Temperature-dependent life table parameters of Aphidius matricariae (Hym.: Braconidae), an important parasitoid of the currant lettuce aphid, Nasonovia ribisnigri (Hem.: Aphididae)

Afrooz Farsi*, Farhan Kocheili, Mohammad Saeed Mossadegh & Arash Raschk

Department of plant protection, faculty of Agriculture, Shahid Chamran University of Ahwaz, Ahwaz, Iran.
*Corresponding author, Email: afrooz.farsi@yahoo.com

Abstract
The effects of temperature on demographic parameters of the aphid parasitoid, Aphidius matricariae (Haldaiy), on lettuce aphid, Nasonovia ribisnigri Mosely, were studied at five constant temperatures, 15, 20, 22, 25 and 27 ± 1°C and a photoperiod of 16L:8D h. The life table parameters were estimated using age-stage, two-sex life table procedure. Moreover, the bootstrap method was used for estimating variance, mean and standard error of the population growth parameters, at studied temperatures. All estimated parameters were considerably affected by temperature. Accordingly, nymphs of N. ribisnigri could not settle and survive on the leaves at 27°C. Thus, mummies were not formed. Developmental time of the parasitoid wasp decreased with increasing temperature from 21.21 days at 15°C to 11.19 days at 25°C. The oviposition periods were 15.21±0.12, 9.47±0.10, 5.91±0.05 and 5.6±0.09 days at the temperatures of 15, 20, 22 and 25°C. The highest value of net reproductive rate (r) and finite rate of increase (λ) were estimated to be 0.251 and 1.285 (d−1) at 20°C, respectively. The highest intrinsic rate of increase (w) was no significant difference among the estimated values regarding intrinsic rate of increase and finite rate of increase at the temperatures of 20, 22 and 25°C. The highest value of net reproductive rate (R0) was 123.06 (offspring/individual) at 15°C and the shortest mean generation time (T) was 13.98 (day) at 25°C. According to the obtained results, the temperatures 20-25°C, can be considered as optimal temperature range for the biological control of the currant lettuce aphid by using A. matricariae.

Keywords: Aphidius matricariae, Nasonovia ribisnigri, demography, temperature
Introduction

Nasonovia ribisnigri (Mosely) (Aphididae) is a primary pest of the lettuce that has spread throughout Europe, Canada, Asia, the Middle East, North and South America (Blackman & Eastop, 2000) and recently invaded the New Zealand (Stufkens & Teulon, 2003; Fagan et al., 2009) and Australia (Diaz & Fereres, 2005). This pest was reported on Crepis sp. (Asteraceae) in the Alborz Mountains of Iran in 1994 (Rezvani, 2001) and for the first time on romaine lettuce fields in Ahwaz, south of Khuzestan province, in 2008 (Bagheri et al., 2014).

Nasonovia ribisnigri colonizes the innermost leaves of the lettuce plants that cannot be treated easily with insecticides resulted in the serious contamination problem, for the simple reason that lettuces with high population of aphids are unsaleable (MacKenzie & Vernon, 1988; Liu, 2004).

The main problem with lettuce aphid is its capacity to act as a vector for viruses, including Gooseberry vein banding virus, Cauliflower mosaic virus, Cucumber virus, and Lettuce mosaic virus (Davis et al., 1997). Mackenzie (1986) and afterwards Morales et al. (2013) have reported that the economic threshold of the lettuce aphid in the fields was 0.5 and 0.07 aphids per plant, respectively. These results show that to avoid critical and heavy damage, insecticide sprays are needed when a very low aphid density is seen in lettuce seedlings soon after transplant. Although, the widespread use of insecticides to control this pest resulted in a serious resistance problem (Palumbo, 2000; Kift et al., 2004). For this reason, biological control has been increasingly considered in the field and greenhouse crops. In California, this invasive aphid has been recognized as a suitable host for a number of indigenous natural enemies (Bugg et al., 2008). Parasitoids and predators along with fungal entomopathogens are potential biocontrol agents against lettuce aphids (Nebreda et al., 2005; Diaz et al., 2007; Smith & Chaney, 2007; Fagan et al., 2010; Shrestha & Enkegaard, 2013; Shrestha et al., 2013; Shrestha et al., 2014).

Especially aphid parasitoids are presently considered as the most effective and reliable biocontrol agents, because of their high population growth rates and ability to react as density-dependent factors (Nebreda et al., 2005). Regarding the parasitoids of the lettuce aphid, Aphidius hieraciorum (Stray) (Hymenoptera: Braconidae) has recently been described as a promising candidate against N. ribisnigri in the United Kingdom and Spain. However, this species is still not commercially available (Nebreda et al., 2005).

Little documentation exists on the efficacy of aphid parasitoids to control of N. ribisnigri in Iran. Based on the survey conducted on the lettuce aphid parasitoids in Khuzestan, Iran, N. ribisnigri individuals were found to be parasitized by two braconid wasp species: Aphidius matricariae (Haliay) and Praon volucr (Haliay). Among them, A. matricariae was the important parasitoid of aphid occurred in the greatest numbers (94%) in association with N. ribisnigri (Farsi et al., 2014). A. matricariae is a broadly oligophagous parasitoid found on the various species of aphids all over the world (Stary, 1988). It is used in commercially in the United Kingdom and elsewhere in Europe for the biological
control of aphids in protected cropping systems. This led to the further attention to consider their potential role in the current lettuce aphid biological control programs in Iran.

Having knowledge on both the population ecology of the target species and its natural enemies are necessary to achieve successful control strategies. Information on the life table is important in aiming to control a given pest species, as it gives the most comprehensive description on the growth, survival and fecundity concisely.

Several factors may influence on the rate of parasitism and subsequently on the development of parasitoids on their host aphids (Jervis & Copland, 1996). Temperature is a key abiotic factor regulating insect population dynamics, developmental rates, and seasonal occurrence (Goodman, 1982). Present study was designed to evaluate the population growth rate and life table parameters of *A. matricariae* based on an age-stage, two-sex life table at five constant temperatures that may be useful for developing biological control of the lettuce aphid in the fields and greenhouses.

**Materials and methods**

**Insect cultures**

The currant lettuce aphid *N. ribisnigri* and its parasitoid *A. matricariae* were collected from lettuce fields in Khuzestan province (Southwestern Iran) in March 2016. The insects were reared on lettuce seedlings (*Lactuca sativa* L. var longifoli) growing in netted hyaline cages (176×70×70 cm) at 25±2°C, 40-60% RH and a photoperiod of 16L: 8D h.

**Biology and life table parameters**

This study was conducted at five constant temperatures: 15, 20, 22, 25 and 27 ± 1°C, 65 ± 5% RH and a photoperiod of 16L: 8D h. Before initiating the experiment, the colony of aphid as host and its parasitoid were kept under the conditions as described above, for one generation.

An opaque cylindrical container (diameter: 7.5 cm; length: 18 cm) containing 4-5 leaf-stage lettuce seedlings kept in vial of water and infested with approximately 100 third instar nymphs of *N. ribisnigri* was used as rearing containers. Each container was covered with fine mesh net for ventilation. To have a cohort of the same age of parasitoid wasps (< 8 h), five male and five female adults (24-48 h old) of *A. matricariae* were released into each container and then removed after 24-h period. The aphids on lettuce were checked daily for the formation of mummies. Mummies were transferred into the plastic petri dishes (diameter: 6 cm; height: 1 cm) and observed daily for adult emergence. Adults were paired after emergence. Twenty-two pairs of *A. matricariae* were used in the life table study. Each pair was transferred to a lettuce seedlings container with 50 third instar nymphs of *N. ribisnigri*. The parasitoids were moved to a new container with the same number of aphids daily. It continued until the death of all parasitoids. Dead males were also steadily replaced with the treated males of the same age. Mummies from different days were recorded and kept separately until the emergence of the adult parasitoids. The date of all emerged offspring was recorded.

**Statistical analysis**

The data were analyzed based on the age stage, two-sex life table procedure (Chi & Liu, 1985; Chi, 1988). The adult pre-oviposition period (APOP) (the duration from adult emergence to first oviposition) and total pre-oviposition period (TPOP) (the duration from egg to first oviposition) were calculated. The age-stage specific survival rates (*s*), the age specific survival rate (*l*), the age-stage specific fecundity (*f*), the age- specific fecundity (*m*) and the population parameters (the intrinsic rate of increase (*r*), the net reproductive rate (*R*), the finite rate of increase (*λ*) and the mean generation time (*T*) were estimated accordingly.

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

\[
\sum_{x=0}^{m} e^{-r(x+1)} l_x m_x = 1
\]

(1)

The finite rate of increase (*λ*), net reproductive rate (*R*) and mean generation time (*T*) were calculated as follows:
Demographic parameters of the aphid parasitoid considerably affected by temperature. Nymphs of *N. ribisnigri* could not settle and survive on the leaves and their growth was incomplete. Accordingly, mummies were not formed at 27°C. Therefore biological characteristics of this parasitoid were recorded only at 15, 20, 22 and 25°C. Form 100 eggs at the beginning of each experiment, 69, 66, 73 and 75 eggs hatched at 15, 20, 22 and 25°C, respectively. The total developmental time, from egg hatch to adult emergence decreased significantly with increasing the temperature, with the longest period recorded at 15°C and the shortest at 25°C (Table 1). Adult longevity was significantly longer at 15°C than that of adults reared at other temperatures (Table 2).

### Table 1. Mean (±SE) developmental time of *Aphidius matricarie* at four constant temperatures

<table>
<thead>
<tr>
<th>Developmental stage</th>
<th>Temperature (°C)</th>
<th>15</th>
<th>20</th>
<th>22</th>
<th>25</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-pupa (day)</td>
<td>13.7±0.33</td>
<td>9.17±0.10</td>
<td>7.62±0.09</td>
<td>6.81±0.09</td>
<td></td>
</tr>
<tr>
<td>Pupa (day)</td>
<td>7.3±0.24</td>
<td>5.15±0.09</td>
<td>4.84±0.10</td>
<td>4.39±0.07</td>
<td></td>
</tr>
<tr>
<td>Pre-adult (day)</td>
<td>21.2±0.44</td>
<td>14.4±0.11</td>
<td>12.45±0.13</td>
<td>11.19±0.13</td>
<td></td>
</tr>
</tbody>
</table>

Means followed by different letters within each row are significantly different according to the paired bootstrap test at 95% confidence interval. The SEs were estimated by 10000 bootstraps.

### Table 2. Mean (± SE) adult pre-oviposition period (APOP), total pre-oviposition period (TPOP), oviposition period, adult longevity and fecundity of *Aphidius matricarie* at four constant temperatures

<table>
<thead>
<tr>
<th>Biological index</th>
<th>Temperature (°C)</th>
<th>15</th>
<th>20</th>
<th>22</th>
<th>25</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female adult longevity (day)</td>
<td>37.3±0.96</td>
<td>25.14±0.66</td>
<td>19.64±0.38</td>
<td>17.75±0.43</td>
<td></td>
</tr>
<tr>
<td>Male adult longevity (day)</td>
<td>39.4±1.95</td>
<td>26.37±0.98</td>
<td>19.1±0.33</td>
<td>17.59±0.26</td>
<td></td>
</tr>
<tr>
<td>APOP (day)</td>
<td>1.26±0.07</td>
<td>1.11±0.05</td>
<td>1.09±0.05</td>
<td>1.10±0.06</td>
<td></td>
</tr>
<tr>
<td>TPOP (day)b</td>
<td>20.9±0.54</td>
<td>14.44±0.15</td>
<td>12.67±0.17</td>
<td>11.15±0.16</td>
<td></td>
</tr>
<tr>
<td>Oviposition days (days)</td>
<td>15.21±0.12</td>
<td>9.47±0.1</td>
<td>5.91±0.05</td>
<td>5.6±0.09</td>
<td></td>
</tr>
<tr>
<td>Fecundity (eggs/female)</td>
<td>249.7±12.62</td>
<td>192.72±12.81</td>
<td>105.15±6.2</td>
<td>102.3±7.02</td>
<td></td>
</tr>
<tr>
<td>Maximum daily fecundity</td>
<td>47</td>
<td>45</td>
<td>50</td>
<td>44</td>
<td></td>
</tr>
</tbody>
</table>

Means followed by different letters within each row are significantly different according to the paired bootstrap test at 95% confidence interval. The SEs were estimated by 10000 bootstraps.

<sup>a</sup> APOP: Adult pre-oviposition period.

<sup>b</sup> TPOP: Total pre-oviposition period.

Except for the adult pre-oviposition period (APOP), total pre-oviposition period (TPOP), oviposition period and fecundity decreased significantly with increasing the temperature. Parasitoids began oviposition at the age of 20.91 d (TPOP) at 15°C. However, oviposition started at age of 11.15 d at 25°C which was the shortest in comparison with the other examined temperatures (Table 2). The oviposition period of *A. matricarieae* was not significantly different between the temperatures of 22 and 25°C. The longest oviposition
period (15.21 day) was recorded at 15°C (Table 2). The highest mean fecundity was 249.74 eggs/female at 15°C and the lowest was 102.3 eggs/female at 25°C. There was no significant difference between fecundity values at temperatures of 22 and 25°C (Table 2).

The age-stage specific survival rate ($s_{xj}$) curve of *A. matricariae* indicates the probability of a newborn larva surviving to age $x$ and stage $j$ (Fig. 1). Due to the variation in the developmental rates among individuals, there are overlaps in the stage survival rate. The probability that a newly laid egg will develop to the adult stage increases with increasing temperature between 15 and 20°C and then decreases at 22 and 25°C. Both females and males at 15°C survived longer than those at other temperatures (Fig. 1).

![Fig. 1. Age-stage survival rate ($s_{xj}$) of *Aphidius matricarieg* at four constant temperatures](image)

The number of offspring produced by an individual of *A. matricariae* in age $x$ and stage $j$ is shown in figure 2. Moreover, age-specific survival rate ($l_x$), age-specific fecundity ($m_x$), and age-specific maternity ($l_xm_x$) show periodic peaks in reproduction (Fig. 2). Based on the estimated data for these curves, the age-specific survival rate ($l_x$) decreased with increase in temperature between 15 and 25°C. The highest peak for age-stage specific fecundity ($f_{xj}$) and age specific maternity ($l_xm_x$) were recorded at 20°C and the age-specific fecundity ($m_x$) was highest at 22 °C (Fig. 2).

The negative effect of a decrease in temperature on reproduction in *A. matricariae* can be observed in the age-specific reproductive curve ($v_{xj}$). The maximum reproductive peak of the females reared at 15°C ($v_{20} = 107/22$) occurred much later than that of females reared at other temperatures (Fig. 3). In contrast, at 25°C, reproductive value reached a peak of 74.58 at age the age of 10 d, earlier than other temperatures. The highest reproductive value at the temperatures of 20 and 22°C was occurred at age of 13 and 11 d, respectively (Fig. 3).

The age-stage life expectancy ($e_{xj}$) of *A. matricariae* at all examined temperatures are presented in figure 4. Based on the results, the age-stage specific life expectancy ($e_{xj}$) of a newborn ($e_{0j}$) is exactly the same, as the mean longevity. Life expectancy decreased gradually with age. Accordingly, the maximum life expectancy of all stages of *A. matricariae* was recorded at 15°C (Fig. 4).
Fig. 2. Age-specific survival rates (l_x), female age-specific fecundity (f_x), adult age-specific fecundity (m_x) and age-specific maternity (l_x m_x) of *Aphidius matricariae* at four constant temperatures.

Fig. 3. Age-stage-specific reproductive value (v_x,j) of *Aphidius matricariae* at four constant temperatures.
The intrinsic rate of increase ($r$), finite rate of increase ($\lambda$), net reproductive rate ($R_0$) and mean generation time ($T$) are presented in Table 3. Temperature had a significant effect on intrinsic rate of increase ($r$). The lowest and highest $r$ value was estimated to be 0.1831 and 0.2507 d$^{-1}$ at 15 and 20 °C, respectively. However, there was a reduction in the value of this parameter at 22 (0.2491 d$^{-1}$) and 25 °C (0.2363 d$^{-1}$) (Table 3).

The estimated values of finite rate of increase ($\lambda$) of *A. matricariae* indicated the same trend as intrinsic rate of increase, among the examined temperatures. The finite rate of increase was greatest at 20°C. Although, there was no significant difference in the intrinsic rate of increase ($r$) and finite rate of increase ($\lambda$) between 20, 22 and 25°C. The mean generation time ($T$) decreased with increasing temperatures, reached the lowest value at 25°C. The net reproductive rate ($R_0$) of *A. matricariae* decreased with increasing temperature from 15 to 25°C. The highest net reproductive rate ($R_0$) was 123.05 offspring/individual at 15°C and the lowest was 27.28 offspring/individual at 25°C (Table 3).

**Table 3.** Comparison of estimated life table parameters of *Aphidius matricarie* at four constant temperatures

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>$r$ (day$^{-1}$)</th>
<th>$\lambda$ (day$^{-1}$)</th>
<th>$R_0$ (offspring/individual)</th>
<th>$T$ (day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>0.1831±0.0062$^b$</td>
<td>1.2010±0.0075$^b$</td>
<td>123.05±16.33$^a$</td>
<td>26.27±0.59$^a$</td>
</tr>
<tr>
<td>20</td>
<td>0.2507±0.0073$^a$</td>
<td>1.2849±0.0094$^a$</td>
<td>105.12±13.66$^a$</td>
<td>18.56±0.25$^a$</td>
</tr>
<tr>
<td>22</td>
<td>0.2491±0.0095$^a$</td>
<td>1.2829±0.0122$^a$</td>
<td>47.53±6.78$^a$</td>
<td>15.49±0.21$^a$</td>
</tr>
<tr>
<td>25</td>
<td>0.2363±0.0154$^c$</td>
<td>1.2666±0.0195$^c$</td>
<td>27.28±5.57$^a$</td>
<td>13.98±0.20$^a$</td>
</tr>
</tbody>
</table>

Means followed by different letters within each column are significantly different according to the paired bootstrap test at 95% confidence interval. The SEs were estimated by 10000 bootstraps.

**Abbreviations:** $r$: Intrinsic rate of increase, $\lambda$: Finite rate of increase, $R_0$: Net reproductive rate, $T$: Generation time.

**Discussion**

Although insects are not subjected to constant or alternating temperatures in nature, controlled laboratory studies can provide a valuable insight into the population dynamics of pests and their natural enemies. One of the main factors influencing the biology, ecology and dynamics of pests and their natural enemies, is temperature (Jervis & Copland, 1996). The
present study demonstrated significant difference in the performance of *A. matricariae*, the parasitoid of lettuce aphid at five constant temperatures. There is no reliable information on the full range of temperatures being suitable for the development and survival of *A. matricariae* on lettuce aphid, *N. ribisnigri*, in Iran.

Our results showed that *A. matricariae* could not develop from egg to adult stage at 27°C, because nymphs of *N. ribisnigri* could not settle and survive on the lettuce. In the current study, we found that an increase in temperature led to a reduction in the developmental time of *A. matricariae*. Zamani et al. (2007) reported that *A. matricariae* could not grow successfully on *Aphis gossypii* Glover and *Myzus persicae* Sulzer at 5 and 35°C from egg to adult. The survival rate of pupa stage was greatest at 25°C and least at 30°C. Moreover, according to the results, TPOP, oviposition periods, fecundity and total longevity of *A. matricariae* dramatically declined as temperature increased from 15 to 25°C. The females were most fecund at 15°C (249.7 eggs).

Fisher (1930) defines the reproductive value as the contribution of an individual to the future population. Earlier occurrence of the maximum reproduction value at 25°C compared to the lower studied temperatures, confirmed that increasing temperature lead to more population increase in high temperatures. Because life expectancy value is calculated using the age-stage survival rate (sₓ), which does not assume the population reaches a stable age-stage distribution, it can be used to predict the survival of a population (Chi & Su, 2006). By using life expectancy, we can predict that both males and females of *A. matricariae* can be expected to live for more than 1 months and 3 weeks at 15 and 25°C, respectively. However, this value could be different under field conditions where both biotic and abiotic factors vary. Tahirri Adabi et al. (2010) have reported that the life expectancy of *A. matricariae* decrease with increasing temperature which it can survive 12 days at 25°C. The Life table is a useful tool for evaluating the effectiveness of natural enemies for controlling pests under various climatic conditions in different habitats (Jervis & Copland, 1996). Among life table parameters (*Rₙ*, *r*, *λ*, *T*), the *r* parameter is especially valuable because it integrates mortality and fertility into a single value.

The maximum intrinsic rate of increase for *A. matricariae* was recorded at 20°C which is considerably higher than that estimated by Reed et al. (1992) (0.092) and Shijko (1989) (0.1550) at the same temperature. Shahrokhii et al. (2004) and Tahirri Adabi et al. (2010) reported the intrinsic rate of increase of *A. matricariae* on *Schizaphis graminum* and *A. fabae* to be 0.24 and 0.41 at 25°C, respectively. One of the major features of latter studies is that the parameters were estimated according to the traditional female age specific theory, which does not consider the role of males in population projection and therefore, may lead to a biased estimation of life-history parameters. However, the mentioned results also were affected by different host species.

According to our results, there was no significant difference between intrinsic rate of increase and finite rate of increase at 20, 22 and 25°C. Based on our results, the moderate temperatures (i.e., 20, 22 and 25°C) were favorable as external factor for *A. matricariae* to has greater survival, longevity and higher reproductive capacity compared with the lower and higher temperatures (i.e., 15 and 27°C). Our results are similar to Pourtaghi et al. (2016) who concluded that at 30°C, the intrinsic rate of increase, net reproductive rate, finite rate of increase, mean generation time of *A. matricariae* with *A. fabae*, as host, were all significantly lower compared to the lower temperatures. They reported that the best temperature was at 20-25°C. van Schelt et al. (2011) also suggested that the number of mummies produced per female of *A. matricariae* on *M. persicae* ssp. *Nicotianae*, was the highest at 20 and then 25°C and it produced only a few mummies with a delayed development and high mortality at 30°C. According to Zamani et al. (2007), the optimal temperature for population growth of *A. matricariae* on *A. gossypii* and *M. persicae* was 25°C. These results showed that this parasitoid cannot undergo very high temperatures during the hot summer months in the greenhouses. Giri et al. (1982) tested an introduced American strain of *A. matricariae* on *M. persicae*. They found an optimum for most parameters at 21°C and a rapid decline above 24°C.

One of the most outstanding features of our study in comparison to other similar ones is that in the current study, the variance and standard error of life table parameters have been...
undertaken both by the bootstrap method (with 10000 repeats). Huang & Chi (2012) have reported that the bootstrap technique is more reliable than the jackknife technique for estimating variances. The variances obtained with the jackknife technique are usually much larger than those were obtained with the bootstrap technique. As a results of frequency data that were estimated by jackknife method, failed in normality test (Ebrahimi et al., 2013).

According to the obtained results here, *A. matricariae* can be considered as a favorable and proper natural enemy for the biocontrol of *N. ribisnigri* at a temperature range of 20-25°C. On the other hand, considering that the current study was the first attempt for evaluation of *A. matricariae* as biological agents of *N. ribisnigri*, more information is necessary to fully understand the other ecological aspects of this species. Thus, more researches should be designed for studying the effect of host plants and other environmental factors on development and efficacy of *A. matricariae*. By understanding these factors, we would able to develop suitable strategies for the biological control of lettuce aphid.

Acknowledgments
We are grateful to the research deputy of Shahid Chamran University of Ahwaz for providing financial support and facilities.

References


Farsi et al.: Temperature-dependent life table parameters of *Aphidius matricariae*
matricariae Haliday on host aphid Schizaphis graminum (Rondani). Proceeding of the 16th Iranian Plant Protection Congress, University of Tabriz, Iran, 37-38.


