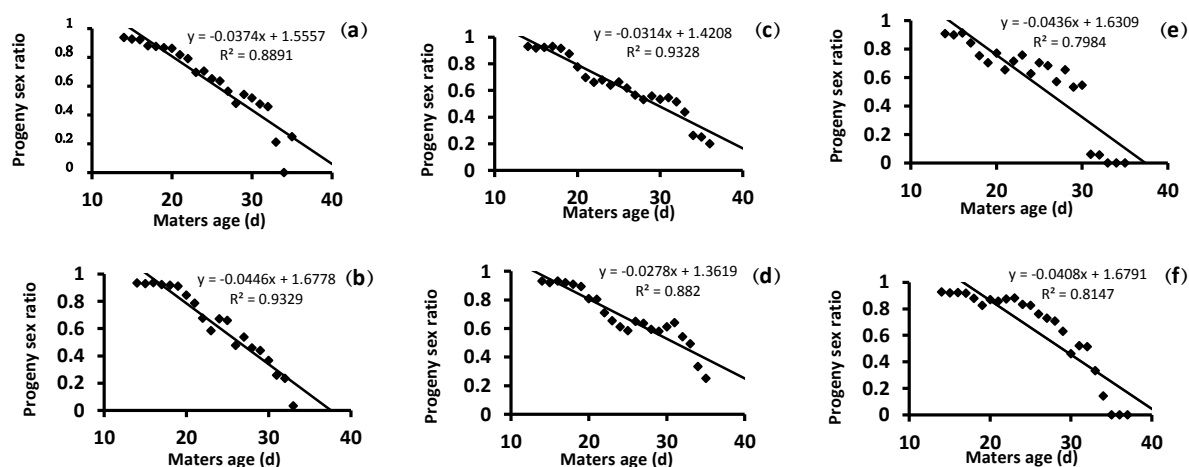


Figure 2. Age-specific sex ratio of two *T. vassilievi* populations on two CSP populations and their reciprocal crosses, a) TT, b) TV, c) VT, d) VV, e) T×V, and f) V×T.

Life tables and survivorship curves of *T. vassilievi*

Age-specific mortality (q_x) of *T. vassilievi* in all treatments increased by age. The results showed that mortality seldom occurs during and prior to oviposition. The survivorship curve of *T. vassilievi* was from type I ($H < 0.5$) in all treatments (Fig.3, Table 3). The life expectancy (e_x) decreased linearly from birth to death (Fig.4). The life expectancy of *T. vassilievi* at birth and emergence, as well as under the curve area of e_x and N_x are shown in Table 3.

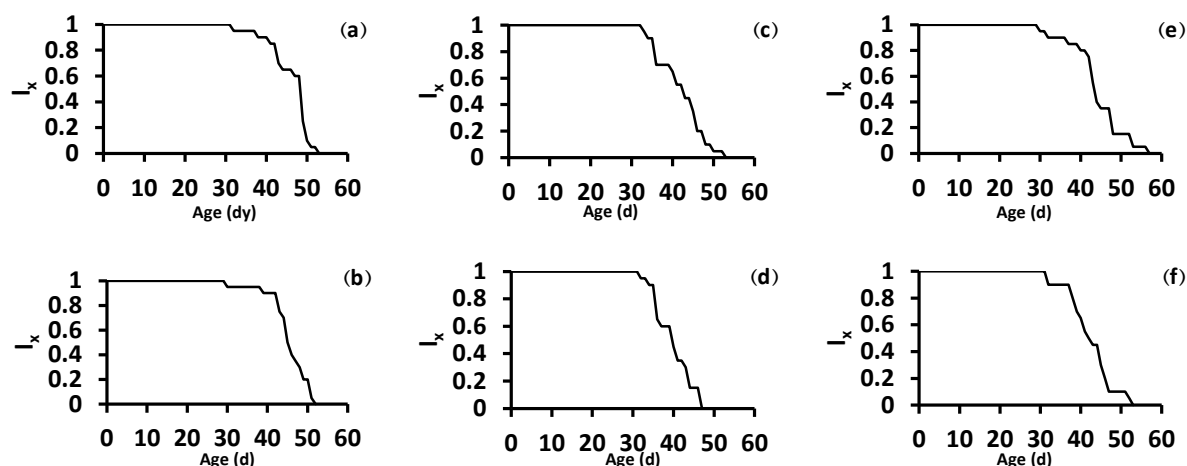


Figure 3. The survivorship curve of two *T. vassilievi* populations on two CSP populations and their reciprocal crosses, a) TT, b) TV, c) VT, d) VV, e) T×V, and f) V×T.

Table 3. Life table statistics of two *T. vassilievi* populations on two CSP populations and their reciprocal crosses under laboratory conditions.

Treatments	TT	TV	VT	VV	T×V	V×T
Entropy	0.078	0.090	0.114	0.097	0.119	0.112
Life expectancy at birth	45.9	45.1	41.8	39.55	43.75	42.05
Life expectancy at adult emergence	31.9	31.1	27.8	25.55	29.75	28.05
Under curve area of N_x (insect-day)	928	912	846	801	885	851
Under curve area of life expectancy e_x	1108.42	1070.47	945.75	832.91	1050.67	956.47

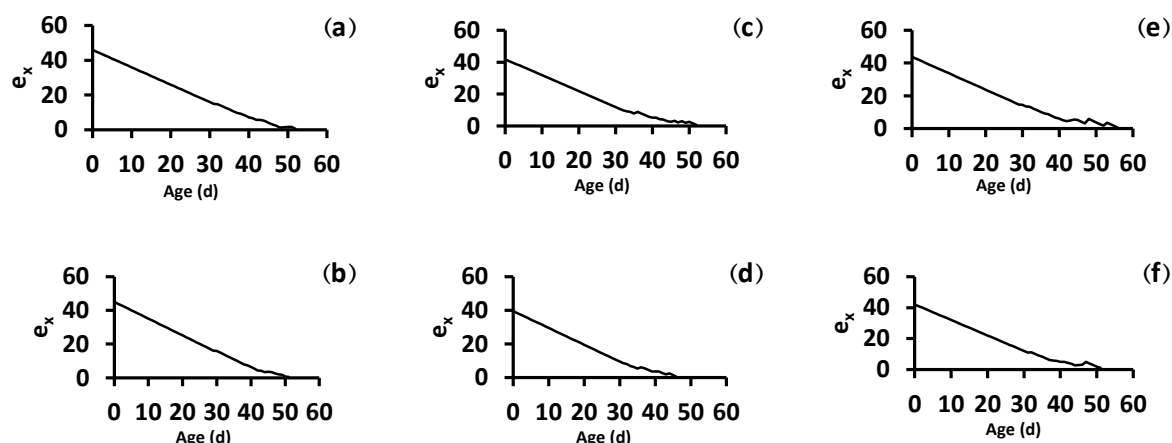


Figure 4. The life expectancy of two *T. vassilievi* populations on two CSP populations and their reciprocal crosses, a) TT, b) TV, c) VT, d) VV, e) T×V, and f) V×T.

Reproduction tables for *T. vassilievi*

The reproductive parameters of *T. vassilievi* on CSP eggs are shown in Table 4. The Varamin population has higher gross and net fecundity and fertility rates than the Tabriz population. The crosses had higher values of these parameters than the main populations, with the highest value

in T×V. The emergence rate of wasps was very high, ranging from 92 to 94%. The mean age of emergence was lower in Tabriz wasps and higher in Varamin wasps than in other treatments. The mean reproductive age for *T. vassilievi* was around 19 days. Other variables are shown in Table 4.

Table 4. Reproductive parameters of *T. vassilievi* on sunn pest eggs.

Treatments	TT	TV	VT	VV	T×V	V×T
Gross fecundity rate	201.53	212.20	229.53	232.56	262.21	250.98
Net fecundity rate	201.39	211.80	229.05	231.80	261.76	250.67
Gross fertility rate	187.20	195.60	211.89	216.52	245.29	234.19
Net fertility rate	187.09	195.26	211.48	215.85	244.97	233.96
Gross hatch rate	0.93	0.92	0.92	0.93	0.94	0.93
Mean age hatch (d)	24.67	24.23	25.97	25.28	24.70	24.95
Mean age gross fecundity (d)	19.17	19.30	19.72	19.82	19.15	19.40
Mean age net fecundity (d)	19.16	19.28	19.69	19.78	19.13	19.38
Mean age gross fertility (d)	19.04	19.11	19.53	19.61	19.01	19.22
Mean age net fertility (d)	19.03	19.09	19.50	19.57	18.99	19.21
Mean egg per day	5.17	5.58	5.89	7.05	6.24	6.44
Mean fertile egg per day	4.80	5.15	5.43	6.56	5.84	6.00
Eggs/female/day	6.31	6.81	8.24	9.07	8.95	5.96
Fertile eggs/female/day	5.86	6.28	7.61	8.45	8.37	5.56

Stable population growth parameters of *T. vassilievi*

Bootstrap estimates of stable population growth parameters of *T. vassilievi* on CSP eggs and their statistical comparisons are shown in Table 5. No significant difference was observed between values in columns 1 and 2, neither between columns 3 and 4. These comparisons refer to host populations and indicate the non-significant effect of the host. In contrast, comparisons between parasitoids of original populations (either between columns 1 and 3 or between columns 2 and 4) indicate significant differences in some parameters. For example, the parasitoid of the Varamin population exhibited a higher level of reproduction (both GRR and R_0) compared to the Tabriz population. On the other hand, *T. vassilievi* from Varamin origin exhibited a higher rate of population increase, finite population increase, birth rate, and shorter doubling time. Crosses showed a higher reproduction rate than both original populations, with a minor advantage of V×T. In addition, their r_m -values were slightly higher than Tabriz parasitoids. Crossing between the two populations resulted in a 13.9 to 18.5% higher net reproduction rate than the maternal populations and 7.7% to 25.2% than the paternal ones. It seems that the reproductive phenotype of the progeny of outcrosses followed the maternal phenotype. The other statistics are also presented in Table 5. Estimates of stable age distribution (C_x) showed that adults make about 1% of a stable population.

215 **Table 5.** Population growth parameters of two populations of *T. vassilievi* on two populations of sunn pest and their reciprocal crosses under
 216 laboratory conditions.

Treatments	TT	TV	VT	VV	T×V	V×T
GRR (female/generation)	168.21±7.24C	172.00±5.06C	188.10±5.93B	190.34±4.03B	208.38±11.06AB	216.38±4.85A
R ₀ (female/generation)	168.14±7.23C	172.00±5.06C	187.95±5.96B	189.86±4.04B	208.23±11.13AB	216.22±4.90A
r _m (d ⁻¹)	0.291±0.0033C	0.296±0.002BC	0.302±0.0023AB	0.303±0.0020AB	0.305±0.0032A	0.302±0.0025AB
λ (d ⁻¹)	1.337±0.0043C	1.345±0.0037BC	1.353±0.0031AB	1.354±0.0027AB	1.357±0.0044A	1.353±0.0033AB
T (d)	17.63±0.13AB	17.37±0.14BC	17.33±0.16BC	17.31±0.10C	17.48±0.13ABC	17.79±0.13A
DT (d)	2.31±0.04A	2.27±0.03AB	2.22±0.03BC	2.21±0.02BC	2.21±0.05C	2.22±0.03BC
b (d ⁻¹)	0.292±0.0033C	0.297±0.0028BC	0.303±0.0023AB	0.304±0.0020AB	0.307±0.0033A	0.303±0.0025AB
d (d ⁻¹)	0.0010±3.4×10 ⁻⁵ C	0.0011±3.02×10 ⁻⁵ BC	0.0012±2.6×10 ⁻⁵ AB	0.0012±2.3×10 ⁻⁵ A	0.0012±3.6×10 ⁻⁵ A	0.0012±2.8×10 ⁻⁵ AB

217 * Means bearing the same capital letters in a row are not significantly different (Bootstrap's pairwise comparisons, α=0.05).

218

219 DISCUSSION

220 In the present study, two geographical populations of *T. vassilievi* were compared in terms of life history parameters by considering two host
 221 populations. On the other hand, out-crosses between populations with the aim of improving parasitoid fitness and breeding parasitoids with superior
 222 characteristics were carried out. Overall, it can be stated that the parasitoids of the Varamin population had a minor advantage over the Tabriz
 223 wasps. The most significant difference was in their reproductive rate, which was 8-15% higher in Varamin wasps. Increased reproduction was due
 224 to 2-days longer oviposition period in the Varamin wasps. However, the daily fecundity rate was similar in both groups and did not differ
 225 significantly. It can therefore be concluded that wasps increase their reproduction by lengthening the oviposition period rather than increasing daily
 226 fecundity; hence, the best way to improve the efficiency of these wasps is to select wasps with longer reproductive periods. Higher fecundity, on
 227 the other hand, reduced female longevity, thus Varamin females lived four days less, while the males lived one day more than the Tabriz population.
 228 The above statements are not true for crosses. The daily and total fecundity of the cross wasps increased independent of the oviposition period, as
 229 they exhibited 20 and 10% higher fecundity compared to Tabriz and Varamin wasps respectively, with similar reproductive periods. This has been
 230 achieved by the introduction of new genes into the genetic pool of the original populations. The reason that males were not affected by crossing,
 231 may be receiving only one copy of their maternal genes.

232

Female longevity is an important qualitative indicator of parasitoids in the field. The longer life span of a parasitoid, the higher encounter to hosts, thus a wasp will have more fortune to find and exploit hosts (Suh *et al.*, 2000). However, higher reproductive effort, results in the exhaustion of females themselves and shortens their lifespan (Krebs and Davies, 1993). This can be deduced by comparing the longevity of the more fecund Varamin population to the Tabriz one. As it can be seen, the Varamin wasps had higher fecundity and at the same time lower life span than the Tabriz wasps which may confirm the above statement.

The average fecundity recorded for *T. vassilievi* in this study is higher than other telenomin species. It was 98.0, 22.4, 29.6, and 63.7 for *T. biproruli*, (James, 1988), *Telenomus calvus* Johnson, (Orr *et al.*, 1986), *T. podisi* Ashmead, and *Trissolcus euschisti* (Ashmead), respectively (Yeargan, 1982). Powell and Shepard (1982) reported 88.1-141.9 broods for different isolates of *T. basalis*. The average progeny number of *T. semistriatus* was reported 88 in Turkey (Kivan and Kilic, 2006), and 210 in Varamin, Iran (Asgari, 2002). Also, it was 85 for Tabriz (Nozad Bonab 2009), and 200 for the Varamin population of *T. grandis* (Amir-Maafi, 2000). The difference between the two populations of *T. vassilievi* was minor and not comparable to the above species. Perhaps one reason is that the physical conditions are quite similar for both populations in the present study while it may be deeply different in the two separate studies on a single species in the above examples. A higher number of daily fecundities may benefit augmentation programs (van Driesche and Bellows, 1996).

The sex ratio of progeny can be changed as parasitoid get older (Bueno *et al.*, 2008; Amir-Maafi and Parker, 2011), because, sperm reserves of the female are depleting and as a result, insemination and consequently the female offspring decreases (Kivan and Kiliç, 2006; Amir-Maafi and Parker, 2011). Higher female progeny benefits the scelionids because reduces the competition between brothers for mating with sisters (Wilson, 1961; Safavi, 1968).

Among the stable population growth parameters of *T. vassilievi*, only the gross and net reproductive rates showed relatively considerable differences among the treatments. In general, cross wasps had higher reproductive rates than original populations, that may be due to flowing new genes in their original pool. The gross and net reproductive rates of *T. grandis* (Amir-Maafi, 2000), and *T. semistriatus* (Asgari, 2002) were 136 and 130 daughters per generation, both less than the values obtained in this study.

The intrinsic rate of population increase (r_m) is a useful indicator of the fitness of a species or population in response to physical and/or nutritional conditions (Southwood and Henderson,

2000). This parameter can be used as a criterion for selecting natural enemies and predicting the success of biocontrol agents (van Lenteren, 2003). The r_m -value of *T. vassilievi* in this study varied between 0.291 and 0.305 d⁻¹, which was slightly higher in Varamin and crossed populations compared to the Tabriz population. It refers mainly to their higher fecundity. Among *Trissolcus* species, the maximum value of r_m has been reported as 0.368 d⁻¹ on *T. grandis* (Nozad Bonab, 2009). The r_m -value of *T. semistriatus* has been 0.226, and 0.227 d⁻¹ for an Iranian and a Turkish population respectively (Asgari, 2002, Kivan and Kilic, 2006). These three species are considered as the most effective species in controlling CSP. Based on R_0 and r_m -values we can rank them as *T. grandis* > *T. vassilievi* > *T. semistriatus*.

The generation time (T) was 17.31-17.79 days for *T. vassilievi* in this study and 13.43 days for *T. grandis* (Amir-Maafi, 2000), which can well explain why *T. grandis* is the most prevalent egg parasitoid species of CSP in Iran (Radjabi and Amir Nazari, 1989). Life history data suggest the high importance of *T. vassilievi* for the biological control of CSP. A highly female-biased sex ratio, high attack rate, and longevity are positive properties for *T. vassilievi*. However, field data at different climatic conditions are essential to prove the role of *T. vassilievi* in large-scale inundation programs. Several field studies indicate the acceptable effect of some telenomins on target pests (Justo *et al.*, 1997; van Lenteren and Bueno, 2003; Asgari *et al.*, 2010; Bagheri Matin *et al.*, 2010; Asgari, 2011).

In conclusion, it can be stated that the host population had no significant effect on parasitism by *T. vassilievi*, however, fecundity was significantly higher in crosses compared to the original populations. This suggests increased fitness of progeny. Similar effects were observed on the thermal phenotypes of this species (Iranipour *et al.*, 2015). This has been demonstrated in some studies (e.g. Carson, 1968; Rasanen and Kruuk, 2007), and nowadays it is accepted as a scientific rule by most biologists and can be used for the artificial selection of parasitoids in the laboratory (Arakawa *et al.* 2004). The intrinsic rate of increase (r_m) of *T. vassilievi* was less variable among treatments of this study and lied between *T. grandis* and *T. semistriatus*. The results of this study revealed that we can benefit from the intra-populations diversity of *Trissolcus* species to obtain more advantageous parasitoids via out-crossing between them.

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REFERENCES

- Abdi, F., Iranipour, S. and Hejazi, M.J. 2017. Reproductive-life table studies on *Trissolcus djadetshkoe* (Hym.: Scelionidae). *Appl. Entomol. Zool.*, 85(1):1-9.
- Ahmadpour S., Iranipour, S. and Asgari, S. 2013. Effects of superparasitism on reproductive fitness of *Ooencyrtus fecundus* Ferriere & Voegelé (Hym. Encyrtidae), egg parasitoid of sunn pest, *Eurygaster integriceps* Puton (Hem. Scutelleridae). *BCPPD.*, 2(2): 97-105.
- Amir-Maafi, M. 2000. An investigation on the host-parasitoid system between *Trissolcus grandis* Thomson (Hym.: Scelionidae) and sunn pest eggs. PhD Thesis, Faculty of Agriculture, University of Tehran, Karaj, Iran. [In Persian with English summary].
- Amir-Maafi, M., Hosseini, M., Tagaddosi, M.V., Nouri, H., Haghshenas, A., Ghazi, M., Pourghz, A., Jamshidi, R., Forouzan, M., and Bagheri, Sh. 2010. The biological control of sunn pest, *Eurygaster integriceps* Put. (Het.: Scutelleridae) using egg parasitoids. Research project, Iranian Research Institute of Plant Protection, Tehran, Iran.
- Amir-Maafi, M. and Parker, B.L. 2011. Biological parameters of the egg parasitoid *Trissolcus grandis* (Hym.: Scelionidae) on *Eurygaster integriceps* (Hem.: Scutelleridae). *J. Entomol. Soc. Iran.*, 30(2): 67-81.
- Arakawa, R., Miura, M. and Fujita, M. 2004. Effects of host species on the body size, fecundity, and longevity of *Trissolcus mitsukurii* (Hymenoptera: Scelionidae), a solitary egg parasitoid of stink bugs. *App. Entomol. Zoolog.*, 39: 177-181.
- Asgari, S. 2002. Comparative fitness of the eggs of *Graphosoma lineatum* (L.) (Pentatomidae) and *Eurygaster integriceps* Put. (Scutelleridae) to the egg parasitoid *Trissolcus semistriatus* Nees (Scelionidae). Ph. D. Thesis. Tarbiat Modares University, Tehran, Iran. [In Persian with English summary].
- Asgari, S. 2011. Inundative release of the sunn pest egg parasitoid and evaluation of its performance. Proceedings of the Biological Control Development Congress in Iran. 27-28 July, Tehran, Iran. Pp. 423–428. [In Persian with English summary].
- Asgari S. and Kharrazi Pakdel, A. 1998. Evaluation of some biological parameters affecting sunn pest egg parasitoid, *Trissolcus grandis* (Thom.) (Hym., Scelionidae). Proceedings of the 13th Iranian Plant Protection Congress, 23–27 August, Karaj, Iran. Vol. 1. p. 28.
- Asgari, S., Safari, M. and Hassani, A.A. 2010. Mass rearing, releasing, and performance of sunn pest egg parasitoids. *Proceedings of the* 19th Iranian Plant Protection Congress, 31 July–3 August, Iranian Research Institute of Plant Protection, Tehran, Iran. p.72.

- 332 Awan, M.S., Wilson, L.T. and Hoffmann, M.P. 1990. Comparative biology of three geographic
333 populations of *Trissolcus basalis* (Hymenoptera: Scelionidae). *Environ. Entomol.*, 19(2):
334 387-392.
- 335 Bagheri Matin, S., Safavi, A., Babakfard, A and Maleki, N. 2010. Study on efficacy of releasing
336 *Trissolcus grandis* Thom. (Hym: Scelionidae) on controlling *Eurygaster integriceps* Put.
337 (Het.: Scutelleridae) in wheat fields of Kermanshah province. *Proceedings of the 19th*
338 *Iranian Plant Protection Congress*, 31 July–3 August, *Iranian Research Institute of Plant*
339 *Protection, Tehran, Iran.* p.32
- 340 Bazavar A., Iranipour S. and Karimzadeh R. 2015. Effect of host unavailability durations on
341 parasitism behavior of *Trissolcus grandis* (Hymenoptera: Scelionidae) egg parasitoid of
342 sunn pest. *J. Appl. Res. Plant Prot.*, 4(1): 41-56.
- 343 Benamolaei, P., Iranipour, S. and Asgari, S. 2015a. Effect of the host embryogenesis on
344 efficiency of *Trissolcus vassilievi*. *BCPP.*, 3(1): 83-100.
- 345 Bena molaei, P., Iranipour, S., and Asgari, S. 2015b. Biostatistics of *Trissolcus vassilievi*
346 (Hym., Scelionidae) developed on sunn pest eggs cold-stored for different durations. *Mun.*
347 *Ent. Zool.*, 10(1): 259-271.
- 348 Bueno, R.C.O., Carneiro, T.R., Pratisoli. D., Bueno, A.D.F. and Fernandes, A. 2008. Biology
349 and thermal requirements of *Telenomus remus* reared on fall armyworm *Spodoptera*
350 *frugiperda* eggs. *Cienc. Rural.*, 38(1): 1-6.
- 351 Carey, J.R. 1993. *Applied Demography for Biologists with Special Emphasis on Insects*. Oxford
352 University Press, UK.
- 353 Carson, H.L. 1968. The population flush and its genetic consequences. In: "*Population Biology*
354 *and Evolution*", (ed.) Lewontin, R.C. Syracuse University Press, Syracuse, New York, pp.
355 123–137.
- 356 Iranipour, S. 2018. A Microsoft Excel program for Bootstrap estimates of reproductive-life
357 table parameters. *J. Crop Prot.*, 7(3): 247-258.
- 358 Iranipour, S., Benamolaei, P., Asgari, Sh and Michaud, J.P. 2015. Reciprocal crosses between
359 two populations of *Trissolcus vassilievi* (Mayr) (Hymenoptera: Scelionidae) reveal
360 maternal effects on thermal phenotypes. *Bull. Entomol. Res.*, 105: 355-363.
- 361 James, D.G. 1988. Fecundity, longevity and overwintering of *Trissolcus biproruli* Girault
362 (Hymenoptera: Scelionidae) a parasitoid of *Biprorulus bibax* Breddin (Hemiptera:
363 Pentatomidae). *J. Austral. Ent. Soc.*, 27: 297–301.
- 364 Justo, H.D., Shepard B.M., and Elsey. K.D. 1997. Dispersal of the egg parasitoid *Trissolcus*
365 *basalis* (Hymenoptera: Scelionidae) in tomato. *J. Agr. Entomol.*, 14: 139–149.

366 Kivan, M. and Kiliç, N. 2006. Age-specific fecundity and life table of *Trissolcus semistriatus*,
 367 an egg parasitoid of the sunn pest *Eurygaster integriceps*. *Entomol. Sci.*, 9: 39-46.

368 Kozlov, M.A. and Kononova, S.V. 1983. Telenominae of the fauna of the USSR (Hymenoptera,
 369 Scelionidae, Telenominae). *Leningrad Nauka Publisher*, 136, 336 pp.

370 Krebs, J.R. and Davies, N.B. 1993. *An Introduction to Behavioural Ecology*. Wiley Blackwell.

371 Laumann, R.A., Moraes, M.C.B., Pareja, M., Alarca, G.C., Botelho, A.C., Maia, A.H.N.,
 372 Leonardecz, E. and Borges, M. 2008. Comparative biology and functional response of
 373 *Trissolcus* spp. (Hymenoptera: Scelionidae) and implications for stink bugs (Hemiptera:
 374 Pentatomidae) biological control. *Biol. Control.*, 44: 32-41.

375 Lotka, A.J. 1907a. Relation between birth rates and death rates. *Science.*, 26: 21-22.

376 Lotka, A.J. 1907b. Studies on the mode of growth of material aggregates. *Am. J. Sci.*, 4(24):
 377 199-216.

378 Mele, A., Avanigadda, D. S., Ceccato, E., Olawuyi, G. B., Simoni, F., Duso, C., Scaccini, D.
 379 and Pozzebon, A. 2024. Comparative life tables of *Trissolcus japonicus* and *Trissolcus*
 380 *mitsukurii*, egg parasitoids of *Halyomorpha halys*. *Biol. Control.*, 195: 105548.

381 Meyer, J.S., Ingersoll, C.G., Mac Donald, L.L. and Boyce, M.S. 1986. Estimating uncertainty
 382 in population growth rates: jackknife vs. bootstrap techniques. *Ecology.*, 67: 1156-1166.

383 Nouri, H., Amir-maafi, M. and Forouzan, M. 2011. Introduction of sunn pest egg parasitoids in
 384 Qazvin, Iran. Proceedings of the Biological Control Development Congress in Iran. 27-28
 385 July, Tehran, Iran, pp. 417–422. [In Persian with English summary].

386 Nozad Bonab, Z. 2009. Effect of temperature on development, fecundity and longevity of
 387 *Trissolcus grandis* Thomson (Hym.: Scelionidae). M.Sc. thesis, Faculty of Agriculture,
 388 University of Tabriz, Tabriz, Iran. [In Persian with English summary].

389 Nozad Bonab, Z., Iranipour, S. and Farshbaf Pourabad, R. 2014. Demographic parameters of
 390 two populations of *Trissolcus grandis* (Thomson) (Hymenoptera: Scelionidae) at five
 391 constant temperatures. *JAST.*, 16 (5): 969-979.

392 Orr, D.B., Russin, J.S. and Borthel, D.J. 1986. Reproductive biology and behavior of *Telenomus*
 393 *calvus* (Hymenoptera: Scelionidae), a phoretic egg parasitoid of *Podisus maculiventris*
 394 (Hemiptera: Pentatomidae). *Can. Entomol.*, 118: 1063-1072.

395 Portilla, M., Morales-Ramos, J. A., Rojas, M. G. and Blanco, C. A. 2014. Life Tables as Tools
 396 of Evaluation and Quality Control for Arthropod Mass Production. In: *Mass Production of*
 397 *Beneficial Organisms: Invertebrates and Entomopathogens*, Academic Press, Cambridge,
 398 MA, USA, pp. 241–275.

- 399 Powell, J.E. and Shepard, M. 1982. Biology of Australian and United States strains of
400 *Trissolcus basalis*, a parasitoid of the green vegetable bug, *Nezara viridula*. *Aust. J. Ecol.*,
401 7: 181-186.
- 402 Radjabi, G. and Amir Nazari, M. 1989. Egg parasites of sunn pest in the central part of the
403 Iranian plateau. *Appl. Entomol. Phytopathol.*, 56: 1–12. [In Persian with English summary].
- 404 Rasanen, K. and Kruuk, L.E.B. 2007. Maternal effects and evolution at ecological time-scales.
405 *Funct. Ecol.*, 21:408–421.
- 406 Safavi, M. 1968. Etude Biologique et Ecologique des Hymenopteres Parasites des Oeufs des
407 Punaises des Cereales. *Entomophaga.*, 13: 381-495.
- 408 Safavi, M. 1973. Etude bio-ecologique des Hymenoptères parasites des oeufs des punaises des
409 cereales en Iran. Ministry of Agriculture and Natural Resources, Tehran, Iran, [In Persian].
- 410 Southwood, T.R.E. and Henderson, P.A. 2000. *Ecological methods*. 3rd edition. Blackwell
411 Science.
- 412 Suh, C.B.C., Orr, D.B. and van Duyn, J.W. 2000. *Trichogramma* releases in North Carolina
413 cotton: Why releases fail to suppress Heliothine pests. *J. Econ. Entomol.*, 93: 1137-1145.
- 414 Taghadosi, M.V., Kharrazi Pakdel, A. and Esmaili, M.M. 1993. A comparative study on
415 reproductive potential of different populations of *Trissolcus grandis* Thomson (Hym.,
416 Scelionidae), on eggs of sunn pest *Eurygaster integriceps* Put. (Het., Scutelleridae). In
417 Proceedings of the 11th Iranian Plant Protection Congress, 27 August - 1 September,
418 University of Guilan, Rasht, Iran. p. 7.
- 419 Teimouri, N., Iranipour, S. and Benamolaei, P. 2019. Effect of Light Intensity and Photoperiod
420 on Development, Fecundity, and Longevity of *Trissolcus grandis* (Hym.: Platygasteridae),
421 Egg Parasitoid of Sunn Pest, *Eurygaster integriceps* Puton (Hem.: Scutelleridae). *J. Appl.*
422 *Res. Plant Prot.*, 8(3): 77-93.
- 423 van Driesche, R.G. and Bellows, T.S.Jr. 1996. *Biological Control*. Chapman and Hall, New
424 York.
- 425 van Lenteren, J.C. 2003. *Quality Control and Production of Biological Control Agents: Theory*
426 *and Testing Procedures*. CABI Publication.
- 427 van Lenteren, J.C. and Bueno, V.H.P. 2003. Augmentative biological control of arthropods in
428 Latin America. *BioControl.*, 48: 123–139.
- 429 Wilson, F. 1961. Adult behavior in *Asolcus basalis* (Hymenoptera: Scelionidae). *Aust. J. Zool.*,
430 9(5): 737-751.
- 431 Yeargan, K.V. 1982. Reproductive capability and longevity of the parasitic wasps *Telenomus*
432 *podisi* and *Trissolcus euschisti*. *Ann. Entomol. Soc. Am.*, 75: 181-183.