J. Crop Prot. 2016, 5 (3): 431-445
doi: 10.18869/modares.jcp.5.3.431

Research Article

Demographic traits of *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae) fed on *Sitobion avenae* Fabricius (Hemiptera: Aphididae)

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Abstract: Lady beetles are the most important predatory species among arthropods, so studying their population parameters gives a clear picture about their life span. The life histories of variegated lady beetle, *Hippodamia variegata* (Goeze), fed on the English grain aphid, *Sitobion avenae* Fabricius, on different host plants were studied under laboratory conditions, at 25 ± 1 °C, 65 ± 5% Relative Humidity and a photoperiod of 16:8 (Light: Dark) h. Developmental, survival and fecundity data were analyzed using the age-stage, two-sex life table method. According to the age-stage, two-sex life table, the net reproductive rates (R_0) of ladybird fed on *S. avenae* reared on *Triticum aestivum* var. tajan, *Hordeum vulgare* var. Dasht, *Zea mays* var. single cross 704 and *Sorghum durra* var. Speed feed were estimated to be 235.38 ± 36.15, 190.74 ± 33.37, 293.54 ± 46.66 and 137.46 ± 23.66 female offspring / female, respectively. Based on the results, the intrinsic rate of increase as an index of population increase of *H. variegata*, was 0.181 ± 0.006, 0.179 ± 0.006, 0.163 ± 0.006 and 0.162 ± 0.006 h^{-1} preyed on host reared on *T. aestivum* var. tajan *Z. mays* var. single cross 704 *S. durra* var. Speed feed and *H. vulgare* var. Dasht, respectively. Our findings demonstrate that by using the age-stage, two-sex life table we can accurately describe the growth, survival and development of the predator. Our finding may provide basic information for developing aphid biological control programs.

Keywords: Two Sex, Demography, *Hippodamia variegata, Sitobion avenae,* host plant

Introduction

Biological control is the major component of Integrated Pest Management (IPM) strategies. The aim of biological control is to reduce pest populations through natural enemies, such as predators, parasitoids and pathogens (Gilkeson and Kelin, 2001). A successful natural enemy is one, which has high reproduction rate, and good searching ability for its host, adaptability in different environmental conditions and synchronization with its host (Buchanan, 1996). Among all beneficial insects and arthropods, lady beetles are the most well-known predators all around the world (William, 2002). In fact, during their adult and larval stages, coccinellids attack to a variety of soft bodied herbivorous pests, including aphids, whiteflies, psyllids, and scales. Moreover they ingest fungal spores, pollen and nectar as complementary or even alternative foods when the preys are rare (Ali *et al.,* 2009). In many studies, it has been shown

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Handling Editor: Jafar Mohaghegh Neyshabori

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Received: 3 April 2015, Accepted: 1 April 2016

that *Hippodamia variegata* (Goeze) is an efficient predator and can be used for the biological control of aphids (Franzman, 2002). This coccinellid is an effective predator of aphids and is used as biocontrol agent against a wide range of aphid species in different crops such as wheat, cotton, tobacco, vegetables and orchards either in outdoor farms or in greenhouses (Cabral *et al.,* 2008). Due to the big size and high feeding capacity, this generalist-variegated beetle is proposed as valuable biological control agent (Kontodimas and Stathas, 2005) and is useful in insect pest management programs.

Due to the importance of predatory ladybird beetles in aphid biological control, it is necessary to investigate the factors influencing the resource quality of aphids as their prey. Among these factors, plant species can affect not only the herbivorous insects feeding on them, but also parasitoids and predators directly or/and indirectly, through multi-trophic interactions (Price *et al.,* 1980). Plant biochemistry may influence the nutritional value of herbivorous insects and in turn affect the various life history traits of their natural enemies (Giles *et al.,* 2002). Prey quality has a direct impact on the growth, development and reproduction of predatory insects (Thompson, 1999), and this effect is displayed by their differential efficiencies (Babu, 1999). The relative suitability of a prey species can be evaluated by measuring its impact on the biological characteristics of the predator (Kalushkov and Hodek, 2001). Preys are categorized as essential, alternative or rejected on the basis of quantitative data on the developmental rate, survival and reproductive capacity (Hodek and Honek, 1996). Recently, some information has become available on the relative suitability of aphid species for some important ladybird beetles (e.g., Takizawa *et al.,* 2000; Evans *et al.,* 2004; Tsaganou *et al.,* 2004; Kalushkov and Hodek, 2001, 2004; Omkar and Srivastava, 2003; Omkar and Bind, 2004; Pervez and Omkar, 2004; Ali and Rizvi, 2007; Golizadeh and Jafari-Behi, 2012). However, supporting data are limited (Wu *et al.,* 2010). Some studies indicated that the suitability of prey was affected not only by the host plant species (Rü and Mitsipa, 2000; Francis *et al.,* 2001; Al-Zyoud *et al.,* 2005), but also by the cultivar (Du *et al.,* 2004).

Demography has been applied to study natural enemies' potential in biocontrol programs (Bellows *et al.,* 1992) and improvement of rearing techniques in the mass production of many species (Carey and Vargas, 1985; Lido and Carey, 1994). A proper assessment of predation potential should include the evaluation of a life table and only life tables can provide a comprehensive description of the development, survival, and fecundity of a population (Farhadi *et al.,* 2011). For most insects, the developmental rates vary among individuals and between the sexes (Istock, 1981; Chi and Liu, 1985; Carey, 1993). Chi and Liu (1985) and Chi (1988) developed an age-stage, two-sex life table that takes into consideration stage differentiation and the male population. The age-stage, two-sex life table has been used to describe the population characteristics of many insect and mite species under the influence of a variety of physical conditions. Chi and Liu (1985) and Chi (1988) also demonstrated that the traditional female age-specific life tables (e.g., Lewis, 1942; Leslie, 1945; Birch, 1948) ignore the males and the stage differentiation.

Although past publications on *H. variegata* have focused mainly on the biological characteristics (Fan *et al.,* 1995; An *et al.,* 2000), functional response (Fan and Zhao, 1988; Feng *et al.,* 2000; Pang *et al.,* 2000), life table (Lanzoni *et al.,* 2004; Kontodimas and Stathas, 2005) and the influence of temperature on its development (Michels and Bateman, 1986; Michels and Flanders, 1992), no studies have been carried out on influence of different host plants of wheat green aphid, *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae) on some population parameters of ladybird, *H. variegata*. Only Wu *et al.* (2010) investigated Influence of five host plants of *Aphis gossypii* Glover on some population parameters of *H. variegata*.

As the fitness of a mass-produced natural enemy depends on many factors as well as food quality, the present research was carried out to determine development, mortality, longevity, reproduction and the most suitable prey for ladybird *H. variegata* as influenced by host plants species in the laboratory.

Materials and Methods

Collecting and rearing of *H. variegata* and *S. avenae*

The English grain aphid, *S. avenae* Fabricius, was collected from wheat fields at the experimental field of Mohaghegh Ardabili University in the suburb of Ardabil city, Iran, in April 2012 and transferred onto four different host plants (*Triticum aestivum* var. *tajan, Hordeum vulgare* var. Dasht, *Zea mays* var. Single cross 704 and *Sorghum durra* var. Speed feed) cultivated in a greenhouse at 25 ± 5 °C, 50–70% RH and natural light conditions at the Department of Plant Protection, College of Agriculture, University of Mohaghegh Ardabili. These four plant species are main hosts of *S. avenae* in Iran.

H. variegata adults used in this study were originally collected from wheat fields at the above mentioned experimental field and brought to the laboratory. Then some pairs of ladybirds were selected for oviposition. Mating pairs were kept together in separate clear plastic cups (15 cm diameter, 8 cm height), with moist filter papers at the bottom (Wu *et al.,* 2010). Each pair was provided with *S. avenae* populations from four different host plants described above and maintained in a growth chamber set at 25 ± 1 °C, 65 ± 5 % RH and 16L: 8Dh photoperiod. Laid eggs of each pair were removed from the culture every 24 h and were kept separately in Petri dishes and were used to rear a new generation. The adult predators and larvae were fed daily with the aphid species. Aphids were replaced daily with fresh ones to avoid microbial contamination (Omkar and James, 2004). Predator populations were reared for at least one generation on aphid prey before being used for life table study.

Pre-imaginal development and survival

Only eggs laid within 24 h were used for the experiments. For investigation of pre-imaginal development and survival on different host plants, groups of about 50 eggs of *H. variegata* were obtained from the adults reared on four different host plants, and placed separately in Petri dishes (15 cm diameter, 8 cm height) in an incubator cabinet at 25 ± 1 °C, 60 ± 10% RH and 16:8h [L: D] photoperiod. Egg hatching and incubation period were recorded daily. After hatching, all emerged first instar larvae for each plant species were carefully transferred and isolated individually into a Petri dish with a fine hairbrush to avoid cannibalism. The first instars were supplied with a specific host plant–aphid complex until their pupation. Aphids and host plant leaves were replaced daily with fresh ones to avoid any microbial contamination. Larval, pupal periods and survival were recorded daily.

Reproductive attributes and longevity

After adult emergence, each pair was isolated in a Petri dish for mating and provided with the above-mentioned specific host plant–aphid complex daily. Eggs were counted daily and transferred to another Petri dish, which was labelled and cultured under the same conditions to calculate egg hatching rates on different host plants. Number of eggs deposited was counted daily and the experiments were continued until the death of all individuals. In the current study, adult pre-oviposition period (APOP: the period of time between the emergence of an adult female insect and the initiation of its oviposition), total pre-oviposition period (TPOP: the duration from egg to first oviposition), oviposition period, total fecundity (eggs during the reproductive period) and adult longevity were recorded. Based on the data obtained from the above experiments, life tables and population growth parameters of *H. variegata* on four host plants were calculated (Birch, 1948; Kontodimas and Stathas, 2005).

Age-stage, two-sex life table

Variables were tested for normality using the Kolmogorov-Smirnov test before subjecting them to analysis (SPSS, 2007). The raw life history data for *H. variegata* on the developmental time of all individuals, including males, females, and those dying before the adult stage, survivorship, longevity, and female daily fecundity of individuals were analyzed according to the theory of age-stage, two-sex life table (Chi and Liu, 1985; Chi, 1988) using the computer program TWOSEX-MSChart (Chi, 2013)

Following Chi and Liu (1985), the age-stage specific survival rate (s_{xj}) (where x = age and j = stage), the age-specific survival rate (l_x), the age-stage specific fecundity (f_{xj}), the age-specific fecundity (m_x), and the population parameters (r_m, the intrinsic rate of increase; λ, the finite rate of increase,; R_0, the net reproductive rate; T, the mean generation time) were calculated accordingly. The age-specific survival rate includes both male and female, the age-specific fecundity, and net reproductive rate were calculated according to Chi and Liu (1985) as:

$$l_x = \sum_{j=1}^{m} s_{xj} \qquad (1)$$

and

$$m_x = \frac{\sum_{j=1}^{m} s_{xj} f_{xj}}{\sum_{j=1}^{m} s_{xj}} \qquad (2)$$

and

$$R_o = \sum_{x=0}^{\infty} l_x m_x \qquad (3)$$

In this paper, the intrinsic rate of increase was estimated using the iterative bisection method and the Euler–Lotka equation with the age indexed from 0 (Goodman, 1982):

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

The mean generation time is defined as the length of time that a population needs to increase to R_0-fold of its original size as the stable age distribution and the stable increase rate are reached, i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$. Thus, it is calculated as T = (ln R_0)/r. The gross reproductive rate (GRR) is calculated as $GRR = \sum m_x$. The finite rate (λ) was calculated as follows:

$$\lambda = e^r \qquad (5)$$

Because life table studies are extremely time consuming and replication is impractical, we used the bootstrap techniques (Efron and Tibshirani, 1993) to calculate the means and standard errors of the population parameters.

Bootstrap technique

In the bootstrap procedure, we randomly take a sample of n individuals from the cohort with replacement and calculate the R_0, *i-boot* for this bootstrap sample as:

$$R_{o,i-boot} = \sum_{x=0}^{\infty} l_x m_x \qquad (6)$$

where the subscript *i-boot* represents the *i*th bootstrap and lx and m_x are calculated from the n individuals selected randomly with replacement. Generally, the data on the same individual are repeatedly selected. We repeat this procedure m times (m > 200, according to Meyer *et al.,* 1986) and compute the mean of these m bootstraps as:

$$R_{o,B} = \frac{\sum_{i=1}^{m} R_{0,i-boot}}{m} \qquad (7)$$

The variance S_B^2 and standard error se $(R_{o,B})$ of these m bootstraps can be calculated as:

$$S_B^2 = \frac{\sum_{i=1}^{m} \left(R_{o,i-boot} - R_{o,B}\right)^2}{m-1} \qquad (8)$$

$$Se\left(R_{o,B}\right) = \sqrt{S_B^2} \qquad (9)$$

The same method is used for the corresponding estimates of the gross reproductive rate, i.e., $GRR_{i\text{-}boot}$, GRR_B, and the variance and standard error of GRR_B.

Effects of host plants on the developmental time, reproduction period and female and male adult longevity were analyzed with one-way ANOVA. If significant differences were detected, multiple comparisons were made using the SNK procedure ($P < 0.05$). Statistical analysis and draw figures were performed using the SPSS v. 16.0 statistical program (SPSS, 2007) and Systat SigmaPlot v. 12.2, respectively.

Results

Age-stage, two-sex life table

The means of developmental periods, adult longevity and fecundity of *H. variegata* fed by aphids reared on four host plants are given in Table 1. All four host plant species of *S. avenae* were suitable for the development of *H. variegata* (Table 1). The mean durations of egg incubation, first, second and fourth instars development times varied significantly. There were also significant differences among the pupal periods on the four aphid host plant species. However, third instar periods did not vary significantly among the four aphid host plants. Moreover, host plant species of *S. avenae* significantly influenced the total developmental period of predators; the complete pre-adult duration was longest (16.31 ± 0.15 days) when reared on *H. vulgare* var. Dasht and shortest (14.89 ± 0.13 days) when reared on *T. aestivum* var. *tajan*. Female and male adults of *H. variegata* when reared on *Z. mays* var. Single cross 704 lived an average of 53.28 ± 1.31 and 47.88 ± 1.47 days, which was slightly longer than that of the female and male adults when reared on *S. durra* var. Speed feed i.e., 39.10 ± 1.54 and 32.66 ± 1.50 days (Table 1). The total recorded immature survival rates were 88, 94, 92 and 86 % on the examined four host plants, respectively.

The APOP of the *H. variegata* was not significantly different regarding the host plants. However, the host plants tested showed significant effects on the TPOP ($P < 0.05$) of this predator, which was the longest on *S. durra* var. Speed feed (20.68 ± 0.33 days) and the shortest on *T. aestivum* var. *tajan* (19.36 ± 0.35 days). There was a significant difference in the total number of eggs per individual of *H. variegata* on the four host plants ($P < 0.05$), which was highest on *Z. mays* var. Single cross 704 (587.31 ± 15.71) and lowest on *S. durra* var. Speed feed (362.47 ± 16.42) (Table 1). Mating happened all along the adult life (Table 1).

Table 1 Developmental durations in days of the different stages, adult longevity, fecundity, preovipostional period, total preovipostional period of *Hippodamia variegata* fed on aphids reared on four host plants at 25 °C.

Host plant	*Triticum aestivum* var. Tajan	*Hordeum vulgare* var. Dasht	*Zea mays* var. Single cross 704	*Sorghum durra* var. Speed feed
Egg (d)	2.18 ± 0.05^{b}	2.20 ± 0.06^{b}	2.54 ± 0.07^{a}	2.48 ± 0.07^{a}
1st instar (d)	2.35 ± 0.08^{b}	2.90 ± 0.10^{a}	2.70 ± 0.09^{a}	2.82 ± 0.09^{a}
2nd instar (d)	2.34 ± 0.08^{b}	2.52 ± 0.08^{b}	2.57 ± 0.09^{b}	2.81 ± 0.08^{a}
3rd instar (d)	1.89 ± 0.10^{a}	1.83 ± 0.11^{a}	1.86 ± 0.08^{a}	1.71 ± 0.09^{a}
4th instar (d)	3.16 ± 0.11^{b}	3.66 ± 0.07^{a}	3.13 ± 0.09^{b}	3.23 ± 0.12^{b}
Pupal period (d)	2.86 ± 0.05^{c}	3.15 ± 0.06^{a}	3.11 ± 0.08^{ab}	2.93 ± 0.05^{bc}
Total pre-adult (d)	14.89 ± 0.13^{b}	16.31 ± 0.15^{a}	15.89 ± 0.14^{a}	16.02 ± 0.09^{a}
Female adult longevity(d)	48.40 ± 1.60^{b}	44.40 ± 1.27^{b}	53.28 ± 1.31^{a}	39.10 ± 1.54^{c}
Male adult longevity (d)	42.28 ± 1.64^{b}	38.40 ± 1.31^{b}	47.88 ± 1.47^{a}	32.66 ± 1.50^{c}
Fecundity (eggs/female)	470.34 ± 19.08^{b}	432.79 ± 14.38^{c}	587.31 ± 15.71^{a}	362.47 ± 16.42^{d}
Oviposition period (d)	31.32 ± 0.25^{b}	29.68 ± 0.18^{b}	36.68 ± 0.19^{a}	24.37 ± 0.28^{c}
APOP[1] (d)	4.32 ± 0.28^{a}	4.27 ± 0.24^{a}	3.88 ± 0.21^{a}	4.63 ± 0.29^{a}
TPOP[2] (d)	19.36 ± 0.35^{b}	20.73 ± 0.33^{a}	19.76 ± 0.23^{ab}	20.68 ± 0.33^{a}

1- APOP: Adult pre-oviposition period, 2- TPOP: total pre-oviposition period. Means followed by the same letters in a row are not significantly different, ($P < 0.05$, SNK).

To illustrate the difference between male and female survival, the survival rates (*sxj*) of both male and female individuals are shown in Fig. 1. The means and standard errors are the summarized descriptive statistics (Table 1), whereas the survival curves depict the detailed survival and stage differentiation process of the cohort. The overlaps between different stages during a development period demonstrate the variable developmental rates among individuals (Fig. 1). For adult male 0.388, 0.508, 0.420, 0.488 and female 0.506, 0.447, 0.508 and 0.382 on mentioned host plants, respectively. The number of offspring produced by an individual *H. variegata* of age *x* and stage *j* is shown in Fig. 2. Because only females produce eggs, there is only a single curve, f_{x7}, which represents females in the seventh life stage. The parameters l_x, m_x, and age-specific maternity (l_xm_x) are also plotted in Fig. 2. The curve of l_x is a simplified version of the age-stage survival rate (s_{xj}). The most daily fecundity (f_{x7}) obtained 16.36, 18.18, 17.00 and 16.84, which occurred in days 42, 39, 41 and 25 respectively. The curves of m_x show roughly periodic peaks in reproduction on barley and corn.

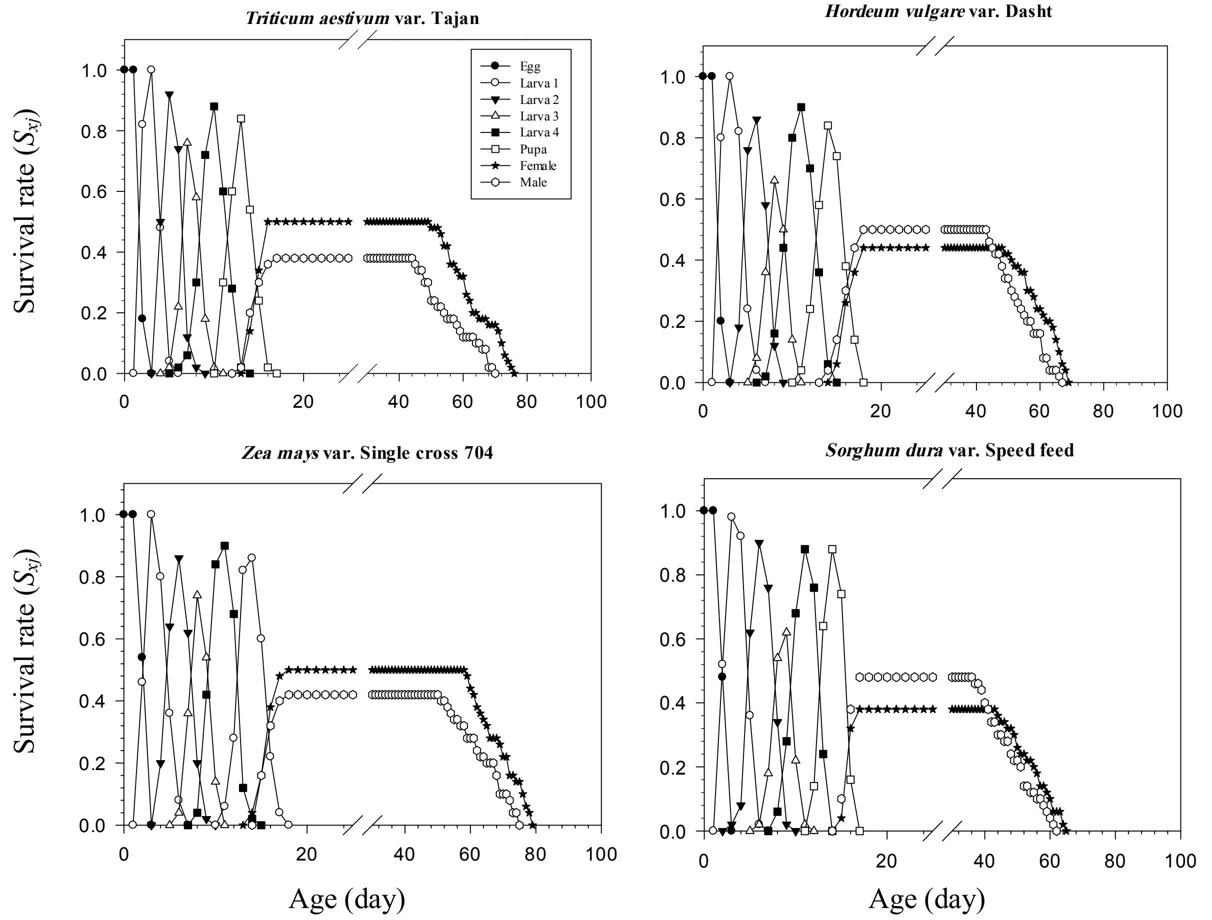

Figure 1 Age-stage specific survival rates of *Hippodamia variegata* fed on aphids reared on four host plants at 25 °C.

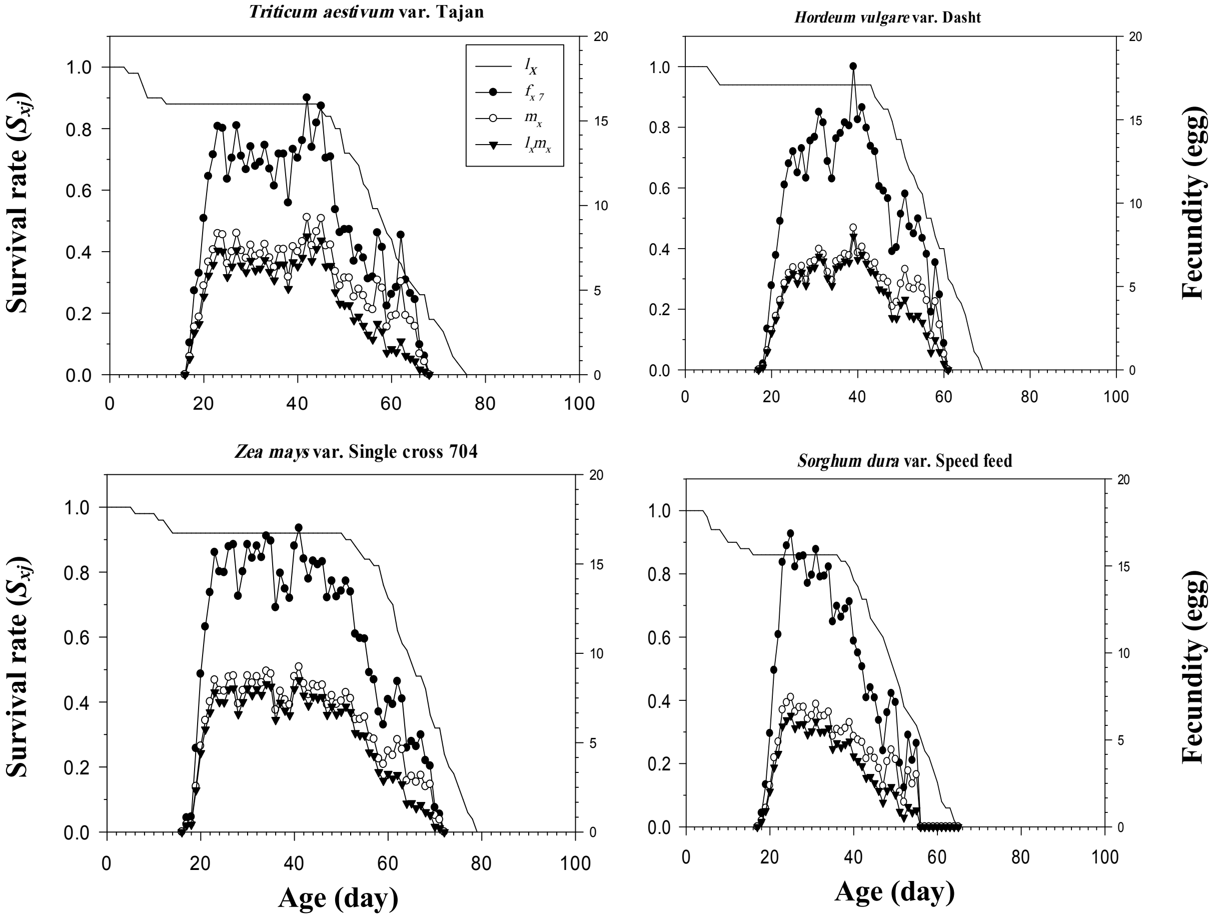

Figure 2 Age specific survival rates (l_x), fecundities (m_x), maternities (l_xm_x) and age-stage specific fecundities (f_{x7}) of *Hippodamia variegata* fed by aphids reared on four host plants at 25 °C.

Population parameters

The means and standard errors of the population parameters that were estimated by employing the bootstrap techniques (Efron and Tibshirani, 1993) are listed in Table 2. The GRR of *H. variegata* showed significant differences among four host plants, and the highest value was observed on *Z. mays* var. Single cross 704 (334.80±48.62 eggs). The R_0 of *H. variegata* was significantly different and highest when fed by aphids reared on *Z. mays* var. Single cross 704 (291.14 ± 46.66) and lowest on *S. durra* var. Speed feed (134.30 ± 23.66) (Table 2). Similarly, the r and λ value exhibited a significant difference on four host plants, which were highest on aphid- *T. aestivum* var. tajan whereas the lowest was on the aphid- *H. vulgare* var. Dasht diet. The T was shortest on the aphid- *S. durra* var. Speed feed diet (29.87 ± 0.33) and longest on aphid- *H. vulgare* var. Dasht (32.03 ± 0.44). Therefore, based on the intrinsic rate of population increase as an index of suitability of prey host plant species on the population increase of *H. variegata*, the suitability in decreasing order was: *T. aestivum* var. tajan > *Z. mays* var. single cross 704 > *S. durra* var. Speed feed > *H. vulgare* var. dasht.

Chi (1988) demonstrated that the relationship between the mean female fecundity (*F*) and the net reproductive rate (R_0) can be described as:

$$R_0 = \left(\frac{N_f}{N}\right)F \qquad (10)$$

where N is the total number of individuals used at the beginning of the life table study (i.e., 50 eggs), and N_f is the number of female adults emerging from these N eggs. It also means $N_f \times F = R_0 \times$ N. In other words, the total number of offspring produced by all females equals the net reproductive rate times the cohort size. In our results i.e., in wheat $N_f \times F$ = 11,758.5 and $R_0 \times$ N = 11,752.5. This minor difference is due to rounding-off. This relationship shows the precision obtainable in the age-stage, two-sex life table analysis.

Discussion

Prey quality consistently influenced the development, reproduction and adult longevity of *H. variegata*. The differences in the life history data of *H. variegata* on four host plant species of *S. avenae* were significant, indicating the major differences in their suitability. In the this study, *H. variegata* completed its development from egg to adult stage in 14.89–16.31 days at 25 °C, depending on the host plant of its prey; this range is shorter than those reported elsewhere at the same temperature on three aphids species [15.16-18.85 days in Golizadeh and Jafari-Behi (2012) or 18.1 days in Lanzoni *et al.* (2004) on *M. persicae*], but longer than those reported by Wu *et al.* (2010) on *A. gossypii* (12.6–14.5 days depending on the host plant of its prey). On the other hand, the pre-adult survival of *H. variegata* ranged from 86.0 to 94.0%, depending on the host plant of its prey and this was higher than the rates reported by others such as 81.0 % (Golizadeh and Jafari-Behi, 2012), 65.9 % (Farhadi *et al.,* 2011), 44.06–58.97 % (Wu *et al.,* 2010), 49.1% (Lanzoni *et al.,* 2004) and 61.8% (ElHag and Zaitoon, 1996). The differences in reported development time and survival rate between different studies can be attributed to the differences in experimental methods, conditions and prey species. In addition, host plants on which the prey fed might affect the nutrition of the prey and in turn affect the predation, development and survival of the predator (Zhang *et al.,* 2010; Wu *et al.,* 2010). Because the variable developmental rate occurring among individuals was incorporated into the age-stage, two-sex life table, the survival curve of a cohort shows stage overlapping (Chi and Yang, 2003). When *H. variegata* was fed on *A. gossypii* that had been reared on five host plant species, the suitability of aphids from various host plants differed for this predator (Wu *et al.,* 2010). Similar inferences were made by Francis *et al.* (2001) for *A. bipunctata* (L.) on *M. persicae*. The difference can be attributed to the nature of the host plants used in the experiment. Francis *et al.* (2001) suggested that host plant allelochemical substances may not only affect the herbivores, but also the pest predators. Lanzoni *et al.* (2004), and ElHag and Zaitoon (1996) used cylindrical containers and plastic containers, respectively, to rear ladybird beetles. In current study, the male adults lived longer compared to the mean longevity of female adults. Female and male adult longevity of *H. variegata* was prey dependent and ranged from 39.10 to 53.28 days and 32.66 to 47.88 days depending on four host plants. Mean female adult longevity on corn was 53.28 days, which was longer than that reported by Golizadeh and Jafari-Behi (2012) (64.75-73.10 days) and Farhadi *et al.* (2011) (44.9 days).

Our results showed that aphid host plant species affected significantly TPOP and oviposition rate of *H. variegata*. Rü and Mitsipa (2000) and Al-Zyoud *et al.* (2005) also obtained similar results. The longevity, and oviposition period and total fecundity of *H. variegata* did vary significantly among four host plants. However, taking into account other reproductive attributes of the predator, our results are different from others. The difference may be attributed to the nature of the host plants used in the experiment.

In this study, total fecundity of *H. variegata* ranged from 362.47 to 587.31 eggs per female, depending on host plant, which was lower than that of Lanzoni *et al.* (2004) (841.7) and (1139.2) on *A. fabae* in Farhadi *et al.* (2011), but higher than that of Kontodimas and Stathas (2005) (76.3–294.4). Also, the recorded total fecundity on Corn, wheat and barley were 587.31, 470.34 and 432.79 eggs, respectively, which were close to the results of Golizadeh and Jafari-Behi (2012).

Table 2 Population parameters of *Hippodamia variegata* fed on aphids reared on four host plants at 25 °C, estimated by using all individuals and the bootstrap techniques.

Parameter	*Triticum aestivum*var. Tajan	*Hordeum vulgare* var. Dasht	*Zea mays* var. Single cross 704	*Sorghum durra* var. Speed feed
r (day^{-1})	0.181 ± 0.006^{a}	0.162 ± 0.006^{c}	0.179 ± 0.006^{b}	0.163 ± 0.006^{c}
λ (day^{-1})	1.199 ± 007^{a}	1.176 ± 0.007^{c}	1.197 ± 0.008^{b}	1.177 ± 0.008^{c}
R_0 (offspring/individual)	235.05 ± 36.15^{b}	183.97 ± 33.37^{c}	291.14 ± 46.66^{a}	134.30 ± 23.66^{d}
T (day)	29.95 ± 0.41^{c}	32.03 ± 0.44^{a}	31.48 ± 0.40^{b}	29.87 ± 0.33^{c}
GRR (offspring)	297.39 ± 39.53^{b}	215.31 ± 36.05^{c}	334.80 ± 48.62^{a}	173.48 ± 28.92^{d}

Means followed by different letters in a row are significantly different, (SNK; $P < 0.05$).
R: the intrinsic rate of increase, λ: the finite rate of increase, R_0: the net reproductive rate, *T:* the mean generation time, *GRR*: gross reproductive rate.

In this study, a decrease was shown in survival rate by spending time in both sexes. The curves of m_x and l_xm_x (Fig. 2) showed roughly periodic peaks in reproduction on sorghum that were similar to those exhibited by *H. variegata*, in study by Farhadi *et al.* (2011). The periodic reproductive peaks are apparent in the raw data of the daily fecundity of individual females, in which reproductive peaks are separated by zeros, which represent periods of no reproduction (Yu *et al.,* 2013).

The population parameters of *H. variegata* are significantly influenced by aphid species. In general, life table can provide a comprehensive description of the development, survival and fecundity of a population. Among the population parameters, the intrinsic rate of increase is the most useful for comparing the population growth potential under specific climatic and food conditions, and it reflects the overall effects of prey on development, reproduction and survival characteristics of a population (Southwood and Henderson, 2000). The values of net reproductive rate (R_0) and intrinsic rate of increase (*r*) were lower than those reported by Kontodimas and Stathas (2005) (R_0 = 425.9, $r = 0.178$) and Farhadi *et al.* (2011) (R_0 = 387.6, $r = 0.204$), but higher than those of Lanzoni *et al.* (2004) (R_0 = 52.75, r = 0.114), and ElHag and Zaitoon (1996) (R_0 = 45.6, r = 0.082). The R_0 value in Golizadeh and Jafari-Behi (2012) was similar (290.97) to the calculated value in the current study (291.14-183.23). The differences in life table parameter values are possibly a result of different experimental conditions, different prey species, different prey species host plants or geographical populations (Kontodimas and Stathas 2005; Farhadi *et al.,* 2011; Golizadeh and Jafari-Behi, 2012).

Meyer *et al.* (1986) discussed the application of the jackknife and bootstrap techniques to population parameters. Based on results for cladoceran species, Meyer *et al.* (1986) suggested that the precision for reporting *r* values should be limited in most cases to two significant figures. According to the means and standard errors of our current and previous studies, we suggest that four significant figures are necessary to confirm the values' differences, precision, and variability. Moreover, the frequency distribution of the net reproductive rate that was estimated by employing the bootstrap technique met the assumptions of normality, which is an important premise for further statistical analysis. Because Yu *et al.* (2013) and Huang and Chi (2012b) zero pseudo values were obtained for R_0 by using the jackknife technique. A R_0 of zero means that the population cannot reproduce offspring and that no intrinsic rate can be estimated. This results in a serious contradiction in the application of the jackknife technique to the estimation of population parameters. Huang and Chi (2012b) mathematically invalidated the use of the jackknife technique in estimating the net reproductive rate. As proven by Chi (1988), based on the two-sex life table, the relationship between R_0 and mean female fecundity (*F*) is given in equation (10), and our data for *N*, N_f, *F* and R_0 (Table 3) were consistent with Eq. (10), for which all individuals are included in the calculation of R_0. In fact, when the bootstrap technique was employed in the calculation of R_0, minor differences were apparent due to the application of the resampling technique.

Chi and Yang (2003) also noticed that the application of a jackknife technique resulted in degrees of discrepancy between the estimated means and their definitions. Eq. (10) is valid for the age-stage, two sex life table, as well as the traditional female age-specific life table. It shows a simple and robust relationship between the common statistics of mean fecundity and the net reproductive rate that was defined more than 100 years ago (Boeckh, 1890).

In using a predaceous ladybird beetle for biological control, individuals in the larval stage are more effective control agents than the adults (Trouve *et al.,* 1997), unless the adults are flightless (Kuroda and Miura, 2003; Seko *et al.,* 2008). Inayat *et al.* (2011) reported that the overall larval feeding rate was twofold greater than that of the adult. In greenhouse conditions, Kuroda and Miura (2003) released *H. axyridis* egg sheets on cucumber plants, and the emerged larvae effectively decreased the density of *A. gossypii*. Therefore, the larval stage of *H. variegata* has the potential to be of use in biological control programs. The advantage of a predation study based on the age-stage, two-sex life table is evident in its proper stage grouping compared to the traditional female age-specific life table. To assess the population growth potentials and the efficacies of insect rearing programs, different methods and parameters have been used. However, in comparing the efficiency of a predator, we have to consider not only the predator's population growth rate but also its predation rate. Although the net reproductive rate R_0 was highest for beetles preying aphids fed on corn, the highest intrinsic rate and the finite rate were observed in beetles that preyed on aphids reared on wheat when the effect of time, i.e., the reproductive age, was considered. A faster intrinsic rate of increase or finite rate does not necessarily represent an efficient predator.

Conclusion

In conclusion, this study showed that all of *S. avenae* from four host plant species were suitable for the growth, development and reproduction of *H. variegata*. Prey host plants affected significantly the biological and ecological characteristics and performance of *H. variegata*. Wheat was the most suitable host among the tested host plants, followed by corn; sorghum and barley were least suitable as host plants. The obtained life history data in this study are of basic importance for efforts to develop a biological control or integrated pest management approach for the examined host plant species. Our study provides an opportunity for better understanding the tritrophic interactions of the plant–aphid–predator relationship and showed that successful biological control of pests should integrate each trophic level. Not only the food prey but also the host plants of prey should be carefully selected in predator's production for biological control. Moreover, age-stage two sex life table information for *H. variegata* must be integrated with its behavioral characteristics and other information, such as its capacity to establish and disperse. The mechanisms on the influence of prey's host plants on the predator remains to be investigated. Like other studies, we demonstrate that an accurate description of the survival, development, and population parameters can be achieved by the age-stage, two-sex life table. Thus, further investigation is needed on predation capacity and functional response.

Table 3 Relation between F and R_0 of *Hippodamia variegata* fed by aphids reared on four host plants at 25 °C.

Host plants	N	N_f	F	R_0	$R_0 = \left(\frac{N_f}{N}\right)F$
*Triticum aestivum*var. Tajan	50	25	470.34	235.05	235.05
*Hordeum vulgare*var. Dasht	50	22	432.79	183.97	183.97
*Zea mays*var. Single cross 704	50	25	587.31	291.14	291.14
*Sorghum durra*var. Speed feed	50	19	362.47	134.30	134.30

N: the total number of individuals used for life table study; N_f: The number of female adults emerged from *N*; R_0: the net reproductive rate; *F:* the mean fecundity of the female.

Acknowledgment

This research was funded by the Department of Plant Protection, University of Mohaghegh Ardabili, which is greatly appreciated.

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ویژگی های دموگرافیک کفشدوزک *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae) با تغذیه از شته سبز گندم *Sitobion avenae* Fabricius (Hemiptera: Aphididae)

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چکیده: کفشدوزک‌ها یکی از مهم‌ترین گونه‌های شکارگر در میان بندپایان می‌باشند. بنابراین مطالعه پارامترهای رشد جمعیت آنها یک تصویر شفافی درباره طول عمر آنها به ما می‌دهد. تاریخچه زندگی کفشدوزک *Hippodamia variegata* با تغذیه از شته سبز گندم *Sitobion avenae* روی گیاهان میزبان مختلف در شرایط آزمایشگاهی در دمای ۱ ± ۲۵ درجه سلسیوس، رطوبت نسبی ۵ ± ۶۵ درصد و دوره‌ی نوری ۱۶ ساعت روشنایی و ۸ ساعت تاریکی مورد بررسی قرار گرفت. اطلاعات دوره نشو و نما، بقاء و باروری با استفاده از جدول زندگی دوجنسی مورد تجزیه و تحلیل قرار گرفتند. بر طبق جدول زندگی دوجنسی نرخ خالص تولیدمثل (R_0) کفشدوزک با تغذیه از گندم (رقم تجن)، جو (دشت)، ذرت (سینگل کراس ۷۰۴) و سورگوم (اسپید فید) به‌ترتیب ۲۳۵/۳۸، ۱۹۰/۷۴، ۲۹۳/۵۴، ۱۳۷/۴۶ ماده/ماده/نسل به‌دست آمد. هم‌چنین براساس نرخ ذاتی افزایش جمعیت (r_m) که به‌عنوان یک شاخص مناسب در افزایش جمعیت این کفشدوزک می‌باشد، گندم نسبت به سایر گیاهان میزبان دارای بیش‌ترین نرخ ذاتی افزایش جمعیت بود و با تغذیه از گیاهان میزبان ذکر شده در بالا به‌ترتیب ۰/۱۸۱، ۰/۱۷۹، ۰/۱۶۳ و ۰/۱۶۲ بر روز به‌دست آمد. نتایج نشان داد که با استفاده از جدول زندگی دوجنسی می‌توان نشو و نما و بقای شکارگر را با دقت توصیف کرد. هم‌چنین این مطالعه برای درک بهتر برهمکنش گیاه - شته- شکارگر فرصت خوبی را ارائه کرده است.

واژگان کلیدی: دو جنسی، دموگرافیک، *Hippodamia variegata*، *Sitobion avenae*، گیاهان میزبان