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Rejuvenation improves the quality of *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae) reared for many generations on *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae)

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Abstract

Background: Domestication usually has negative effects on insect performance, especially when they are reared continuously for many generations. Rejuvenation can reduce the negative effects of domestication in the parasitoid, *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae) reared for 30 generations (G) on *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae). Life table and parasitism parameters in the primary colony (G31–G45) were compared with the respective colony rejuvenated with field-collected individuals.

Results: There were significant differences in life history traits between domesticated and rejuvenated populations. The highest (38.4 eggs/female) and lowest (13.3 eggs/female) fecundity was observed in rejuvenated G31 and domesticated G45, respectively. The highest values of the life table and parasitism parameters were observed in rejuvenated G31 without significant difference with G32, G33 and G34. The relationship between finite parasitism rate (ω) and generation number in both rejuvenated and domesticated populations were fitted to the cubic regression model, indicating the parasitism potential of *T. brassicae* increased significantly after adding feral individuals but decreased remarkably over the generations.

Conclusions: Therefore, it seems that adding 10% feral individuals re-established the reproductive performance of the wasps at least for four generations, and it needs to be repeated routinely or it needs to be made by adding a higher rate of feral individuals. However, this issue should be investigated by more studies in which different rates of feral individuals are added to the primary colony.

Keywords: *Trichogramma brassicae*, *Sitotroga cerealella*, Mass rearing, Feral population, Generation-dependent demography

Background

There is an increasing interest globally for using natural enemies against pests so that many of these organisms are cultured and traded by companies in many countries. To achieve and maintain successful biological control, these organisms need to be checked qualitatively both during production and after being released, because they may lose some attributes after continuous mass rearing

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that are necessary for biocontrol agents being released in an augmentative program (Yazdanpanah et al. 2022). Natural enemies applied for the control of pests under field conditions are being reared in insectaries for many generations, and their potential may decrease and cause the biological control program to fail. Long-term mass rearing under such conditions may promote inbreeding and lead to inefficiency under field conditions (Hopper et al. 1993). Domestication usually causes insects to experience homogeneous environment that lacks the challenges of natural conditions. In some cases, the targeted traits are so essential for success of natural enemies under field conditions (Bartlett 1984). Whether quality changes occur in continuous rearing should be determined prior to inundative release programs and to support recommendations for routinely rejuvenating commercial cultures using wild insects (Smith 1996), prevent inbreeding and conserving the gene pool (van Lenteren 2003).

The egg-parasitoid, *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae) is one of the widely used biocontrol agents in Iran (Moghaddassi et al. 2019) and in other countries (Cônsoli et al. 2010), commonly mass reared on various factitious hosts, such as the Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) (Wang et al. 2014). In a previous studies, a large decrease in the quality of *T. brassicae* over long-term mass rearing was found (Ghaemmaghami et al. 2021). To find whether rejuvenation can reduce the negative effects of domestication in *T. brassicae* wasps continuously mass reared for many generations was endeavored. The present study aimed to compare life table and parasitism parameters of the domesticated and rejuvenated populations of *T. brassicae* under long-term mass rearing. This could deepen our knowledge for improving biological control programs using high-quality parasitoid.

Methods

Insects rearing

A colony of Angoumois grain moth, *S. cerealella*, was established on barley grains under ambient temperature (25 ± 1 °C) in a biocontrol laboratory of the Technical and Vocational Training Center of Estahban, Fars province, Iran. Emerged adults were transferred to funnels (diameter 20 cm) covered with a fine mesh net over the mouth. After mating, the eggs were collected on papers placed under the open side of the funnel. The domesticated population data were extracted from Ghaemmaghami et al. (2021). To obtain a stock to initially create the primary colony of *T. brassicae*, egg traps, pieces of white papers (21 × 11 cm) containing *S. cerealella* eggs, were placed on tomato farms in Karaj (51°00′ E, 35°48′ N), Iran, in May 2017. The traps were recollected after 48 h, and the parasitized eggs were incubated in a growth chamber set at 25 ± 1 °C, 65 ± 5% RH and a 16:8 h (L:D) photoperiod until the emergence of *T. brassicae* adults (G0), which were then reared in rectangular plastic containers (35 × 20 × 15 cm) on *S. cerealella* eggs under the same conditions mentioned above. The parasitoids were reared sequentially for 45 generations, and for tested generations, a cohort of parasitized eggs were separated.

To rejuvenate the colony, after 30 generations of domestication, field-collected parasitoids were added to the colony. Feral individuals of *T. brassicae* were collected using egg traps as mentioned above. The parasitized eggs were separately added to a part of primary population in 1:10 ratio (feral: primary). The first generation in the rejuvenated population corresponded to the 31st generation in the domesticated one. The rearing conditions were similar to those for primary colony.

Assessment procedure

Around 80 one-day-old parasitized eggs were harvested randomly from the primary (≈ 1000 wasps) and rejuvenated colony (≈ 1000 wasps) and kept in a glass container (6 cm in diameter, 5 cm in height) until the emergence of the adult wasps. Male and female wasps were then paired and placed in glass cylinders (10 × 1.6 cm) containing about 150 one-day-old host eggs (stuck to paper tape; 1 × 5 cm). The wasps were supplied with diluted honey on cotton rolls as a carbohydrate source during oviposition. If a male died, it was replaced by a newly emerged (< 24 h old) male from the stock colony. These individuals were excluded from analyses. The wasps were checked daily until the death of the last individual and the number of parasitized eggs, development time, adult longevity, fecundity and their mortality and survival rate were estimated. These procedures were repeated for generations 31, 32, 33, 34, 35, 36, 40 and 45 of the primary colony and simultaneously for the respective generations in the rejuvenated population. All experiments were carried out in an incubator set at 26 ± 1 °C, 65 ± 5% RH and a photoperiod of 16:8 h (L:D).

Data analysis

The life history data of all individuals were analyzed using age-stage, two-sex life table theory (Chi 1988). Data analysis and population parameters including gross reproductive rate (GRR), net reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ) and mean generation time (T) were calculated by TWOSEX-MSChart program (Chi 2019). A bootstrap procedure was used to estimate the variances and the standard errors of population parameters (Huang and Chi 2012). To obtain stable estimates, 100,000 bootstrap samples were used. Bootstrap values of different generations of *T. brassicae* were

then compared via paired-bootstrap procedure (Bahari et al. 2018).

Data obtained on daily parasitism rates of the total cohort were used to estimate the parasitism parameters for each of the different generations. The estimated parameters included net parasitism rate (c_0), transition rate (Q_p), stable parasitism rate (ψ) and finite parasitism rate (ω). c_0 describes the mean number of hosts parasitized by an individual parasitoid during its entire life span. Q_p is the transformation rate from host population to parasitoid offspring. ψ is the total parasitism capacity of a stable population with the same total size. The finite parasitism rate (ω) estimates the parasitism potential of a parasitoid population by combining its growth rate (λ), age-stage parasitism rate (c_{xj}) and stable age-stage structure (a_{xj}) (Chi and Yang 2003).

Parasitism rate data were analyzed using the computer program CONSUME-MSChart (Chi 2019). The bootstrap resampling method (100,000 bootstraps) was used to estimate the variances and the standard errors of the parameters. Comparison of parasitism parameters was done based on paired-bootstrap test using TWOSEX-MSChart program (Chi 2019).

One-way ANOVA was used to analyze fecundity and durations of different life stages of the domesticated and rejuvenated populations of *T. brassicae,* and in the case of significant differences, mean comparisons were made using Tukey's test (SPSS-Inc, 2009). Mean comparison among corresponding generations was analyzed using *t* tests using SPSS program (SPSS-Inc 2009). Domesticated population data were extracted from Ghaemmaghami et al. (2021).

Results

Life duration, survival rate and fecundity

Except for domesticated G45, none of generations in domesticated and rejuvenated populations had significant differences in the female longevity and total life span with rejuvenated G31. Domesticated G45 had shorter female longevity (3.75 d) than rejuvenated G31 (5.24 d), and a shorter total life span (14.12 d) than rejuvenated G31 (15.49 d) and G32 (15.50 d). Rejuvenated G31 had longer male adult longevity (5.48 d) than domesticated G40 (4.05 d) and G45 (4.06 d) (Table 1).

There were significant differences between domesticated and rejuvenated populations in terms of oviposition days of the wasps (Table 1). The length of oviposition days ranged from 3.84 d in rejuvenated G31 to 2.55 d in domesticated G45. Mean comparison of oviposition days between corresponded generations

Table 1 Mean (±SE) duration of different life stages (day) and fecundity (eggs±SE) in different generations of the primary and rejuvenated populations of *Trichogramma brassicae* on *Sitotroga cerealella* eggs

Population	Generation	Number of individuals	Adult longevity (Female)	Adult longevity (Male)	Total life span (day)	Oviposition days	Fecundity
Rejuvenated population	31	76	5.2 ± 0.4^{a}	$5.5\pm0.3^{a*}$	$15.5\pm0.3^{a*}$	$3.8\pm0.2^{a**}$	$38.4\pm3.2^{a**}$
	32	74	5.0 ± 0.3^{ab}	$5.3\pm0.3^{ab*}$	$15.5\pm0.3^{a*}$	$3.7\pm0.2^{a**}$	$35.1\pm2.9^{ab**}$
	33	75	4.8 ± 0.3^{ab}	5.0 ± 0.3^{ab}	$15.3\pm0.3^{ab*}$	$3.6\pm0.2^{ab**}$	$33.0\pm2.7^{abc**}$
	34	72	4.6 ± 0.3^{ab}	4.8 ± 0.3^{ab}	15.2 ± 0.2^{ab}	$3.5\pm0.2^{abc*}$	$31.0\pm2.7^{abcd**}$
	35	73	4.2 ± 0.3^{ab}	4.7 ± 0.3^{ab}	15.0 ± 0.2^{ab}	3.1 ± 0.2^{abcd}	$25.9\pm2.4^{bcde**}$
	36	74	4.1 ± 0.3^{ab}	4.4 ± 0.2^{ab}	14.8 ± 0.2^{ab}	3.1 ± 0.2^{abcd}	$24.7\pm2.2^{cdef**}$
	40	77	$4.9\pm0.3^{ab**}$	4.6 ± 0.2^{ab}	14.9 ± 0.3^{ab}	3.2 ± 0.2^{abcd}	$22.2\pm1.7^{efgh**}$
	45	75	$4.4\pm0.2^{ab*}$	4.4 ± 0.3^{ab}	14.6 ± 0.2^{ab}	2.8 ± 0.1^{bcd}	$17.9\pm1.3^{fgh**}$
Domesticated population	31	74	4.6 ± 1.5^{ab}	4.5 ± 0.3^{ab}	14.7 ± 0.2^{ab}	2.9 ± 0.1^{bcd}	18.8 ± 1.3^{fgh}
	32	75	4.5 ± 1.5^{ab}	4.4 ± 0.3^{ab}	14.6 ± 0.2^{ab}	2.8 ± 0.1^{bcd}	18.3 ± 1.3^{fgh}
	33	76	4.4 ± 1.5^{ab}	4.2 ± 0.2^{ab}	14.6 ± 0.2^{ab}	2.9 ± 0.1^{bcd}	18.0 ± 1.3^{fgh}
	34	74	4.4 ± 1.5^{ab}	4.3 ± 0.2^{ab}	14.6 ± 0.2^{ab}	2.8 ± 0.1^{bcd}	17.8 ± 1.3^{fgh}
	35	77	4.4 ± 1.5^{ab}	4.1 ± 0.2^{b}	14.4 ± 0.2^{ab}	2.8 ± 0.1^{bcd}	17.6 ± 1.3^{fgh}
	36	75	4.4 ± 1.5^{ab}	4.2 ± 0.2^{ab}	14.5 ± 0.2^{ab}	2.8 ± 0.1^{bcd}	17.4 ± 1.3^{fgh}
	40	76	4.0 ± 1.3^{ab}	4.0 ± 0.2^{b}	14.3 ± 0.2^{ab}	2.7 ± 0.1^{cd}	15.9 ± 1.3^{gh}
	45	75	3.7 ± 1.4^{b}	4.1 ± 0.2^{b}	14.1 ± 0.2^{b}	2.5 ± 0.1^{d}	13.3 ± 1.1^{h}
	F		2.143	2.516	2.673	5.310	15.795
	df1,df2		15,633	15,343	15,1182	11,577	15,633
	P		0.007	0.002	< 0.001	< 0.001	< 0.001

The means followed by the same letter in each column (including both rejuvenated and domesticated population) are not significantly different ($P > 0.05$, Tukey's test). The means with one or twoasterisk in the respective generations are different according to independent sample *t* tests at $\alpha = 0.05$ and 0.01, respectively

showed significant differences in G31 ($t=3.427$; d$f=1.72$; $P=0.004$), G32 ($t=3.266$; d$f=1.74$; $P=0.001$), G33 ($t=2.777$; d$f=1.5$; $P=0.001$) and G34 ($t=2.668$; d$f=1.71$; $P=0.004$). Fecundity was different in the rejuvenated and domesticated populations. The highest (38 eggs/female) and lowest (13 eggs/female) fecundities were observed, respectively, in rejuvenated G31 without significant difference with G32, G33 and G34 and domesticated G45 without significant difference with G31, G32, G33, G34, G35, G36 and G40 (Table 1). However, the sex ratio was not affected by rejuvenation, and non-significant difference was found between rejuvenated and domesticated populations (Fig. 1). Although the sex ratio was not statistically significant, domesticated populations tend to have higher female ratio every generation.

The age-stage-specific survival rates (s_{xj}) of *T. brassicae* (Fig. 2) showed the survivorship and stage differentiation as well as the variable developmental rate. The mean number of offspring produced by *T. brassicae* individuals of the age x and stage j per day was shown with the age-stage-specific fecundity (f_{xj}) in Fig. 3. The start of oviposition of the first female in all of generations occurred at the age 11 days. The daily fecundity of *T. brassicae* ranged from 13.27 eggs in G45 to 19.61 eggs in G31. The highest and lowest age-specific survival rates (l_x) at age of adult emergence of *T. brassicae* after adding feral population were observed at age 11 days in G34 (0.90) and G45 (0.81), respectively (Fig. 3).

Population growth (life table) parameters

Based on the age-stage, two-sex life table procedure, the population (life table) parameters were estimated using the data of the entire cohort for each generation of the two populations (Table 2). Significant differences in population growth parameters were found among different generations of *T. brassicae* in primary and rejuvenated populations. The highest values of *GRR* (26.13 eggs/individual), R_0 (20.71 eggs/individual), r (0.239 day^{-1}), λ (1.271 day^{-1}) and T (12.65 days) were observed in rejuvenated G31, and the lowest ones were in domesticated G45 with 9.91eggs/individual, 7.82 eggs/individual, 0.167 day^{-1}, 1.181 day^{-1} and 12.29 days, respectively (Table 2).

Parasitism capacity

Comparing parasitism parameters between populations before and after adding feral individuals showed that some generations in the rejuvenated population had more parasitism capacity than others both in the rejuvenated and domesticated populations (Table 3). The highest values for net parasitism rate (c_0), stable parasitism rate (ψ) and finite parasitism rate (ω) were observed in rejuvenated G31 with 20.71 hosts/parasitoid, 0.279 hosts/parasitoid and 0.355 hosts/parasitoid/day, respectively. Domesticated G45 had the lowest values for c_0 (7.82

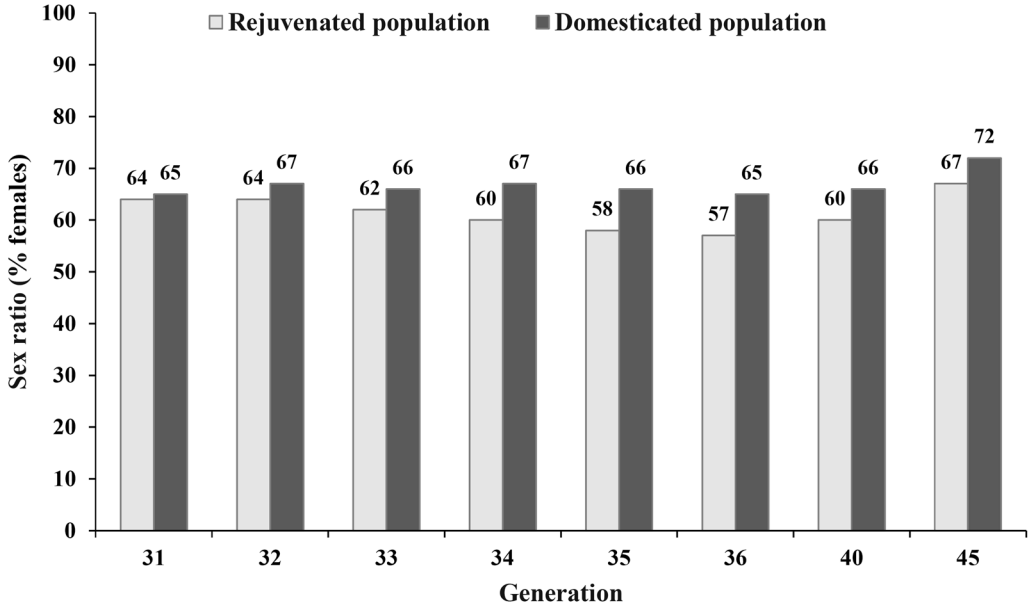

Fig. 1 Sex ratio (% emerged females) of different generations of *Trichogramma brassicae* reared on *Sitotroga cerealella* eggs in both domesticated and rejuvenated populations

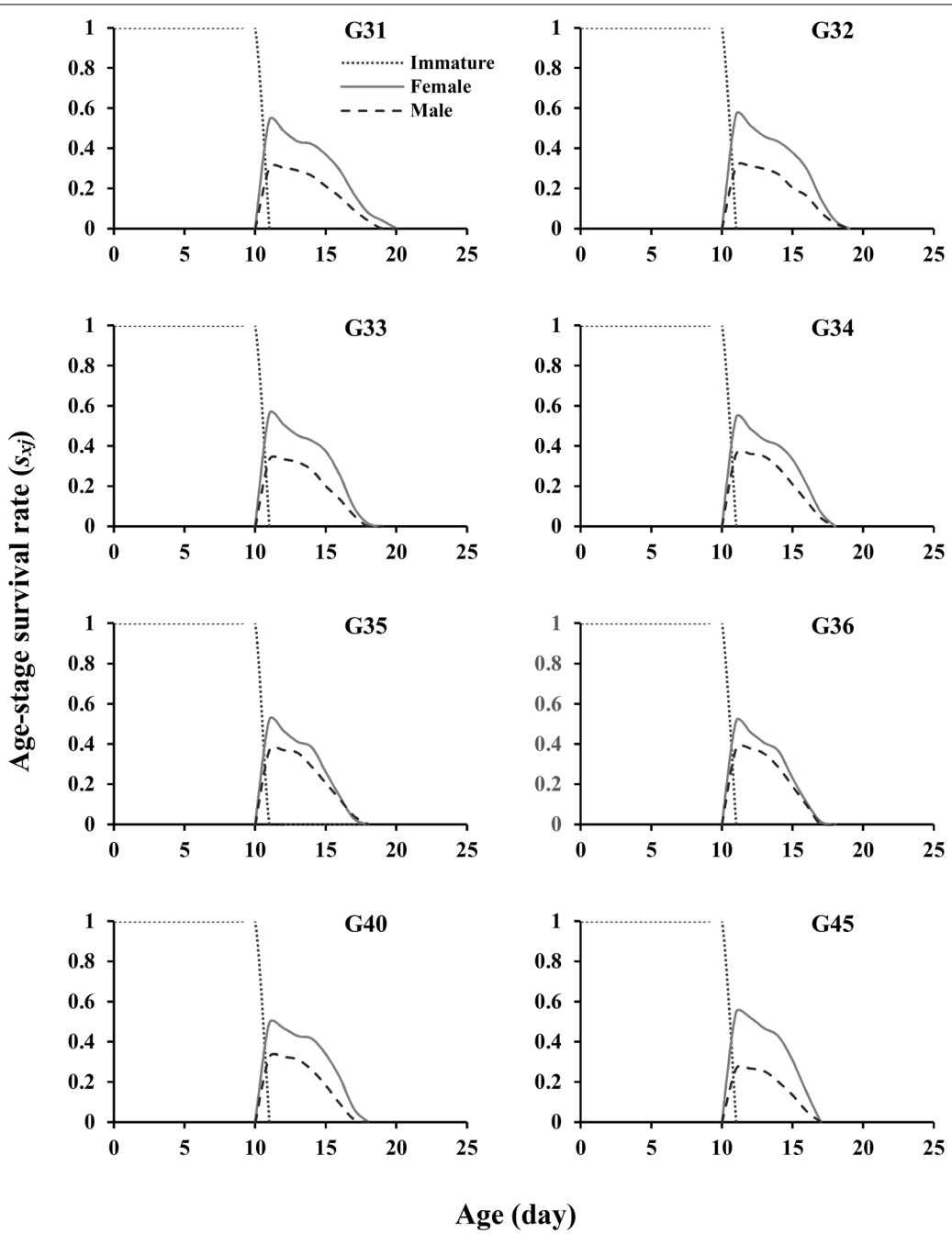

Fig. 2 Age-stage survival rate (s_{xj}) in different generations (G) of the rejuvenated *Trichogramma brassicae* on *Sitotroga cerealella* eggs

hosts/parasitoid), ψ (0.202 hosts/parasitoid) and ω (0.238 hosts/parasitoid/day) (Table 3). The transition rate values (Q_p) for all generations were close to 1 ($R_0 \approx c_0$), because *T. brassicae* almost always lays one egg in each *S. cerealella* egg.

The age-stage-specific parasitism rate (c_{xj}) describes the mean number of *S. cerealella* that had been parasitized by individual *T. brassicae* at age *x* and stage *j*. The peaks of curves declined over generations. The highest and lowest number of the parasitized hosts in the rejuvenated population were observed in G31 (19.61 hosts/parasitoid) and G45 (13.27 hosts/parasitoid), respectively, at age of 11 days (Fig. 4).

The regressions between finite parasitism rate and generation number in the rejuvenated and domesticated populations were fitted to a cubic regression

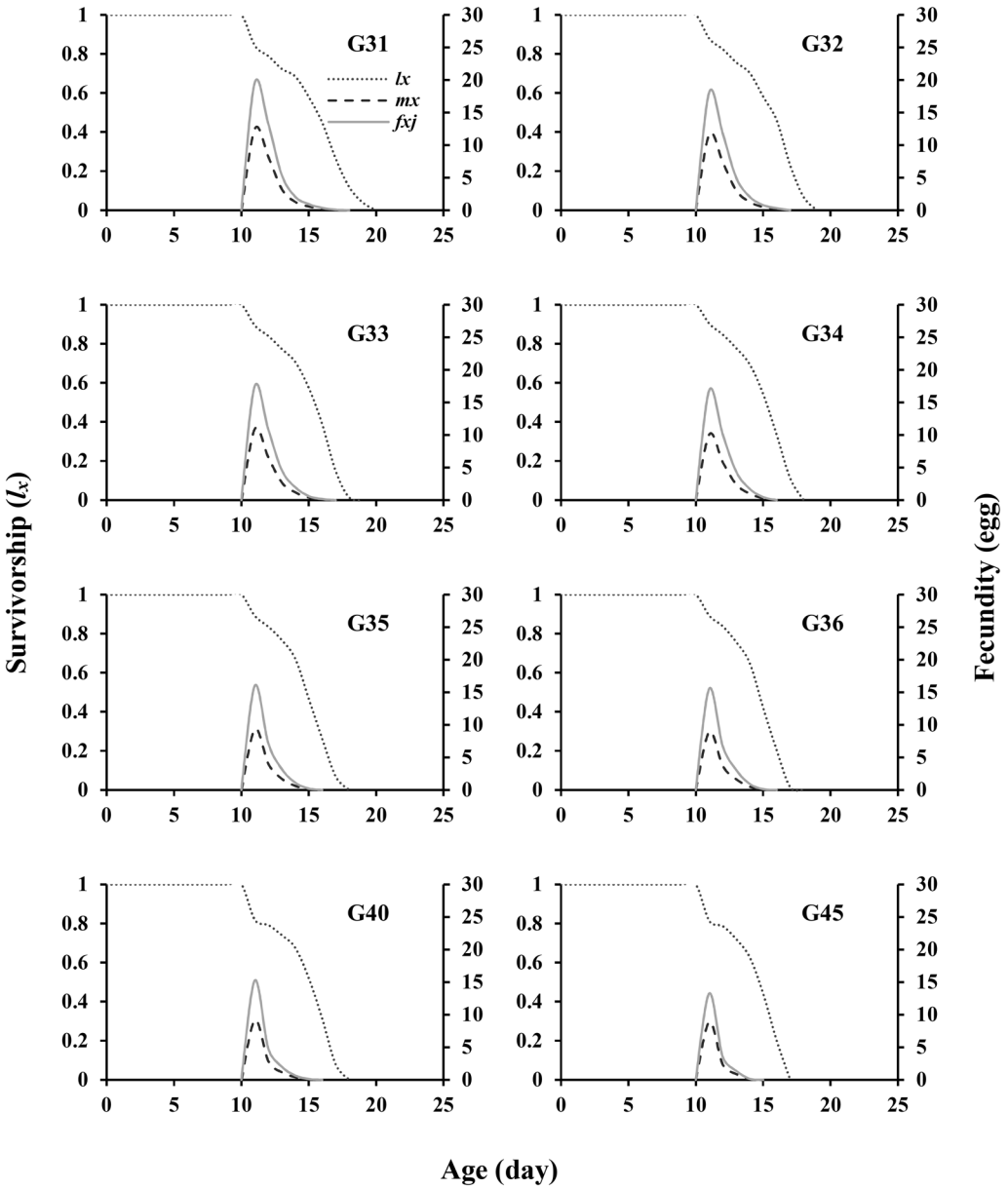

Fig. 3 Age-specific survivorship (l_x), age-stage-specific fecundity of female (f_{xj}) (eggs) and age-specific fecundity (m_x) in different generations (G) of the rejuvenated *Trichogramma brassicae* on *Sitotroga cerealella* eggs

model (Fig. 5). The merit of the model was supported by the high value of the coefficient of determination (R^2) for the domesticated ($F = 144.903$, $P < 0.01$, $R^2 = 0.984$) and rejuvenated ($F = 43.057$, $P = 0.002$, $R^2 = 0.970$) populations, indicating the parasitism potential of *T. brassicae* increased significantly after adding feral individuals but decreased markedly over subsequent generations.

Discussion

The success of a biological control, particularly augmentative biological control, depends on the effectiveness of natural enemies that have been released. These biocontrol agents may have been produced in mass rearing facilities over many generations. Developing the best rearing strategy is complicated by the 'paradox of captive breeding' in which increased quantity generally

Table 2 Life table parameters (Means ± SE) of different generations of *Trichogramma brassicae* reared on *Sitotroga cerealella* eggs in both primary and rejuvenated populations

Population	Generation	GRR (eggs/individual)	R_0 (eggs/individual)	r (d^{-1})	λ (d^{-1})	T (d)
Rejuvenated population	31	26.13 ± 3.14^{a}	20.71 ± 2.79^{a}	0.239 ± 0.011^{a}	1.271 ± 0.014^{a}	12.65 ± 0.04^{a}
	32	24.11 ± 2.87^{a}	19.95 ± 2.61^{a}	0.237 ± 0.010^{a}	1.267 ± 0.013^{ab}	12.65 ± 0.04^{a}
	33	21.90 ± 2.62^{ab}	18.49 ± 2.40^{ab}	0.231 ± 0.010^{ab}	1.260 ± 0.013^{abc}	12.63 ± 0.03^{a}
	34	19.62 ± 2.52^{abc}	16.78 ± 2.32^{ab}	0.224 ± 0.011^{abc}	1.251 ± 0.014^{abc}	12.60 ± 0.03^{a}
	35	15.82 ± 2.14^{bcd}	13.47 ± 1.95^{bc}	0.208 ± 0.012^{bcd}	1.231 ± 0.014^{bcd}	12.49 ± 0.03^{b}
	36	14.88 ± 2.01^{cde}	12.69 ± 1.82^{bc}	0.204 ± 0.012^{bcde}	1.226 ± 0.014^{cde}	12.47 ± 0.03^{bc}
	40	13.68 ± 1.71^{cdef}	10.95 ± 1.51^{cde}	0.193 ± 0.011^{def}	1.213 ± 0.014^{def}	12.40 ± 0.03^{c}
	45	12.25 ± 1.39^{def}	9.81 ± 1.26^{cde}	0.185 ± 0.011^{def}	1.203 ± 0.013^{def}	12.30 ± 0.02^{d}
Domesticated population	31	12.46 ± 1.43^{def}	9.93 ± 1.27^{cde}	0.186 ± 0.011^{def}	1.204 ± 0.013^{def}	12.31 ± 0.02^{d}
	32	12.50 ± 1.40^{def}	9.99 ± 1.26^{cde}	0.186 ± 0.010^{def}	1.205 ± 0.013^{def}	12.31 ± 0.02^{d}
	33	12.20 ± 1.35^{def}	9.93 ± 1.23^{cde}	0.186 ± 0.010^{def}	1.204 ± 0.012^{def}	12.31 ± 0.02^{d}
	34	12.21 ± 1.37^{def}	9.85 ± 1.25^{cde}	0.185 ± 0.010^{def}	1.204 ± 0.013^{def}	12.30 ± 0.02^{d}
	35	11.92 ± 1.36^{def}	9.41 ± 1.20^{cde}	0.182 ± 0.010^{def}	1.199 ± 0.013^{def}	12.30 ± 0.02^{d}
	36	11.66 ± 1.35^{def}	9.29 ± 1.20^{cde}	0.181 ± 0.011^{def}	1.198 ± 0.013^{def}	12.30 ± 0.02^{d}
	40	10.84 ± 1.26^{ef}	8.78 ± 1.13^{de}	0.176 ± 0.011^{ef}	1.192 ± 0.013^{ef}	12.30 ± 0.02^{d}
	45	9.91 ± 1.12^{f}	7.82 ± 1.01^{e}	0.167 ± 0.011^{f}	1.181 ± 0.013^{f}	12.29 ± 0.02^{d}

Means marked with the same letters within the same column (including both rejuvenated and domesticated population) are not significantly different (Paired-bootstrap, $\alpha = 0.05$)

Table 3 Parasitism parameters (Means ± SE) of different generations of *Trichogramma brassicae* reared on *Sitotroga cerealella* eggs in both primary and rejuvenated populations

Population	Generation	c_0 (hosts/parasitoid)	Q_p	ψ (host/parasitoid)	ω (hosts/parasitoid/day)
Rejuvenated population	31	20.71 ± 2.79^{a}	≈ 1	0.279 ± 0.017^{a}	0.355 ± 0.025^{a}
	32	19.95 ± 2.61^{a}	≈ 1	0.275 ± 0.016^{a}	0.349 ± 0.024^{a}
	33	18.49 ± 2.40^{ab}	≈ 1	0.269 ± 0.016^{a}	0.339 ± 0.023^{a}
	34	16.78 ± 2.32^{ab}	≈ 1	0.261 ± 0.016^{ab}	0.326 ± 0.024^{ab}
	35	13.47 ± 1.95^{bc}	≈ 1	0.243 ± 0.016^{bc}	0.300 ± 0.024^{bc}
	36	12.69 ± 1.82^{bc}	≈ 1	0.239 ± 0.016^{bcd}	0.293 ± 0.023^{bcd}
	40	10.95 ± 1.51^{cde}	≈ 1	0.227 ± 0.015^{bcd}	0.275 ± 0.021^{bcd}
	45	9.81 ± 1.26^{cde}	≈ 1	0.220 ± 0.013^{bcd}	0.265 ± 0.019^{cd}
Domesticated population	31	9.93 ± 1.27^{cde}	≈ 1	0.220 ± 0.013^{bcd}	0.265 ± 0.019^{bcd}
	32	9.99 ± 1.26^{cde}	≈ 1	0.221 ± 0.013^{bcd}	0.266 ± 0.019^{bcd}
	33	9.93 ± 1.23^{cde}	≈ 1	0.220 ± 0.013^{bcd}	0.265 ± 0.019^{cd}
	34	9.85 ± 1.25^{cde}	≈ 1	0.220 ± 0.013^{bcd}	0.264 ± 0.019^{cd}
	35	9.41 ± 1.20^{cde}	≈ 1	0.216 ± 0.013^{cd}	0.259 ± 0.019^{cd}
	36	9.29 ± 1.20^{cde}	≈ 1	0.215 ± 0.013^{cd}	0.258 ± 0.019^{cd}
	40	8.78 ± 1.13^{de}	≈ 1	0.211 ± 0.013^{cd}	0.251 ± 0.019^{cd}
	45	7.82 ± 1.01^{e}	≈ 1	0.202 ± 0.012^{d}	0.238 ± 0.017^{d}

Means marked with the same letters within the same column (including both rejuvenated and domesticated population) are not significantly different (Paired-bootstrap, $\alpha = 0.05$)

decreases quality (van Lenteren 2003). A decrease in the quality of the sequentially reared *Trichogramma* spp. has been found by different authors (Taghikhani et al. 2019). This problem is not limited exclusively to *Trichogramma* species and many natural enemies have been reported to experience this issue (Bellutti 2011). Routinely introducing field-collected individuals to the domesticated colonies of natural enemies is one commonly used method to keep genetic diversity over generations.

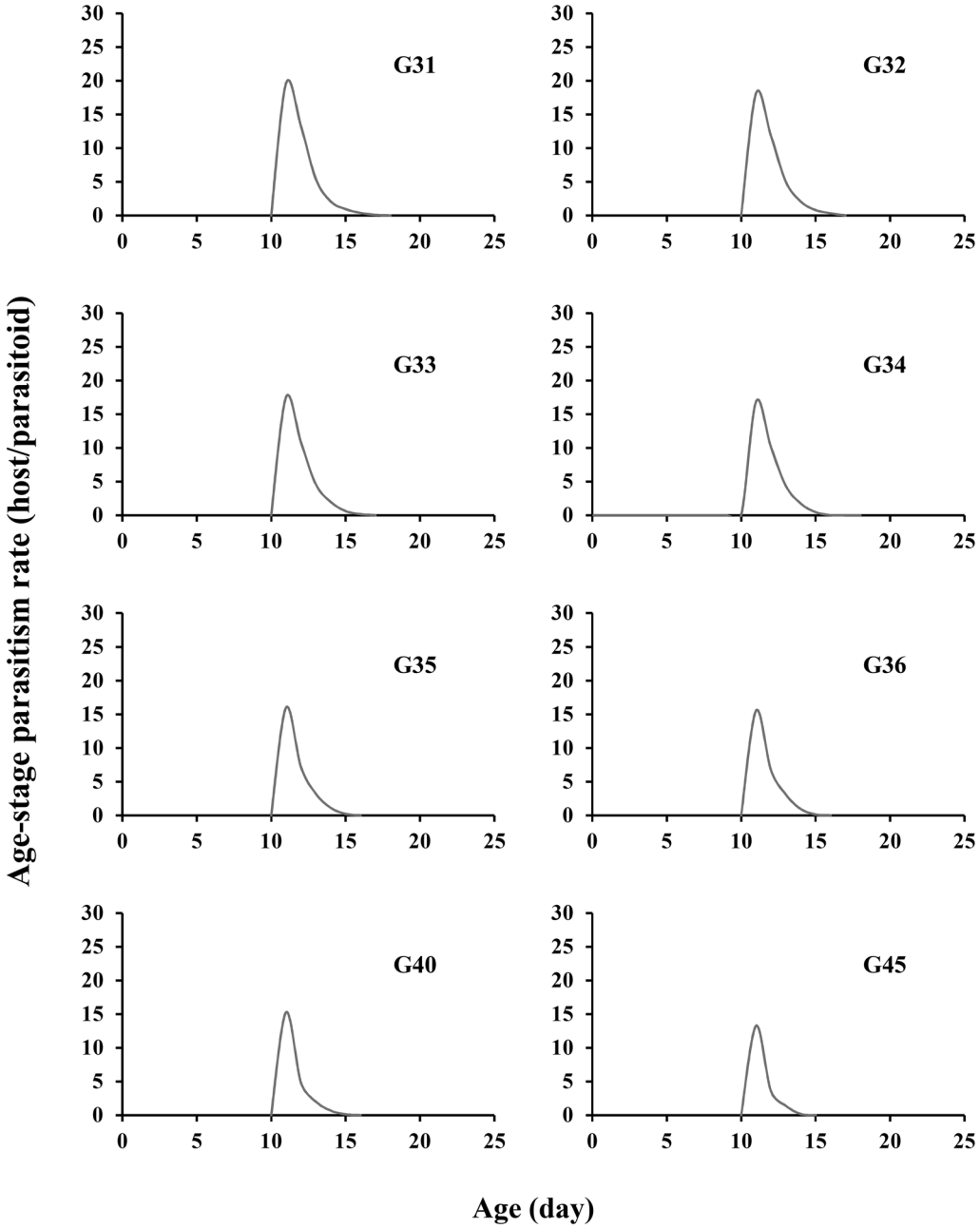

Fig. 4 Age-stage parasitism rate (c_{xj}) in different generations (G) of the rejuvenated *Trichogramma brassicae* on *Sitotroga cerealella* eggs

In our previous studies, a high reduction in the efficiency of *T. brassicae* over 45 generations of rearing, including a decrease in population and parasitism parameters was found (Ghaemmaghami et al. 2021). Here, the quality was improved in a primary colony of *T. brassicae* rejuvenated by adding feral individuals. Although most generations in the rejuvenated group had non-significant differences in the longevity with the primary population, females in the rejuvenated group laid more eggs than the domesticated. Cônsoli et al. (2010) mentioned that several factors may affect fecundity in *Trichogramma* spp., including host species, factitious or artificial hosts, egg size, age and nutrition. In the present study, the domesticated and rejuvenated populations both had the same condition, and any variation in the fecundity can be related just to add wild individuals. It seems that by increasing the rate of feral individuals added to primary colony, the process of reducing the quality of the wasp

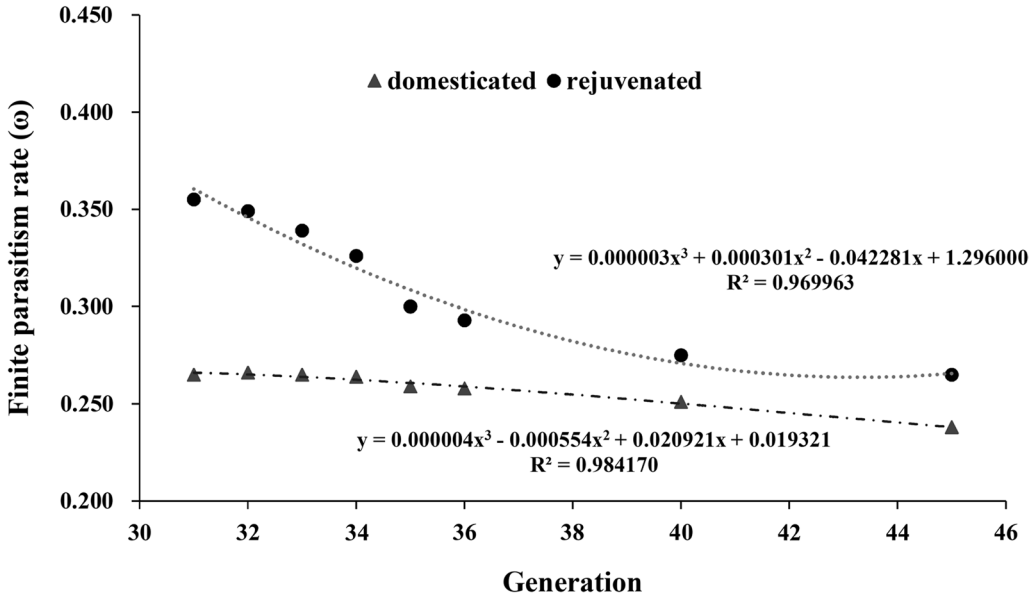

Fig. 5 Regression curve of finite parasitism rates (*ω*) with generations of *Trichogramma brassicae* reared on *Sitotroga cerealella* eggs in both domesticated and rejuvenated populations

can be slowed down. However, this issue should be investigated by more studies in which different rate of feral individuals are added to the primary colony.

Although non-significant differences in the population growth parameters (*GRR*, R_0, *r*, λ and *T*) were found among rejuvenated G31–G34, the rejuvenation drastically improved the population growth parameters, and they had higher population parameters than domesticated group. However, van Lenteren (2003) declared if the rearing conditions remain the same in the laboratory, the introduced wild individuals will be subjected to the same process of genetic selection. Declined parasitism parameters of *T. brassicae* after four generations of the rejuvenation may reinforce this inference.

Domestication can have remarkable evolutionary payoffs. For instance, it can induce both plastic and genetic modifications that limit the capacity of an organism to thrive in nature (Gering et al. 2019). Recent works showed that feral taxa undergo rapid evolutionary changes at loci controlling an array of fitness-related traits, including morphology, behavior and development (Moyers et al. 2017). Gene flow between domesticated and wild populations leads to important, diverse and context-dependent effects in fitness of recipient populations, which in turn can have important and unexpected roles in subsequent adaptation to changing (e.g., feral) environments (Gering et al. 2019). Domestication puts insects in a homogeneous environment where the challenges of natural selection are lacking (Cohen 2000), and in some cases, traits necessary for fitness are lost. Bartlett (1984) discussed the elimination of diapause genes and 'startle response' genes. Such inadvertent selection can be exacerbated by founder effect, where small starter population size leads to higher rates of genetic drift. These pitfalls are a legitimate concern for researchers and biological control practitioners who are interested in the use of augmentative biological control where laboratory-cultured natural enemies are to be used. Generally, cascading changes in the genetic pattern of a population reared in a novel environment is inevitable (van Lenteren 2003), and it is expected that natural selections reduce the genetic variability of such populations (Miyatake 1998). Moyers et al. (2017) stated that the process of domestication of wild species can result in an increase in the number, frequency and/or proportion of deleterious genetic variants that are fixed or segregating in the genomes of domesticated species for these species.

Sex ratio is an important trait in parasitoids influencing the financial profitability of mass rearing. In other word, produced male parasitoids in an augmentative release program have no pest control benefits. Generally, a reduction in the proportion of female individuals may happen in long-term mass rearing programs (van Lenteren 2003). Here, no effect of rejuvenation on sex ratio was found. Also, in our previous study, a clear declining trend in ratio of the produced females was not observed (Ghaemmaghami et al. 2021).

Conclusion

Optimizing mass rearing of arthropods for augmentative release programs is an extremely complex challenge. An ideal captive population should be able to adapt well to both the breeding environment and the field conditions where they need to control pests. Indeed, many of parasitoids, especially *Trichogramma* spp., are difficult to rear, creating a high potential for laboratory adaptation and for a large tradeoff with field performance. It seems adding feral individuals could reshape the reproductive performance of the wasps at least for four generations, and it needs to be repeated routinely. Furthermore, the quality may also be improved by adding a higher rate of feral individuals. However, this issue should be investigated by more studies in which different rate of feral individuals are added to the primary colony.

Abbreviations

L: Lightness; D: Darkness; RH: Relative humidity; G: Generation; GRR: Gross reproductive arte; R_0: Net reproductive rate; r: Intrinsic rate of increase; λ: Finite rate of increase; T: Mean generation time; APOP: Adult pre-oviposition period; TPOP: Total pre-oviposition period; s_{xj}: Age-stage survival rate; f_{xj}: Age-stage-specific fecundity of female; l_x: Age-specific survivorship; m_x: Age-specific fecundity; C_0: Net predation rate; Q_p: Transformation rate; ψ: Stable predation rate; ω: Finite predation rate; c_{xj}: Age-stage predation rate; a_{xj}: Stable age-stage structure.

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Author contributions

EG involved in writing, investigation, data collection and data analysis; YF involved in supervision, review and editing and project administration; AB involved in formal analysis and review and editing; AAT involved in review and editing; GVPR involved in final review and editing and improvement. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

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