Article

Group-rearing did not affect the life table and predation rate of *Phytoseiulus persimilis* (Acari: Phytoseiidae) fed on *Tetranychus urticae*

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Abstract

To better understand the effect of individual- and group-rearing conditions on predator performance, we studied the life table and predation rate of the predatory mite, *Phytoseiulus persimilis* Athias-Henriot, after the mites had been individually- or group-reared on two-spotted spider mites, *Tetranychus urticae*, eggs at $25\pm1^{\circ}$ C, $65\pm5^{\circ}$ RH and a photoperiod of 16: 8 (L:D) h. The net reproductive rate (R_0), intrinsic rate of increase (r), net predation rate (C_0), finite predation rate (ω) in the individually-reared predators were 40.61 offspring, 0.2594 d⁻¹, 437.3 *T. urticae* eggs, and 4.8668 preys/d, respectively. Similar values were obtained when the predators were reared in groups ($R_0 = 43.10$ offspring, r = 0.2837 d⁻¹, $C_0 = 420.9$ *T. urticae* eggs, and $\omega = 5.9054$ preys/d). Mean adult longevities were 28.42 and 25.29 d for group-reared male and female predators, respectively; these values were significantly shorter than those of individual-reared mites (49.87 d for male and 36 d for female). Our results showed that *P. persimilis* mites could be group-reared in biological control programs without negative effect on their growth and predation potential.

Key words: Life table, consumption rate, individual-rearing, group-rearing, predatory mites

Introduction

The two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), is an important polyphagous and cosmopolitan pest threatening many agricultural crops in fields and greenhouses (Helle & Sabelis 1985; Bolland *et al.* 1998; Zhang 2003). Predacious mites of the family Phytoseiidae are important biological control agents of herbivorous mites, thrips and whiteflies (McMurtry *et al.* 2013). *Phytoseiulus persimilis* Athias-Henriot is a well- known effective predator with a considerable ability to suppress prey populations (Van lenteren 2003). It predates on *Tetranychus* spp. and is classified among type I lifestyle phytoseiids. This lifestyle contains specialized predators attacking spider mites with complicated webs (McMurtry *et al.* 2013).

Life table is an important tool for population ecology and pest management and offers comprehensive descriptions of survival rate, development, stage differentiation, reproduction and life expectancy of a population (Chi & Liu 1985; Chi 1988). Life table of the predatory mite *P. persimilis* (Laing 1968; Amano & Chant 1977; Bjornson & Keddie 1999; Escudero & Ferragut 2005) as well as its predation rate (Takafuji & Chant 1976; Amano & Chant 1977; Rasmy *et al.* 1991; Vanas *et al.* 2006; Tello *et al.* 2009; Moghadasi *et al.* 2013) have already been studied using traditional methods. The traditional female age-specific life table, however, has important

limitations (Chi & Liu 1985; Chi 1988; Huang & Chi 2012). Because stage differentiation is common to mite populations and some mite stages are non-predatory (e.g., egg and larval stages in *P. persimilis*; Amano & Chant 1977), life table and predation rate data have to be collected to take the stage structure and stage-specific predation rate into consideration (Yu *et al.* 2013). To achieve this, the age-stage, two-sex life table theory (Chi & Liu 1985; Chi 1988) and its application for predator-prey relationships (Chi & Su 2006; Huang & Chi 2012; Tuan *et al.* 2015) have been developed.

The aim of this study is to construct the age-stage, two-sex life table for *P. persimilis* and to explore its predation rate within a life table framework. In general, life tables are constructed for recording life history data of each individual of a cohort until they reach adulthood and then one male and a female are paired in order to record their survival and reproductive potential. Unlike such unnatural experimental conditions, many insects and mites live in colonies or groups. Thus, the sex ratio and many other natural conditions have been ignored in most life table studies based on individuals. Although animals should expect competition for shared resources, mates and diseases transmission as a cost, benefits of group-living affect vigilance, foraging behavior, predation risk, mating opportunities and hence reproductive success (Krause & Ruxton 2002; Earley & Dugatkin 2010). In addition, group living may cause social interactions and affect the predator's performance (Rubenstein 1978; Avilés & Tufino 1998; Holbrook *et al.* 2000; Salomon & Lubin 2007; Lihoreau & Rivault 2008; Le Goff *et al.* 2010). In this study two kinds of life table experiments (i.e. individual-and group-reared) were constructed to understand predator-prey relationships in a more realistic situation. The information collected in this study will be useful for successful biological control programs.

Material and Methods

Rearing and experimental condition

The laboratory population of *P. persimilis* was originally obtained from Koppert (NL) and reared on detached leaves of common bean, *Phaseolus vulgaris* L., infested by the two-spotted spider mite, *Tetranycus urticae* (TSSM). The predatory mites were maintained on artificial arenas consisting of piled up detached leaves on a plastic laminate tile placed on a water-saturated foam cube kept in a plastic box half-filled with water. Moist tissue paper was wrapped around the edges of the tile to prevent the mites from escaping (Schausberger 1997). The predatory mites were fed at two-day intervals by adding spider mite-infested bean leaves to the arenas. All the experiments were conducted in a growth chamber with $25 \pm 1^{\circ}$ C and $65\% \pm 5$ RH and photoperiod of 16:8 (L:D) h.

Life table study

Individual-reared life table

Gravid females of the predatory mite were collected from the stock colony and transferred to 6-cm Petri dishes, each consisting of a bean leaf placed upside down on water-saturated cotton and provided with mixed life stages of *T. urticae*. After 24 h, 31 newly laid eggs were collected and transferred individually into experimental glass cages, each consisting of a circular cavity of 20 mm in diameter and 5 mm in height with fine gauze at the bottom and closed on the upper side by a microscope slide (Schausberger 1997). According to preliminary tests, protonymphs and deutonymphs of the predator were fed with seven eggs of TSSM, daily. TSSM eggs were used as prey in our experiments because of the following reasons: (1) When supplied with all stages of two spotted spider mite, immature stages (protonymph and deutonymph) of *P. persimilis* consumed more eggs and no deutonymphs and

adults of *T. urtice*, (Takafuji & Chant 1976); (2) According to Blackwood *et al.* (2001), *P. persimilis* females preferred eggs rather than larvae. Similar results also were demonstrated by other studies (Pernando & Hassell 1980; Moghadasi *et al.* 2013); (3) Eggs are immobile and easier for the immature stages of the predator to consume; and (4) Nutritional benefit of eggs for developing immatures seems to be higher than for other stages (Sabelis 1985; Badii *et al.* 2004; Furuichi *et al.* 2005). Developmental time and survival of all individuals were recorded every 24 h. After emergence of the adults, males and females were paired and checked daily for survival and the number of eggs produced. During the adult stage, 35 eggs of TSSM were supplied daily to each pair.

Group-reared life table

To study effects of group-living on life table parameters, instead of only using one egg in each of the experimental units, five eggs of the predatory mites were provided with 40 TSSM eggs in an experimental cage. To determine the sex ratio of *P. persimilis*, and hence the proportion of predator males and females in a group, 100 eggs randomly taken from the stock colony were put into Petri dishes and fed until adulthood. Once mounted on microscope slides, the mites were studied in order to determine their gender by their morphological characteristics (i.e. presence of sperm transfer organ on chelicerae and having less than three ventral plates in males). To reduce potential competition in space in the group treatment, dimensions of each experimental cage were increased proportionately (i.e., cages were 35 mm in diameter and 5 mm height). Developmental time and mortality of pre-adult stages were checked daily. After reaching adulthood, four females were paired with just a single male (based on the preliminary sex ratio test) to make a unit group and then survival and oviposition of all the four females in each group were recorded until the last individual died. 110 TSSM eggs were provided for each unit group daily. The total number of *P. persimilis* eggs used to construct the group-reared life table was 42.

Predation rate of the predator

In both the above-mentioned life table experiments, the number of consumed TSSM eggs by immature and adult predators was checked daily. To estimate predation rates of males and females separately, predation rates of 22 males were studied individually in a separate experiment. To obtain predation by females, average daily predation of each male was subtracted from the number consumed by a pair.

Data analysis

The raw life history data for *P. persimilis* were analyzed using the TWO-SEX MS Chart program (Chi 2015b), based on the age-stage, two-sex life table theory (Chi & Liu 1985) and the method described by Chi (1988). The age-stage specific survival rate (s_{xj}) (where x= age and j = stage), age-stage specific fecundity (f_{xj}) , age-specific survival rate (l_x) , age-specific fecundity (m_x) , and population parameters $(r, intrinsic rate of increase; <math>\lambda$, finite rate of increase; R_0 , net reproductive rate; T, mean generation time) were calculated accordingly. The age-specific survival rate (l_x) for both females and males and age-specific fecundity (m_x) for females were also calculated (Chi & Liu 1985):

and

$$=\sum_{i=1}^{p} s_{xi} \tag{1}$$

$$m_{x} = \frac{\sum_{j=1}^{p} s_{xj} f_{xj}}{\sum_{i=1}^{\beta} s_{xj}}$$
(2)

where β is the number of stages.

The net reproductive rate is defined as the total number of offspring that an individual can produce during its lifetime and is calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{3}$$

The intrinsic rate of increase was calculated using the iterative bisection method and the Euler-Lotka equation with the age indexed from 0 (Goodman 1982):

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$$
(4)

Mean generation time represents the period that a population requires to increase to R_0 -fold of its size as time approaches infinity and the population settles down to a stable age-stage distribution. This parameter is calculated as

$$T = \frac{\ln R_0}{r} \tag{5}$$

The finite rate of increase also is calculated as

$$\lambda = e^r \tag{6}$$

In the group-reared experiment, the number of laid eggs was divided by the number of living females. As for extra egg (s) after division, these were accrued to the females randomly. The groupreared life table data were analyzed according to Chang et al. (2016). The means and standard errors of population parameters, as well as developmental time and fecundity of individuals in both experiments were calculated by the bootstrap method using 100,000 bootstraps (Akca et al. 2015; Polat-Akköprü et al. 2015). The results of treatments were compared using a paired bootstrap test based on the confidence interval of the treatment difference (Efron & Tibshirani 1993; Polat-Akköprü et al. 2015). The daily consumption of all individuals (females, males and those died before adulthood) was analyzed to calculate the predation rate according to Chi & Yang (2003) and Yu et al. (2005), using the computer program CONSUME-MSChart (Chi 2015a). The age-specific predation rate (k_{y}) is the mean number of TSSM eggs consumed by P. persimilis at age x and was calculated as follows (Chi & Yang 2003):

$$k_{x} = \frac{\sum_{j=1}^{\beta} s_{xj} c_{xj}}{\sum_{i=1}^{\beta} s_{xj}}$$
(7)

The net consumption (predation) rate (C_0) shows the mean number of prey consumed by an average individual predator during its life span and was calculated according to Chi & Yang (2003):

$$C_0 = \sum_{x=0} k_x l_x \tag{8}$$

The transformation rate from prey population to predator offspring (Q_p) , which is the ratio of the net predation rate to the net reproductive rate and gives the mean number of prey needed for a predator to produce an offspring, was calculated as follows (Chi & Yang 2003):

$$Q_p = \frac{C_0}{R_0} \tag{9}$$

To compare the predation capacity of a predator on different prey, Chi et al. (2011) and Yu et al. (2013) defined the finite predation rate (ω) as

$$\omega = \lambda \psi = \lambda \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} c_{xj}$$
(10)

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where λ is the finite rate of the predator population, ψ is the stable predation rate, a_{xj} is the proportion of individuals belonging to age x and stage j, c_{xj} is the age-stage specific predation rate.

In the group-reared experiment, female predation rates were achieved by subtraction of the male predation rates from those of each unit. Then the total female predation was divided by the number of surviving females (to obtain predation rate per female). If there were extra eaten prey after division, they were accrued to the female(s) randomly. Standard errors of predation parameters and differences among predation parameters were compared via CONSUME-MSChart (Chi 2015a) based on the bootstrap method. In addition, the life table and predation rate data from both experiments were used to project the population growth and predation capacity of *P. persimilis* using the program TIMING-MSChart (Chi 2015c) based on the method described in Tuan *et al.* (2014). The predation capacity at time *t* is calculated according to Liu *et al.* (2017) as follows:

$$p(t) = \sum_{j=1}^{\beta} \left(\sum_{x=0}^{\infty} c_{xj} n_{xj}(t) \right)$$
(11)

where n_{xj} is the number of individuals of age x and stage j and c_{xj} is the mean consumption rate of individuals of n_{xj} .

Results

Life table study

Of all 31 eggs used at the beginning of individual-rearing test, 28 eggs hatched. In the group-reared experiment, 39 out of 42 eggs hatched. The developmental period for pre-adult stages and longevity of adult males and females are shown in Table 1. Female adults of *P. persimilis* lived 36.00 days on average when rearing individually, which was significantly longer than that of group-reared ones with 25.29 d average longevity. Similarly, male adult longevity was significantly higher when mites were kept individually (49.87 d) than in a group (28.42 d). The age-stage specific survival rate (s_{xj}) is the probability that a newborn will survive to age *x* and stage *j* and shows the change of stage structure during the life history of the predatory mite. Stages overlapping in survival curve reflect a variable developmental rate among individuals. Females emerged from age 4 to 8 d in individual-reared cohort and from age 4 to 6 d in group-reared cohort, respectively (Fig. 1). The number of eggs produced during the oviposition period was 74.05 and 67.03 eggs in individual- and group-reared experiments, respectively (Table 2). In the individual-reared cohort, the APOP (adult pre-oviposition period) was 1.23 d, i.e., the mated females needed 1.23 d to begin reproduction, while the APOP was 1.07 d in the group-reared cohort (Table 2).

Fig. 2 illustrates the age-specific survival rate (l_x) , female age-stage specific fecundity (f_{x5}) , the age-specific fecundity (m_x) and age-specific maternity (l_xm_x) in *P. persimilis*. The l_x curve is a simplified and combined version of the age- stage survival rate (s_{xj}) . Although the individual-reared females lived longer (Fig. 1), oviposition periods in two experiments were similar. Life expectancy (e_{xj}) estimates the time individuals of age x and stage j are expected to live and are plotted in Fig. 3. Based on this, life expectancy for a new born was 37.74 and 26.02 d for individual- and grouped-reared mites, respectively. Survival rate of individuals in the laboratory affected mainly due to aging, so that the trend decreased with age from the larval stage in both experiments. The intrinsic rate of increase (r), finite rate of increase (λ) , net reproductive rate (R_0) and mean generation time (T) using bootstrap method are compared in Table 3. There were no significant differences in population parameters between the two treatments, although the grouped-reared mites had higher values of r and λ .

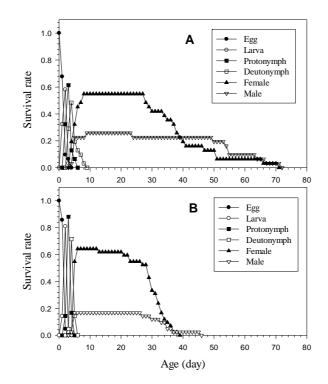


FIGURE 1 Age-stage survival rate (s_{xj}) of *Phytoseiulus persimilis* reared on *Tetranychus urticae* eggs: A. individual-reared treatment, B. group-reared treatment at $25\pm 1^{\circ}$ C, $65\%\pm 5$ RH and a photoperiod of 16:8 (L: D) h.

TABLE 1. Developmental time of different stages and adult longevity of *Phytoseiulus persimilis* reared on *Tetranychus urticae* eggs at $25\pm1^{\circ}$ C, $65\%\pm5$ RH and a photoperiod of 16:8 (L:D) h.

Davialammental time (dav)	Indiv	Individual- reared		p- reared	— P	
Developmental time (day)	Ν	$Mean \pm SEM$	N	$Mean \pm SEM$	F	
Egg	29	1.68 ± 0.09 $^{\rm a}$	40	1.85 ± 0.05 $^{\rm a}$	0.16	
Larva	28	1 ± 0 ^a	39	$1\pm0~^{a}$	1	
Protonymph	25	1.2 ± 0.11 $^{\rm a}$	36	1.22 ± 0.07 $^{\rm a}$	0.87	
Deutonymph	2 5	1.52 ± 0.17 $^{\rm a}$	34	1 ± 0 $^{\rm b}$	0.003	
Tota pre-adult	25	5.36 ± 0.27 $^{\rm a}$	34	5.05 ± 0.07 $^{\rm a}$	0.28	
Adult male	8	49.87 ± 4.95 $^{\rm a}$	7	28.42 ± 2.55 ^b	0.001	
Adult female	17	36.00 ± 2.82 ^a	27	25.29 ± 1.06^{b}	0.0008	

Standard errors were estimated by using 100,000 bootstraps. Means followed by different letters are significantly different between two treatments using the paired bootstrap test at the 5% significance level.

Predation rate

The predation rate of different stages and sexes of *P. persimilis* fed on TSSM eggs are listed in Table 4. Consumption rate was estimated from the protonymphal stage after the non-consuming stages (egg and larval) and increased toward adulthood. There was a significant difference in predation rate between females and males in both treatments and it was higher in individual-reared mites (Table 4). The age-stage predation rate (c_{y}) indicates the mean number of eggs consumed by a predator of age

x and stage j. As it can be seen in Fig. 4, the highest peak was on days 22 and 23 for females' predation in individual- and group-reared treatments, respectively. After the oviposition period, predation rate of the females decreased (Fig. 2 and 4). Curves of age-specific survival rate (l_x) , age-specific predation rate (k_x) and age-specific net predation rate (q_x) are plotted in Fig. 5. As shown in the figure, the eggs and larvae of the predator were incapable of prey consumption. The net predation rate was 437.3 and 420.9 TSSM eggs per individual when the predators were reared individually or as a group, respectability. Mites in the individual-reared cohort needed 10.77 prey eggs to produce one offspring (Q_p) , which was not significantly different from the number of prey required to do so in group-reared mites (9.77) (Table 5).

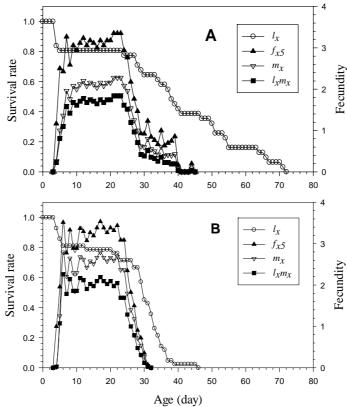


FIGURE 2. Age-specific survival rate (l_x) , age-stage fecundity of female (f_{x5}) (eggs/female), age-specific fecundity (m_x) and age- specific maternity $(l_x m_x)$ A. individual-reared treatment, B. group-reared treatment at $25\pm 1^{\circ}$ C, $65\%\pm 5$ RH and a photoperiod of 16:8 (L: D) h.

TABLE 2. Reproductive characteristics of *Phytoseiulus persimilis* reared on *Tetranychus urticae* eggs at $25 \pm 1^{\circ}$ C, $65\% \pm 5$ RH and a photoperiod of 16:8 (L:D) h.

<u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u><u></u></u>	Individual-reared		Group	D		
Statistics	Ν	Mean \pm SEM	N	$Mean \pm SEM$	- r	
APOP (d)	17	1.23 ± 0.10 $^{\rm a}$	27	1.07 ± 0.05 $^{\rm a}$	0.16	
TPOP (d)	17	6.58 ± 0.37 $^{\rm a}$	27	6.15 ± 0.091 $^{\rm a}$	0.29	
Oviposition period (d)	17	24.11 ± 1.18 ^a	27	$22.03\pm0.84~^{\rm a}$	0.15	
Mean fecundity (egg per female)	17	74.05 ± 3.58 ª	27	67.03 ± 2.54 ^a	0.11	

Standard errors were estimated by using 100,000 bootstraps. Means followed by the same letters are not significantly different between two treatments using the paired bootstrap test at the 5% significance level.

Population and predation projection

To simulate the changes in the population size, stage structure and predation capacity of *P. persimilis* fed on TSSM eggs, data from life tables and predation rate were used to project the population growth as shown in Figs. 6 and 7. The figures show population growth is faster when predatory mites are reared as a group. For example on day 20, the total papulation size was 3.0534 in log scale (it approximated 1130 individuals) in the group-reared treatment, which was higher than the value of 2.8407 in individual-reared treatment (about 692 individuals). The number of prey consumed was also higher in the group-reared treatment (3.6604 in log scale, i.e., about 4,575 TSSM eggs) in comparison with the 3.4006 (i.e., about 2,515 TSSM eggs) in individual-reared treatment on day 20 (Fig. 7).

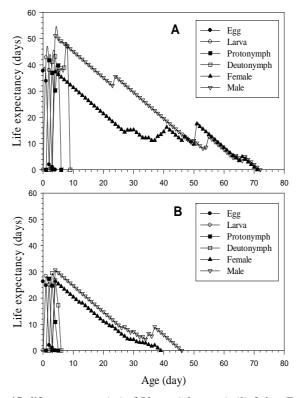


FIGURE 3. Age-stage specific life expectancy (e_{xj}) of *Phytoseiulus persimilis* fed on *Tetranychus urticae* eggs: A. individual-reared treatment, B. group-reared treatment at $25 \pm 1^{\circ}$ C, $65\% \pm 5$ RH and a photoperiod of 16:8 (L: D) h.

TABLE 3. Population parameters (Means \pm SEM) of *Phytoseiulus persimilis* at 25 \pm 1°C, 65% \pm 5 RH and a photoperiod of 16:8 (L: D) h.

	Individual- reared	Group- reared	D
Population parameters	Mean ± SEM	Mean ± SEM	— P
<i>r</i> (d ⁻¹)	0.2594 ± 0.0182 ^a	0.2837 ± 0.0117^{a}	0.24
λ (d ⁻¹)	1.2961 ± 0.0235 ^a	1.3281 ± 0.0155 $^{\rm a}$	0.24
R_0 (offspring/individual)	40.61 ± 6.91 ^a	43.10 ± 5.20^{a}	0.78
<i>T</i> (d)	$14.28\pm0.56~^{\rm a}$	13.27 ± 0.18 a	0.07

Standard errors were estimated by using 100,000 bootstraps. Means followed by the same letters are not significantly different between two treatments using the paired bootstrap test at the 5% significance level.

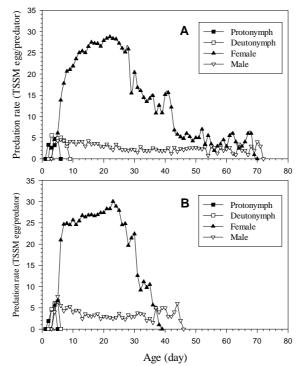


FIGURE 4. Age-stage predation rate (*cxj*) of *Phytoseiulus persimilis* fed on *Tetranychus urticae* eggs during population growth: A. individual-reared treatment, B. group-reared treatment at $25 \pm 1^{\circ}$ C, $65\% \pm 5$ RH and a photoperiod of 16:8 (L: D) h.

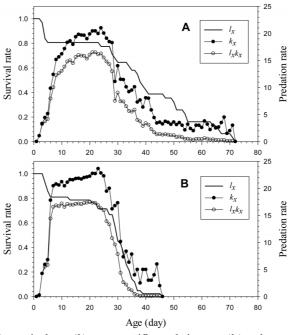


FIGURE 5. Age- specific survival rate (l_x) , age- specific predation rate (k_x) and age-specific net predation rate (q_x) of *Phytoseiulus persimilis* fed on *Tetranychus urticae* eggs during population growth: A. individual-reared treatment, B. group-reared treatment at $25\pm 1^{\circ}$ C, $65\%\pm 5$ RH and a photoperiod of 16:8 (L: D) h.

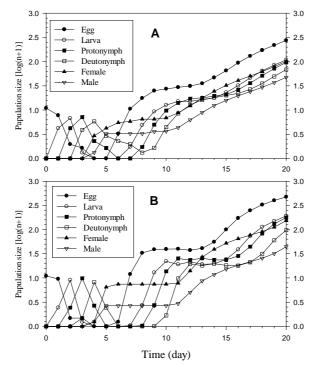


FIGURE 6. Changes in stage structure of Phytoseiulus persimilis fed on Tetranychus urticae eggs during population growth: A. individual-reared treatment, B. group-reared treatment at 25±1°C, 65%±5 RH and a photoperiod of 16:8 (L: D) h.

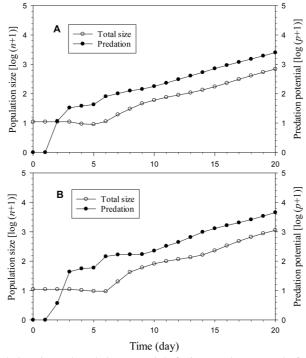


FIGURE 7. Total population size and predation potential of Phytoseiulus persimilis fed on Tetranychus urticae eggs based on total population: A. individual-reared treatment, B. group-reared treatment at 25±1°C, 65%±5 RH and a photoperiod of 16:8 (L: D) h.

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Sex Stage	Store	Ν	Individual- reared N		Group- reared	— P
	Stage	IN	$Mean \pm SEM$		$Mean \pm SEM$	— r
	Protonymph	17	$4.23\pm0.71^{\text{ a}}$	27	$5.93\pm0.65~^a$	0.07
Female Deutonymph Adult	17	8.76 ± 1.20 $^{\rm a}$	27	6.15 ± 0.24 $^{\rm b}$	0.03	
	Adult	17	$715.76 \pm 34.08 \ ^{a}$	27	$610.30 \pm 24.02 \ ^{\text{b}}$	0.01
Protonymph	8	2.75 ± 1.10 $^{\rm a}$	7	$3.96\pm0.61~^{\rm a}$	0.33	
Male	Deutonymph	8	$4.5\pm0.83~^{\rm a}$	7	5.28 ± 0.42 $^{\rm a}$	0.39
	Adult	8	137.125 ± 9.61 ^a	7	106.90 ± 9.32^{b}	0.02

TABLE 4. Mean (\pm SEM) *Tetranychus urticae* eggs eaten by different stages/sexes of *Phytoseiulus persimilis* at 25 \pm 1°C, 65% \pm 5 RH and a photoperiod of 16:8 (L:D) h.

Standard errors were estimated by using 100,000 bootstraps. Means followed by different letters are significantly different between two treatments using the paired bootstrap test at the 5% significance level.

TABLE 5. Mean (± SEM) of net predation rate (C_0 , no. preys), transformation rate (Q_p , no. preys per viable predator egg), stable predation rate (ψ , no. preys) and finite predation rate (ω , preys/d) of different stages of *Phytoseiulus persimilis* reared on *Tetranychus urticae* eggs at 25± 1°C, 65%± 5 RH and a photoperiod of 16:8 (L:D) h.

Parameters	Individual- reared	Group- reared	Р	
	$Mean \pm SEM$	$Mean \pm SEM$		
C_0	437.3 ± 61.4 ^a	$420.9\pm44.6~^{a}$	0.83	
Q_p	10.77 ± 0.54 $^{\rm a}$	9.77 ± 0.23 a	0.07	
ψ	$3.7550 \pm 0.4651 \ ^{\rm a}$	$4.4467 \pm 0.3010 \ ^{\rm a}$	0.22	
ω	$4.8668 \pm 0.6853 \ ^{\rm a}$	$5.9054 \pm 0.4652 \ ^{\rm a}$	0.22	

Standard errors were estimated by using 100,000 bootstraps. Means followed by the same letters are not significantly different between two treatments using the paired bootstrap test at the 5% significance level.

Discussion

Life table analyses give the most comprehensive picture of population parameters such as survivorship, development, and reproduction. This study evaluated the life history and predation parameters of specialized predator of spider mites, P. persimilis, when fed on two spotted spider mite eggs both when mites are held in groups and individually. There was no significant treatment difference between total pre-adult developmental times although it tended to be shorter in the groups. Lihoreau & Rivault (2008) showed that isolated Blatella germanica L. nymphs (males and females) reached adulthood significantly later than grouped nymphs. Also Van Impe (1984) reported that developmental time of *T. urticae* males decreased with increasing the number of individuals. Similarly, in this study when kept in group, duration of immature stages of P. persimilis was 5.05 d which was shorter than those kept individually (5.36 d). Adult life span in both males and females was longer in this study compared with those reported by Moghadasi et al. (2016) on rose leaf discs. Furthermore, living together influenced adult longevity so that in both females and males the longevity decreased. When reared in groups, mating may increase. Multiple mating will cost energy and thus affect longevity negatively. Martin & Hosken (2004) reported that in Saltella sphondylli (Diptera: Sepsidae), male fly longevity was 24.25 d with one copulation and 15.85 d with six copulations, whereas males that had no copulation lived longer (27.90 d). In N. californicus, females

with multiple mating had a shorter life span compared to those with a single copulation (Gotoh *et al.* 2008). Also similar studies suggested that sexual activities had negative effects on *Drosophila melanogaster* longevity (Partridge & Farquhar 1981; Cordts & Partridge 1996).

			Population parameters			Conditions		
Source	prey	Stage	R_0	$r(d^{-1})$	$\lambda \left(d^{\text{-1}} \right)$	$T(\mathrm{day})$	$T(^{\circ}C)$	RH (%)
This study (individual-reared)	T. urticae	Egg	40.61	0.258	1.29	12.31	25±1	65±5
This study (group-reared)	T. urticae	Egg	43.10	0.283	1.33	13.27	25±1	65±5
Takafuji & Chant 1976	T. pacificus	Female	63.24	0.317	1.37	-	25	90-70
Takahashi & Chant 1994 ¹	T. pacificus	All stages	66.83	0.4198	1.52	13.68	26	80±10
Takahashi & Chant 1994 ²	T. pacificus	All stages	71.09	0.4260	1.53	13.42	26	80±10
Takahashi & Chant 1994 3	T. pacificus	All stages	66.69	0.4343	1.54	12.81	26	80±10
Takahashi & Chant 1994 ⁴	T. pacificus	All stages	55.69	0.4103	1.50	12.67	26	80±10
Escudero & Ferragut 2005	T. urticae	All stages	45.61	0.373	-	12.85	25±1	80-70
Escudero & Ferragut 2005	T. turkestani	All stages	43.02	0.367	-	12.79	25±1	80-70
Escudero & Ferragut 2005	T. ludeni	All stages	40.78	0.424	-	11.57	25±1	80-70
Escudero & Ferragut 2005	T. evansi	All stages	4.37	0.106	-	14.21	25±1	80-70
Tello et al. 2009	T. cinnabarinus	Egg	1.23	0.019	1.019	11.11	29	45±5
Vangansbeke et al. 2013	T. urticae	All stages	42.3	0.118	-	-	15	65
Vangansbeke et al. 2013	T. urticae	All stages	58	0.235	1.26	-	20	65
Moghadasi et al. 2016	T. urticae	T. urticae	33.48	0.296	1.34	11.83	25 ± 1	75±5

TABLE 6. Review of population parameters of Phytoseiulus persimilis in different sources.

P. persimilis from Sicily (Italy)¹, California (USA)², Sydney (Australia)³ and Valparaiso (Chile)⁴

Pre-oviposition period, oviposition period and fecundity are informative parameters in demography due to the fact that they can predict the first reproduction at the population level and the number of prospective offspring in the next generation. Fecundity of *P. persimilis* was higher than that investigated by Kazak *et al.* (1989); Escudero & Ferragut (2005); Mohamed & Omar (2011) and Moghadasi *et al.* (2016). The differences could be attributed to different experimental situations, plant species and so forth. *Phytoseiulus persimilis* females need copulation and unmated mites cannot produce eggs (Takafuji & Chant 1976; Amano & Chant 1977). Individual-reared females lived longer than group-reared ones though the difference between their oviposition periods was not significant. On the other hand, their life span increased without producing any offspring. Accordingly, it seems that oviposition potential in *P. persimilis* females is similar and they do not use all their consumed food and energy for producing offspring. Statistical analyses showed that there were no significant differences in reproductive parameters between two treatments and living in a group exerted no influence on this predator's reproductive parameters.

During the reproduction period, females need more food due to offspring production. We estimated the amount of prey consumption during and after oviposition period. During oviposition period, average consumption rate for gravid females was 19.89 and 23.84 *T. urticae* eggs per day in individual- and group- reared treatments, respectively. Then a dramatic decrease happened with 4.41 and 6.53 eggs, respectively consumed in the post-oviposition period. The results are in agreement with those of Takafuji & Chant (1976) who reported consumption of 17.6 and 3.8 protonymphs of *Tetranychus pacificus* by *P. persimilis* during oviposition and post-oviposition periods. Females fed on eggs 5 times more than males in both treatments, whereas a value of 11 times for this predator

was reported when they were held on rose discs (Moghadasi *et al.* 2016). Rasmy *et al.* (1991); Naher *et al.* (2005) and Khalequzzaman *et al.* (2007) have shown higher prey consumption in females of *P. persimilis* compared to males for *T. urticae* on raspberry, bean and eggplant.

In the Chi & Liu model (1985), data of both sexes and variable developmental rates among individuals are used to evaluate population parameters. Like other factors, prey species and experimental condition may affect intrinsic rate of increase (*r*). McMurtry & Croft (1997) demonstrated that the intrinsic rate of increase of Phytoseiidae is sometimes below 0.1, but increases to 0.25 when fed on spider mites or pollen. For instance, it was 0.106 d⁻¹ when supplied with all stages of *T. evansi* (Escudero & Ferragut 2005); or as it was reported by Tello *et al.* (2009), feeding on *T. cinnabarinus* eggs decreased it to 0.019 d⁻¹ (Table 6). Net reproductive rate (R_0) of *P. persimilis* was 1.23 offspring in 29 °C and 42% humidity (Tello *et al.* 2009), whereas it was 40.69 offspring in 25 °C and 65 RH in this study (Table 6). The mean numbers of *T. urticae* eggs consumed by protonymphs and deutonymphs of this specialist predator were 3.02 and 4.95 per day, respectively. Tello *et al.* (2009) reported 3 and 7 consumed eggs of *T. cinnabarinus* for this two developmental stages of *P. persimilis*, respectively. Consumption of female protonymphs and deutonymphs when supplied with 25 *T. pacificus* protonymphs have been recorded as 5.6 and 6.8, respectively (Takafuji & Chant 1976) which is more than the amount in this study (3.54 and 5.56).

Group rearing may have positive effects. For instance, Le Goff et al. (2010) showed that while being in a group (two to six individuals), daily reproduction and web production were significantly higher in T. urticae females than when held individually. Lihoreau & Rivault (2008) showed that being in a group increases the oothecae production and nymphal development in aggregating species, Blattella germanica while two non-aggregating species (B. lituricollis Walker and B. biligata Walker) were not affected by group living. Effects of colony size also were investigated in social spider mites and results have shown that the greater the increase in colony size, the higher the probability of offspring surviving to maturity and reproducing (Avilés & Tufino 1988; Salomon & Lubin 2007). Our result showed that although there was no significant difference between most of the reproductive and population parameters of *P. persimilis* when group- vs. individual-reared, being in a group and living with peers improved some parameters and caused shorter pre-adult and preoviposition periods. Despite no significant differences were observed in population parameters and predation capacities between two individual- and group-reared treatment, the population size and total predation potential were higher in group-reared cohort than that in individual-reared cohort. These results may be explained as that joined effect of the shorter preadult duration, higher survival rate, earlier reproduction (APOP and TPOP) became more significant over the time. This information will be useful for mass-rearing of P. persimilis for practical application.

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