

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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31 growth parameters in egg parasitoids of common sunn pest (CSP), *Eurygaster integriceps* Puton
32 (Hem., Scutelleridae), and related stinky bugs. These are dominantly on *Trissolcus* spp. and
33 *Telenomus* spp. (Hymenoptera: Scelionidae) (Asgari and Kharrazi Pakdel 1998; Laumann *et al.*
34 2008; Amir-Maafi and Parker, 2011, Nozad-Bonab *et al.* 2014, Bazavar *et al.* 2015, Benamolaei
35 *et al.* 2015 a, b, Abdi *et al.*, 2017, Teimouri *et al.* 2019), and *Ooencyrtus* spp. (Hymenoptera:
36 Encyrtidae) (Ahmadpour *et al.* 2013, Mele *et al.* 2024).

37 There is little information about intra- and inter-specific variation of survival value and
38 reproductive potential of egg parasitoids of CSP, and it is limited to few studies. In the 1970s,
39 several species of CSP's egg-parasitoids, collected from different regions of the world, were
40 transferred to the former Soviet Union and compared with native species, especially *Trissolcus*
41 *grandis* (Thomson), in laboratory and field conditions. The overall result of this study showed
42 that native species had superiority and it was due to the adaptation of native species to climatic
43 and seasonal conditions (Nouri *et al.*, 2011). Awan *et al.* (1990) compared three geographical
44 populations of *T. basalis* (Wollaston) collected from France, Italy, and Spain regarding
45 biological and behavioral characteristics. The emergence rate of adult wasps from *Nezara*
46 *viridula* (L.) eggs was significantly higher in the French population than in the Italian and
47 Spanish ones. The development of immature stages of the Italian population was significantly
48 longer than the other two populations. Taghadosi *et al.* (1993) and Nozad Bonab *et al.* (2014)
49 observed differences among populations of *T. grandis* of Tehran-Alborz-Qazvin and East
50 Azarbaijan provinces respectively. A comparison of biostatistics of Scelionidae by Amir-Maafi
51 (2010) during 2004-2006 in different provinces of Iran revealed significant differences between
52 species and populations of the wasps. Fecundity, oviposition period, and gross and net
53 reproductive rates differed between species or populations. The net fecundity of *T. vassilievi*
54 (Mayr) from Lorestan and Tehran was 240.8 and 227.5 eggs respectively, which was 2.5 times
55 as much as the other populations. The highest intrinsic rate of increase of *T. grandis*, *T.*
56 *semistriatus* (Nees), and *T. vassilievi* was recorded for Golestan, West Azarbaijan, and Tehran
57 provinces, respectively.

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

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

68 MATERIAL AND METHODS

69 Cultures of *Eurygaster integriceps* Puton

70 Adult bugs were collected on several occasions at the end of the winter from mountains around
71 Tabriz and Varamin before leaving the resting sites. Collectings of specimens were continued
72 in wheat fields during post diapause phase. The collected insects were transferred to a
73 greenhouse unit of the Department of Plant Protection, Faculty of Agriculture, University of
74 Tabriz. Transparent rectangular cubic plastic containers (20×30×9cm) equipped with a mesh
75 cap for ventilation were used for the rearing of both populations. Dry wheat grain was used as
76 a foodstuff and soaked cotton balls as a water source. The paper strips folded fan-like to be
77 served as an oviposition substrate. These insects were exposed to 25±2 °C, 40±10% RH, and
78 16: 8 h L: D photoperiod (Iranipour *et al.* 2015).

79 Cultures of *Trissolcus vassilievi* (Mayr)

80 In this study, two populations of *T. vassilievi*, namely original populations, one from Tabriz
81 (1360 AMSL, 46°E, 38°N) and the other from Varamin (918 AMSL, 51°E, 35°N) were
82 examined. To collect egg parasitoids, host egg traps (yellow cardboards, 5×15 cm, folded twice
83 to construct a Δ-shaped structure) were used (Safavi, 1973). The traps were tied to wheat ears
84 and removed after one week, then the parasitized eggs were transferred to glass vials (1.5×10
85 cm) and kept in a growth chamber (Iran Khodsaz Co., IKH.RH model) under constant
86 conditions (26±1 °C, 50±5% RH and 16:8 h L:D photoperiod). The emerged wasps were
87 identified by the identification key of Kozlov and Kononova (1983). After rearing for one
88 generation, males and females of the second generation from the same population were
89 randomly coupled and each pair was transferred to a similar vial supplied by host eggs of either
90 population. Small drops of honey were used to feed the wasps.

92 Fecundity-life table studies

93 Ten clutches of 24-hour-old CSP eggs (14 eggs per clutch) from each population were exposed
94 to 48-hour-old mated *T. vassilievi* females of second-generation of each population. After 24
95 hours, females were removed and the host eggs were kept as a life table cohort in so-called
96 growth chambers to determine their fate. The experiment was conducted as a factorial
97 experiment in a completely randomized design framework, with two factors including wasp
98

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

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

110

111 Measures of stable population growth parameters

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

$$114 \quad H = \frac{\sum_{x=0}^{\omega} e_{x} d_x}{e_0} \quad \text{Eq.1}$$

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

$$122 \quad \sum_{x=0}^{\omega} e^{-r_m x} l_x m_x = 1 \quad \text{Eq.2}$$

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

126

127 Statistical analyses

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

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

138
 139 **RESULTS**

140 **Life history parameters of *T. vassilievi***

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

145 **Table 1.** Analysis of variance of life history components of two populations of *T. vassilievi* on
 146 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

147 * df for all treatments=1,76.

148
 149 Analysis of variance showed that there was a significant difference in the longevity of both
 150 females and males when crosses were included as well (Tabriz population, Varamin population,
 151 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
 152 male longevity). The highest longevity of females and males was observed in Tabriz and
 153 Varamin wasps, respectively (Table 2).

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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

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* 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.

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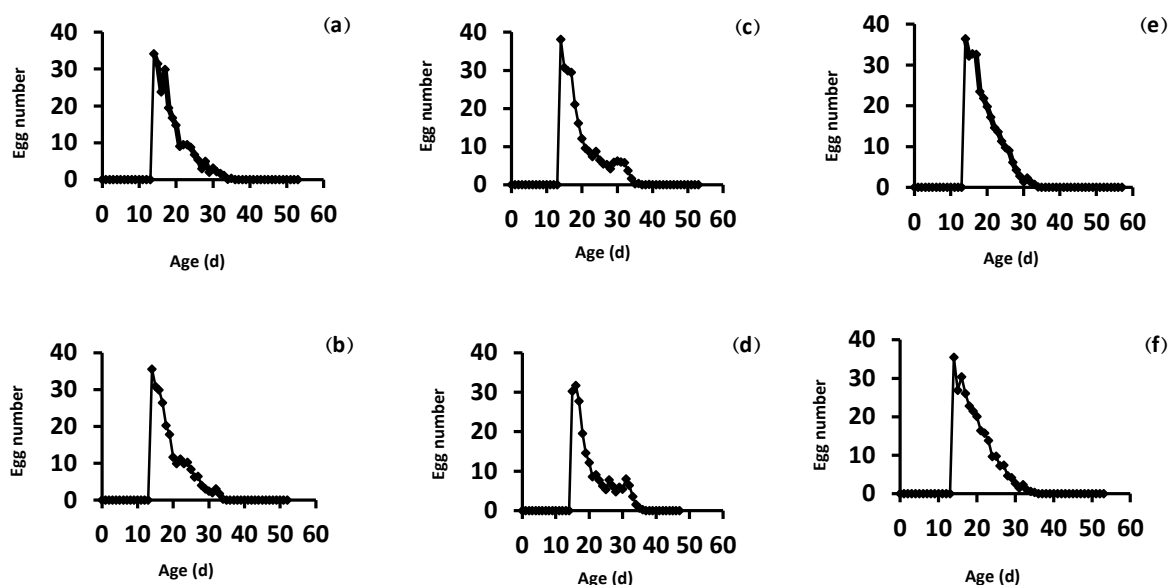
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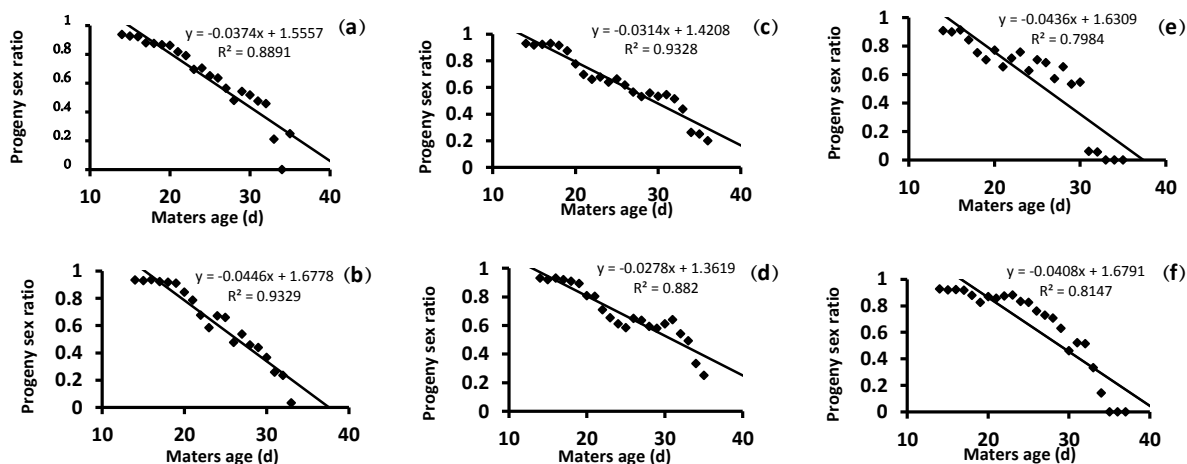
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Female wasps from the crosses showed intermediate longevity of the two populations so their differences were not significant with either population. However, the male progeny of crosses had a shorter lifespan than their parents (Table 2). Females lack 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).



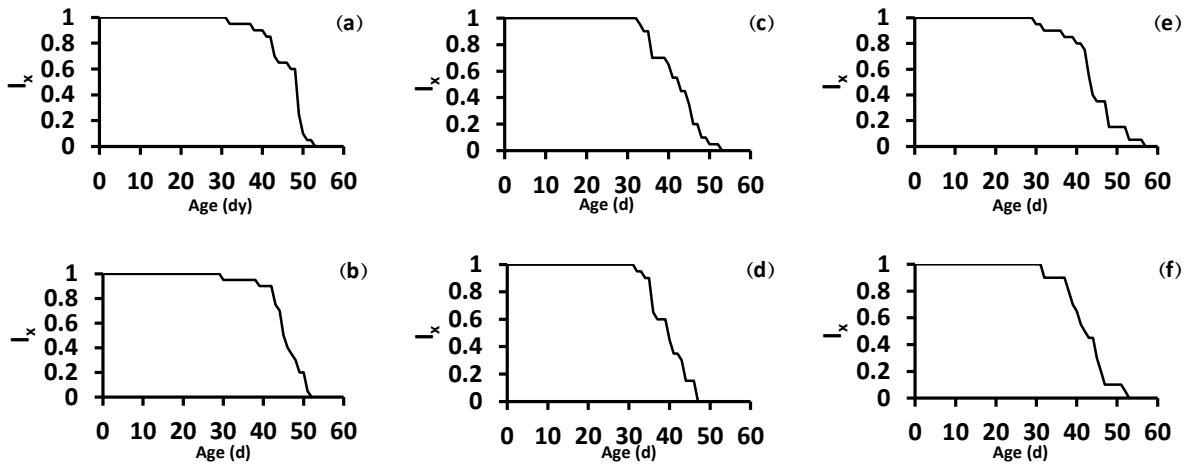
166 **Figure 1.** The trend of Oviposition of two *T. vassilievi* populations on two CSP populations
 167 and their reciprocal crosses, a) TT, b) TV, c) VT, d) VV, e) T×V, and f) V×T.
 168



169 **Figure 2.** Age-specific sex ratio of two *T. vassilievi* populations on two CSP populations and
 170 their reciprocal crosses, a) TT, b) TV, c) VT, d) VV, e) T×V, and f) V×T.
 171

172 Life tables and survivorship curves of *T. vassilievi*

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



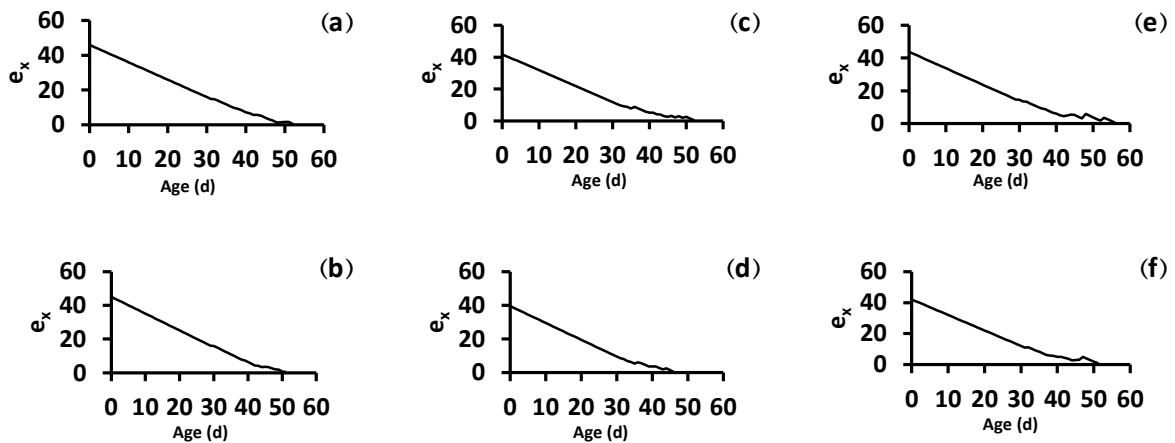
178 **Figure 3.** The survivorship curve of two *T. vassilievi* populations on two CSP populations and
 179 their reciprocal crosses, a) TT, b) TV, c) VT, d) VV, e) T×V, and f) V×T.

180

181 **Table 3.** Life table statistics of two *T. vassilievi* populations on two CSP populations and their
 182 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

183



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

186

187 **Reproduction tables for *T. vassilievi***

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

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

195 **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

196 **Stable population growth parameters of *T. vassilievi***

197 Bootstrap estimates of stable population growth parameters of *T. vassilievi* on CSP eggs and
 198 their statistical comparisons are shown in Table 5. No significant difference was observed
 199 between values in columns 1 and 2, neither between columns 3 and 4. These comparisons refer
 200 to host populations and indicate the non-significant effect of the host. In contrast, comparisons
 201 between parasitoids of original populations (either between columns 1 and 3 or between
 202 columns 2 and 4) indicate significant differences in some parameters. For example, the
 203 parasitoid of the Varamin population exhibited a higher level of reproduction (both GRR and
 204 R_0) compared to the Tabriz population. On the other hand, *T. vassilievi* from Varamin origin
 205 exhibited a higher rate of population increase, finite population increase, birth rate, and shorter
 206 doubling time. Crosses showed a higher reproduction rate than both original populations, with
 207 a minor advantage of V×T. In addition, their r_m -values were slightly higher than Tabriz
 208 parasitoids. Crossing between the two populations resulted in a 13.9 to 18.5% higher net
 209 reproduction rate than the maternal populations and 7.7% to 25.2% than the paternal ones. It
 210 seems that the reproductive phenotype of the progeny of outcrosses followed the maternal
 211 phenotype. The other statistics are also presented in Table 5. Estimates of stable age distribution
 212 (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

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

240 The average fecundity recorded for *T. vassilievi* in this study is higher than other telenomin
241 species. It was 98.0, 22.4, 29.6, and 63.7 for *T. biproruli*, (James, 1988), *Telenomus calvus*
242 Johnson, (Orr *et al.*, 1986), *T. podisi* Ashmead, and *Trissolcus euschisti* (Ashmead),
243 respectively (Yeorgan, 1982). Powell and Shepard (1982) reported 88.1-141.9 broods for
244 different isolates of *T. basalis*. The average progeny number of *T. semistriatus* was reported 88
245 in Turkey (Kivan and Kilic, 2006), and 210 in Varamin, Iran (Asgari, 2002). Also, it was 85
246 for Tabriz (Nozad Bonab 2009), and 200 for the Varamin population of *T. grandis* (Amir-Maafi,
247 2000). The difference between the two populations of *T. vassilievi* was minor and not
248 comparable to the above species. Perhaps one reason is that the physical conditions are quite
249 similar for both populations in the present study while it may be deeply different in the two
250 separate studies on a single species in the above examples. A higher number of daily fecundities
251 may benefit augmentation programs (van Driesche and Bellows, 1996).

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

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

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

265 2000). This parameter can be used as a criterion for selecting natural enemies and predicting
266 the success of biocontrol agents (van Lenteren, 2003). The r_m -value of *T. vassilievi* in this study
267 varied between 0.291 and 0.305 d^{-1} , which was slightly higher in Varamin and crossed
268 populations compared to the Tabriz population. It refers mainly to their higher fecundity.
269 Among *Trissolcus* species, the maximum value of r_m has been reported as 0.368 d^{-1} on *T.*
270 *grandis* (Nozad Bonab, 2009). The r_m -value of *T. semistriatus* has been 0.226, and 0.227 d^{-1} for
271 an Iranian and a Turkish population respectively (Asgari, 2002, Kivan and Kilic, 2006). These
272 three species are considered as the most effective species in controlling CSP. Based on R_0 and
273 r_m -values we can rank them as *T. grandis* > *T. vassilievi* > *T. semistriatus*.

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

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

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