PREY DENSITY DEPENDENT LIFE TABLE OF *APHIDOLETES APHIDOMYZA* RONDANI (DIP., CECIDOMYIIDAE) FEEDING ON *APHIS CRACCIVORA* KOCH (HEM., APHIDIDAE) UNDER LABORATORY CONDITIONS

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Abstract: The life table provides an integrated and comprehensive description of development times, survivorship, and reproduction of a population. Life table parameters of aphidophagous midge, *Aphidoletes aphidimyza* Rondani (Dip., Cecidomyiidae) on different densities (5, 10, 20, 40, 60, 80) of third instar nymphs of *Aphis craccivora* Koch as prey, were studiedat (25±1°C, 70±5% relative humidity (RH) and a photoperiod of 16L : 8D h). There were no significant differences among the adult pre-ovipositional periods (APOP) at different prey densities. The total pre-ovipositional period (TPOP) of female *A. aphidimyza* was reduced significantly as prey density increased. The oviposition period was significantly different at varying prey densities. It was 4.333±0.211 and 5.625±0.324 days at the lowest and highest prey densities, respectively. Female longevity was also significantly different at varying prey densities. Fecundity was directly dependent on prey density ($R^2 = 0.990$). The lowest fecundity was obtained at a density of 5 prey (52.5±1.544 eggs) and the highest was at a density of 80 prey, per day (121.375±4.301 eggs). The intrinsic rate of increase (r) was prey density dependent ($R^2 = 0.958$), and ranged from 0.122±0.017 to 0.193±0.014 d^{-1} as prey density increased. The net reproductive rate (R_0) was significantly increased as prey density increased. The peak reproductive values showed that female aphidophagous midges at the age of 15, 16, 17, 18, and 19 days made the highest contribution to the population at different prey densities. It was concluded that the increase in the densitits of third instar nymphs of *A. craccivora* had significant effects on demographic parameters of *A. aphidimyza.*

Key words: *Aphis craccivora*, *Aphidoletes aphidimyza*, intrinsic rate, prey density, reproductive values

INTRODUCTION

The cotton aphid, *Aphis gossypii* Glover (Hemiptera., Aphididae) as a cosmopolitan and polyphagous species, is widely distributed in tropical, subtropical, and temperate regions. This aphid is a pest of cotton, cucurbits, and citrus. *A. gossypii* principally attacks vegetables in fields and greenhouses (Leclant and Deguine 1994)**.**

The cowpea aphid, *A. craccivora* Koch (Hemiptera: Aphididae), as a cosmopolitan pest attacks several host plants, especially Fabaceae. It is considered as a major pest of important economic crops such as alfalfa, beans, and cowpea, *Vigna unguiculata* L. in Asia, Africa, and Latin America (Singh and Jackai 1985; Pettersson *et al.* 1998). In the tropics, it is one of the relatively few aphid species with pest status (Blackman and Eastop 1984). It has been reported that this aphid can transmit some plant pathogenic viruses (Coceano and Peressini 1989; Chen *et al.* 1999). Understanding the factors controlling the aphid's development and implementing this information into forecast models, may increase the efficacy and success of control tactics (Kührt *et al.* 2006).

The aphidophagous midge, *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) is a specialist predator of aphids. This midge is commonly used in biological control programs (Markkula and Tittanen 1985). Since 1973, it has been used for biological control of aphid populations in greenhouses (Asyakin 1973; Markkula *et al.* 1979; Kulp *et al.* 1989). It shows great promise as a biological control agent because of its high degree of density-dependency (El-Titi 1973), its inclination to kill more aphids than it consumes (Uygun 1971), and its compatibility with many pesticides (Warner and Croft 1982; Whalon and Eisner 1982).

The potential of the predatory midge, *A. aphidimyza*, as a control agent of aphids on greenhouse vegetables, has been studied in several countries such as Germany (Mayr 1973; El-Titi 1974); the Union of Soviet Social Republics (USSR) (Asyakin 1977; Bondarenko and Moiseev 1978); the Netherlands (van Lenteren *et al.* 1979): Finland (Markkula and Tittanen 1980); Canada (Gilkenson and Klein 1981) and Norway (Hofsvang and Hågvar 1982). Life table parameters of various *A. aphidimyza* populations have been studied on *A. fabae. A. fabae* preys on bean seedlings (*Vicia faba* L.) (Havelka and Zemek 1999).

The life table provides an integrated and comprehensive description with details of development times, sur-

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vival rates of each growth stage, fecundity and life expectancy of a population. The life table is often used by scientists as a method of projecting the growth of populations and predicting the population dynamics and population size (Chi 1990; Carey 1993; Medeiros *et al.* 2000; Southwood and Henderson 2000; Carey 2001). Also, the collection of life table data for related species of different trophic levels in a food chain is a basic and important task for conservation (Bevill and Louda 1999; Gabre *et al.* 2005) and pest management (Naranjo 2001). Life table analysis is a standard ecological method to estimate demographic parameters relevant to population dynamics (Legaspi 2004).

Population growth rate is a basic ecological characteristic that is usually described as the intrinsic rate of increase (r); an estimate of population growth potential introduced by Birch (1948). Among the life table parameters, intrinsic rate of increase is a key demographic parameter useful for predicting the population growth potential of an animal under a given environmental condition (Ricklefs and Miller 1999; Southwood and Henderson 2000). The intrinsic rate of increase may help predict the outcomes of pest–natural enemy interactions (Roy *et al.* 2003). The physiological qualities of an animal relative to its capacity to increase can be summarized with (r) (Andrewartha and Birch 1954). Besides being a measure of population growth, r has been widely used as a bioclimatic index (Hulting *et al.* 1990), in the estimation of insect response to resistant plants and in the comparison of different food types that predators consumed (Engel 1990). Furthermore, construction of life fertility tables may help improve pest management (Toapanta *et al.* 2005).

The main purpose of this study was to determine the impact of different densities of third instar nymphs of *A. craccivora* on the biological and life table parameters of a *A. aphidimyza*, population under laboratory conditions. The life table parameters can be used to estimate the rate of increase in a natural or released population (El Hag and Zaitoon 1996).

MATERIALS AND METHODS

Rearing prey and predator

Third instar nymphs of *A. craccivora* were collected from Black locust (*Robinia pseudoacacia* L.) and reared on black-eyed bean (*Vigna unguiculata* L.) at the College of Agriculture in the University of Guilan (Northern Iran). Larvae of *A. aphidimyza* were collected from the colony of *A. craccivora* in an infested black-eyed bean field. The predators were reared for one generation on different instars of *A. craccivora* before starting the life table experiments.

Experimental conditions

All aphids and predator stocks were kept in a growth chamber at 25±1°C, 70±5% relative humidity (RH), and a photoperiod of 16:8 (L:D) h.

Life table study

Experiments were done, after rearing the population under constant laboratory conditions as mentioned above, for one generation. To obtain the eggs of the predator, a stock culture of *A. aphidimyza* was kept in the laboratory and visited frequently during the day. Newly hatched 1st instar larvae of *A. aphidimyza* were transferred and placed individually in experimental, transparent plastic containers (15x13x3 cm). The larvae were offered densities of 5, 10, 20, 40, 60, and 80 third instar nymphs of *A. craccivora* every day to study their life table parameters. The duration of the successive development stages and the mortality were recorded. The number of prey consumed was counted daily at each prey density level to determine the total number of prey eaten (from 1st instar larva to adult). Prior to pupation, mature larvae were transferred to larger transparent, plastic containers (19x16x6 cm) to produce cocoons in a 2–3 cm layer of moistened fine sand. The sand had been disinfected in an autoclave (20 minutes at 120°C). The cocoons were left in these containers until the emergence of adults (Havelka and Zemek 1988). After adult emergence, the gall midges from the same prey densities were allowed to mate, and then were transferred to individual experimental arenas as described earlier in the pupal stage. Adults were fed on a few strips of papers (1x7 cm) soaked in a sucrose solution placed on the corners of the containers. The containers contained the same prey densities as in their immature stages. The aphidophagous midge mortality and number of eggs laid were recorded daily until all adults died. The number of replicates was 20 for both larval and adult stages, at each prey density.

Statistical analysis

Data were analyzed using an age-stage, two-sex life table theory. Therefore, developmental time of all individuals and female daily fecundity were analyzed according to the age-stage, two-sex life table theory (Chi and Liu 1985; Chi 1988).

The age-stage specific survival rate (s_{xj}) (where x – age and j – stage), the age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), the age-specific fecundity (m_x), and the population parameters (r, the intrinsic rate of increase; λ, the finite rate of increase, $\lambda = e^r$; R_0, the net reproductive rate; T, the mean generation time, and Gross Reproductive Rate (GRR), Gross reproductive rate) were calculated accordingly. In the age stage, two-sex life table, the l_x and m_x were calculated according to Chi and Liu (1985) as:

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

and

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

where:

k – the number of stages.

In this paper, the intrinsic rate of increase was calculated using the iterative bisection method from:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \qquad (3)$$

with age indexed from 0 (Goodman 1982). The age-stage life expectancy (e_{xj}) for individuals of age x and stage j was calculated according to the method described in Chi and Su (2006). The mean generation time is the time length that a population needs to increase to R_0 – times of its 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 GRR is calculated as GRR = $\sum m_x$. Data analysis and population parameters were calculated using the TWOSEX-MSChart program designed in visual BASIC for the Windows operation system (Chi 2005). The TWOSEX-MSChart is available at http://140.120.197.173/Ecology/prod02.htm (Chung Hsing University) and http://nhsbig.inhs.uiuc.edu/wes/chi.html (Illinois Natural History Survey). We used Duncan's procedure to compare the differences among treatments, following the description of Sokal and Rohlf (1995).

RESULTS

The adult pre-oviposition periods that is, the duration from adult emergence to first oviposition, was not significant at different prey densities provided to immature stages and adults. The total pre-oviposition period, that is, the duration from egg to first oviposition, was significantly higher in females fed on 5, 10, 20, 40, and 60 prey per day during their larval stage, than females fed on 80 prey per day as larva on lower prey densities during their larval stage (F = 2.64; df = 5, 41; p < 0.043).

The oviposition period was also significantly different among females fed on various prey densities per day during their larval stage (F = 2.69; df = 5, 40; p = 0.035). The density provided to immature stages and adults had a significant effect on female longevity (F = 2.74; df = 5, 45; p = 0.032). The fecundity was directly dependent on prey density ($R^2 = 0.990$) and affected significantly by prey density (F = 232.689, df = 1, 4, p = 0.0001) (Fig. 1). The total fecundity of females fed on 5 prey per day during their larval stage, was significantly lower than those fed on 10 prey per day. Those females fed on 60 and 80 prey per day during their larval stage had significantly higher fecundity than those fed on 20 and 40 prey per day (F = 45.89; df = 5, 41; p = 0.0001) (Table 1).

Results showed that increasing prey density had significant effects on the intrinsic rate of increase (r), the finite rate of increase (λ) and the net reproductive rate. Feeding on 5 and 10 prey per day during the larval stage led to a lower r than other densities (F = 3.08; df = 5, 119; p = 0.012). However, r values were directly dependent on prey density (F = 103.001, df = 1, 4, p = 0.0005) (Fig. 2). The finite rate of increase (λ) differed significantly with increasing prey density (F = 2.68; df = 5, 119; p = 0.025). The net reproductive rate (R_0) was significantly density dependent (F = 44.446, df = 1, 4, p = 0.003) (Fig. 3). It increased with increasing prey density ($R^2 = 0.961$). Similar results were found on GRR on different prey densities. The mean generation time (T) was not affected significantly by prey density (F = 1.12; df = 5, 119; p = 0.353) (Table 2).

The age-stage specific survival rates (s_{xj}) show the probability that a newborn will survive to age x and develop to stage j (Fig. 4). Because of the variability in devel-
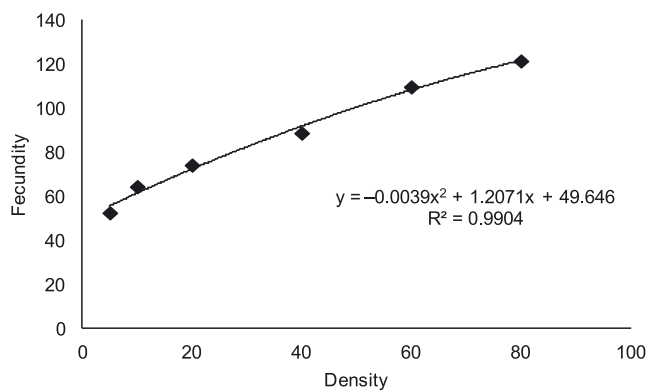

Fig. 1. Direct relationship between fecundity of *A. aphidomyza* and different densities of third instar nymphs of *A. craccivora*

Table 1. Biological parameters, longevity, and fecundity of *A. aphidimyza* adults reared on different densities of *A. craccivora* (mean ±SE)

Prey density	APOP	TPOP	Oviposition period [day]	Female longevity [day]	Fecundity [eggs/female]
5	1±0 a	20.83±1.077 a	4.333±0.211a	5.333±0.211 a	52.5±1.544 a
10	1±0 a	19.62±0.822 a	4.875±0.295 ab	5.875±0.295 ab	64.375±2.719 b
20	1±0 a	19.43±1.131 a	5.143±0.261 b	6.143±0.261 b	74.143±3.501 c
40	1±0 a	19.22±0.572 a	5.222±0.222 b	6.333±0.236 b	88.667±4.802 c
60	1±0 a	18.75±0.590 a	5.375±0.183 b	6.375±0.183 b	109.625±4.229 d
80	1±0 a	17.25±0.313 b	5.625±.324 b	6.625±0.324 b	121.375±4.301 d

APOP – adult pre-oviposition period; TPOP – total preoviposition period (from egg to first oviposition). Within columns, values followed by the same letter do not differ significantly (p <0.05) using Duncan's procedure
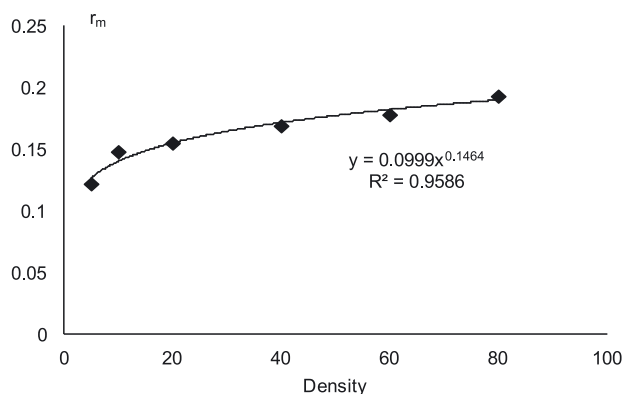
Fig. 2. Relationship between intrinsic rate increase (r) of *A. aphidomyza* and different densities of third instar nymphs of *A. craccivora*
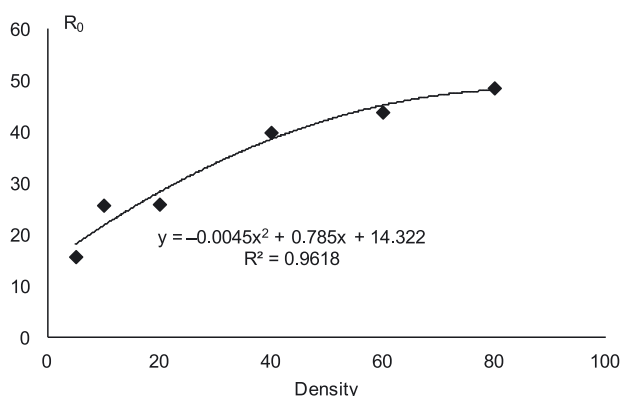

Fig. 3. Density dependent net reproductive rate (R_0) of *A. aphidomyza* fed on different densities of third instar nymphs of *A. craccivora*

Table 2. The population parameters: Intrinsic rate of increase (d^{-1}), finite rate of increase (d^{-1}), net reproductive rate (offspring/individual), mean generation time (day), and gross reproductive rate (offspring/individual) of *A. aphidimyza* reared withon different densities of *A. craccivora*

Prey density	Intrinsic rate of increase (r)	Finite rate of increase (λ)	Net reproductive rate (R_0)	Mean generation time (T)	Gross reproductive rate (GRR)
5	0.122±0.017 a	1.129±0.019 a	15.75±5.54 a	23.13±1.11 a	82.34±14.35 b
10	0.148±0.014 a	1.159±0.017 ab	25.75±7.31 ab	22.17±0.84 a	111±35.25d
20	0.155±0.019 ab	1.167±0.022 abc	25.95±8.2 ab	21.45±1.46 a	81.67±16.15 b
40	0.169±0.013 ab	1.184±0.015bc	39.9±10.33 ab	22.01±0.57 a	94.96±26.35 c
60	0.178±0.015 b	1.195±0.018 bc	43.85±12.43 ab	21.43±0.65 a	89.89±23.69 c
80	0.193±0.014 b	1.213±0.017 c	48.55±13.74 b	20.28±0.37 a	77.05±27.52 a

Within columns, values followed by the same letter do not differ significantly (p < 0.05) using Duncan's procedure

opmental rates among individuals, there were overlaps in the stage survival rate curves. Based on the age-stage, two-sex life table, the age-stage specific life expectancy (e_{xj}) gives the expected life span an individual of age x and stage j can live after age x (Fig. 5). For example, the life expectancy of a newborn aphidophagous midge was 20.95 days when fedon 10 prey per day during the larval stage. The contribution of an individual of age *x* and stage *j* to the future population is described by the age-stage reproductive value (v_{xj}) (Fig. 6). However, the peak reproductive value appeared at the ages of: 18 days on 5 prey /day, 16 days on 10 prey/day, 15 days on 20 prey/

day, 19 days on 40 prey/day, 17 days on 60 prey/day, and 18 days on 80 prey/day, during their larval stage. This showed that females at the age of 18, 17, 18, 19, and 16 days made the highest contribution to the population when reared on (80, 60 and 5), (40 and 10), and 20 prey densities per day, respectively.

We calculated the age-specific survival rate (l_x) and fecundity rate (m_x) using equations (1) and (2). The curve of l_x is a simplified version of the age-stage survival rate (s_{xj}) and describes the change in the survival rate of the cohort with age. The age-stage specific fecundity rate (f_{xj}) of the female adult *A. aphidimyza* is also shown in figure 7.
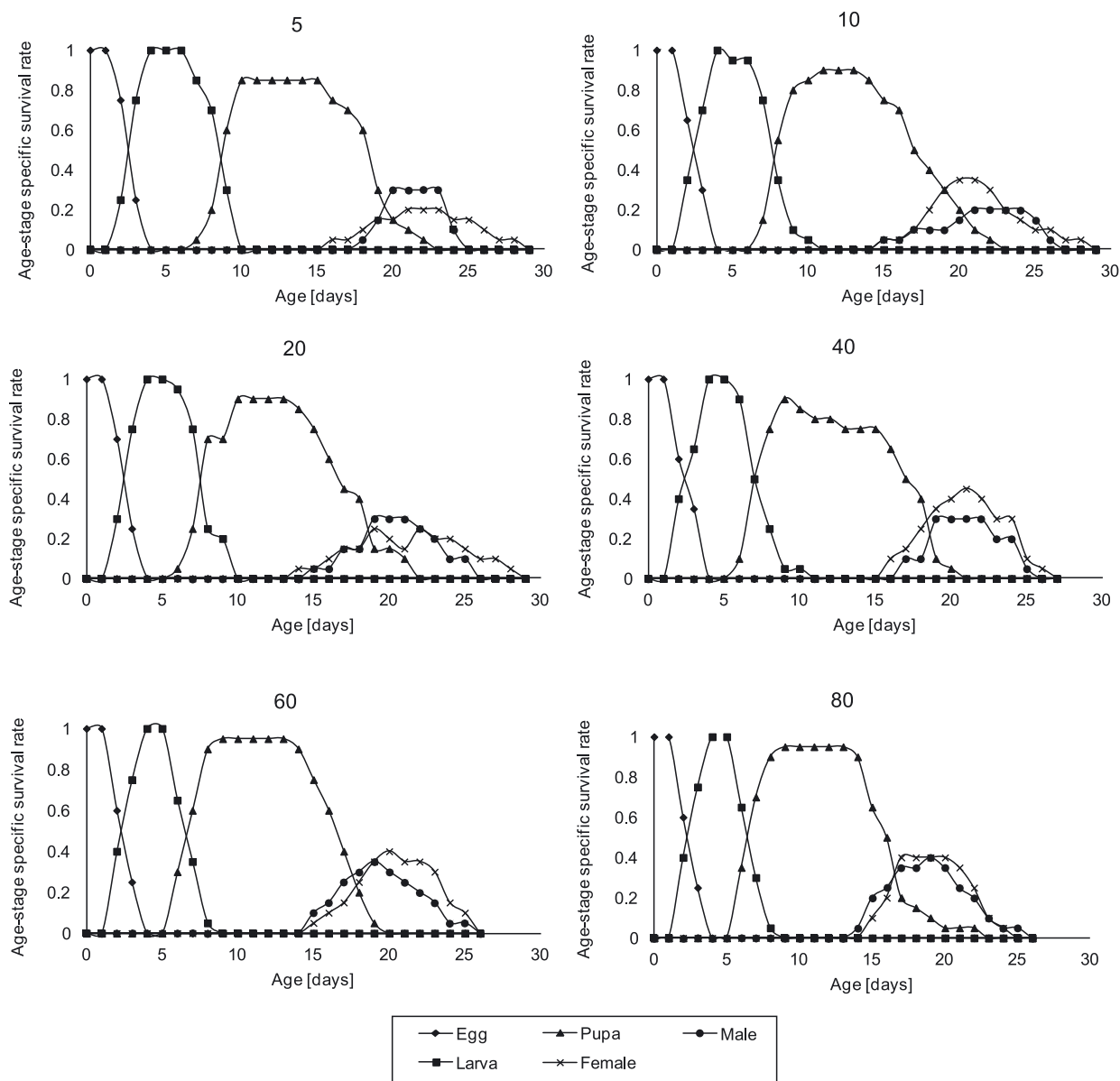
Fig. 4. Age-stage specific survival rate of *A. aphidimyza* fed on different densities of *A. craccivora* at 25±1°C, 70±5% relative humidity, photoperiod 16:8 h (L:D) (the numbers above the figures means prey density)
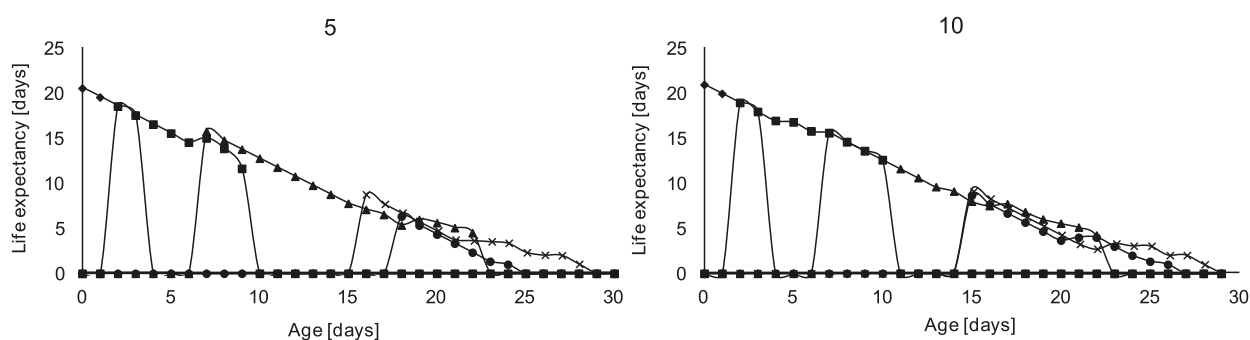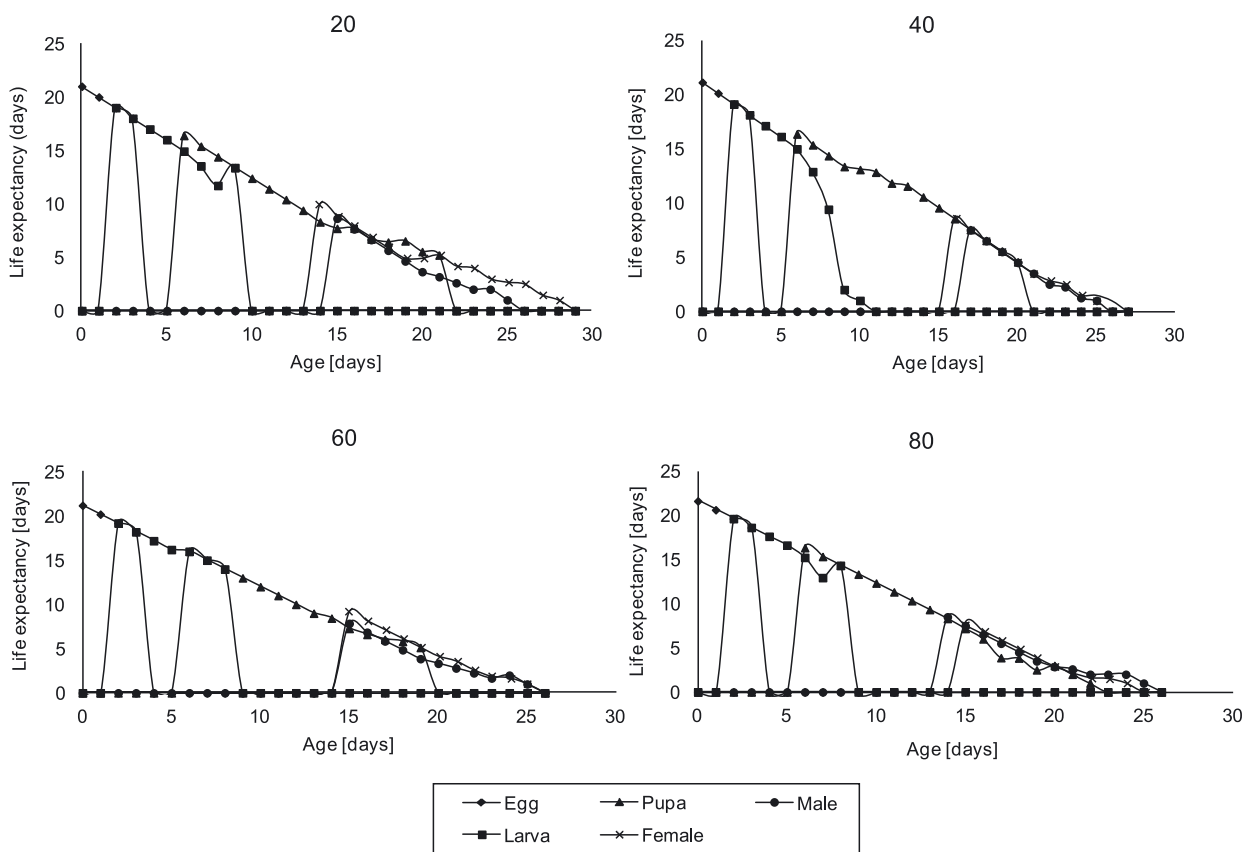

Fig. 5. Age-stage-specific life expectancy of *A. aphidimyza* fed on different density of *A. craccivora* at 25±1°C, 70±5% relative humidity, photoperiod 16:8 h (L:D)

Fig. 5. Age-stage-specific life expectancy of *A. aphidimyza* fed on different density of *A. craccivora* at 25±1°C, 70±5% relative humidity, photoperiod 16:8 h (L:D)
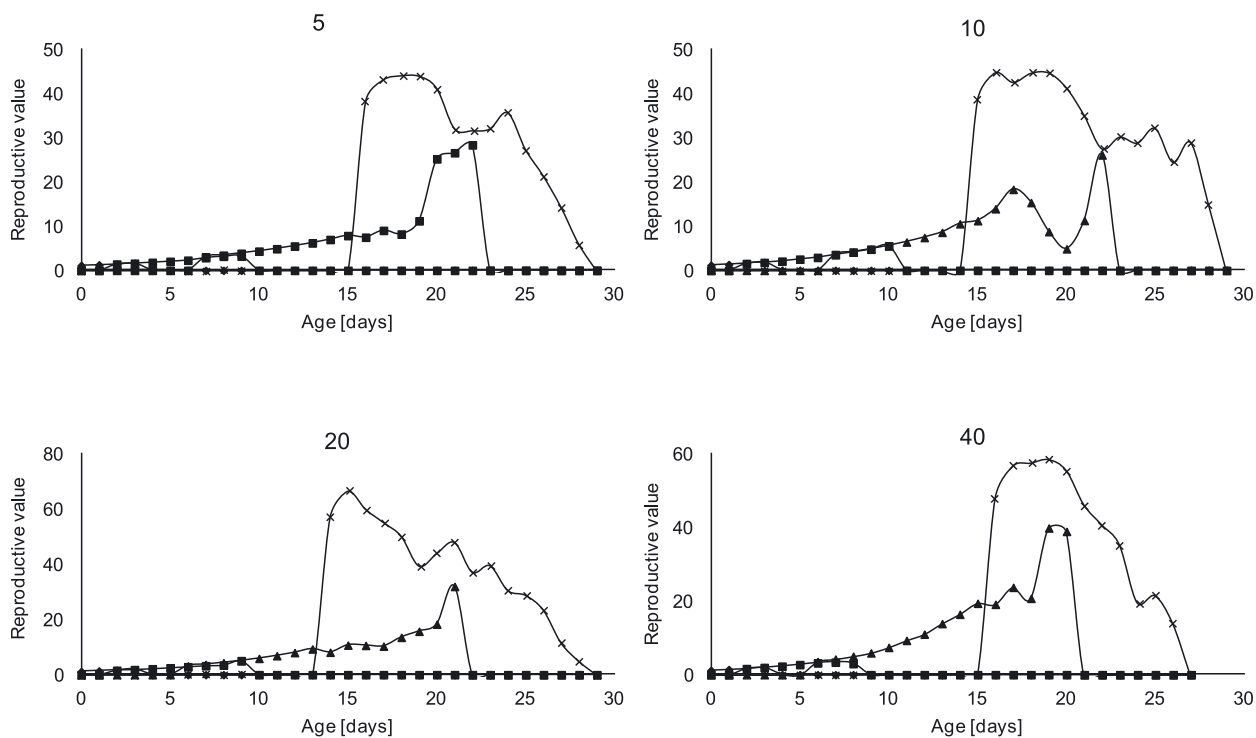

Fig. 6. Age-stage-specific reproductive value of *A. aphidimyza* fed on different density of *A. craccivora* at 25±1°C, 70±5% relative humidity, photoperiod 16:8 h (L:D)

Fig. 6. Age-stage-specific reproductive value of *A. aphidimyza* fed on different density of *A. craccivora* at 25±1°C, 70±5% relative humidity, photoperiod 16:8 h (L:D)
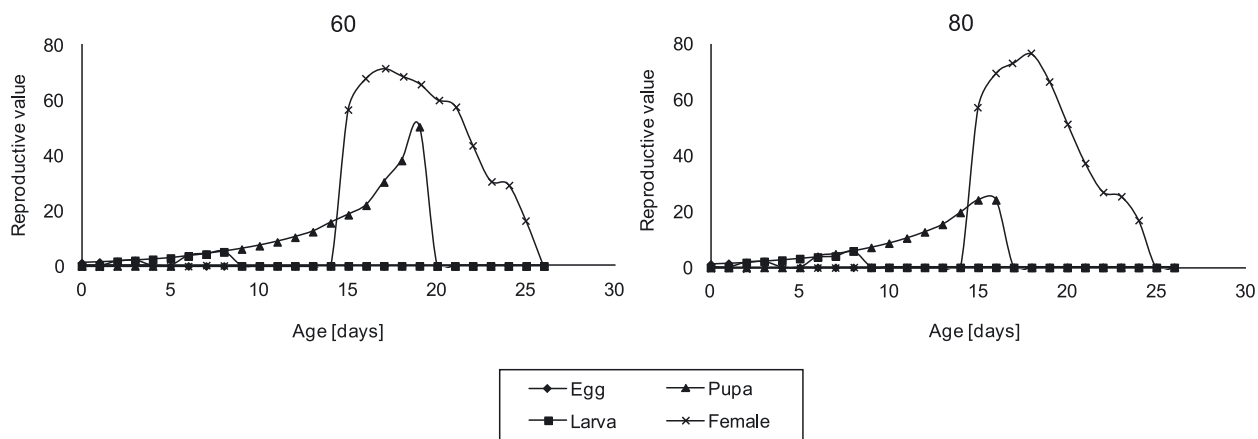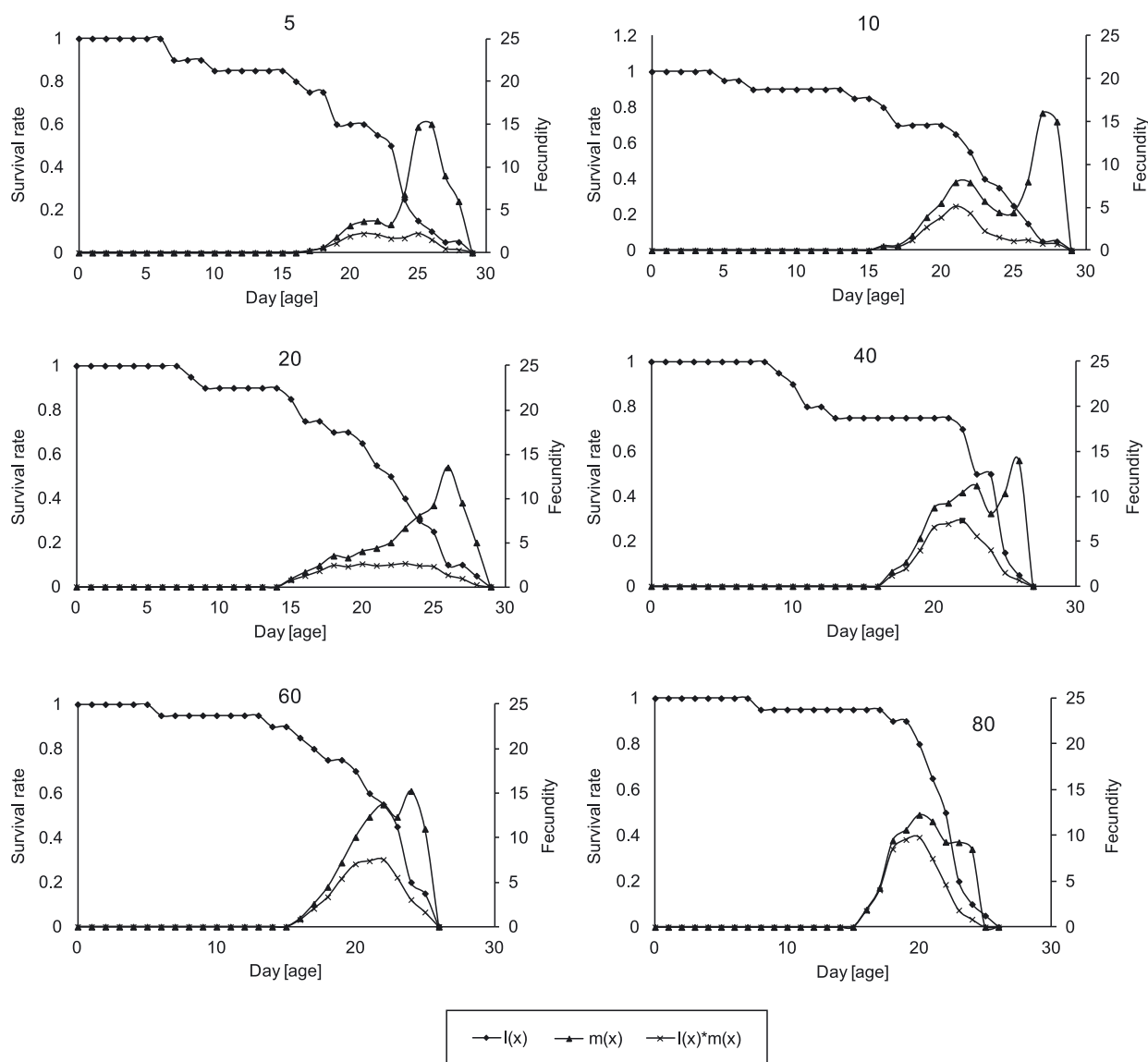

Fig. 7. Age-specific survival rate (l_x), female age-specific fecundity (f_x), age-specific fecundity (m_x) and age-specific maternity ($l_x m_x$) of *A. aphidimyza* fed on different density of *A. craccivora* at 25±1°C, 70±5% relative humidity, photoperiod 16:8 h (L:D).

DISCUSSION

Gabre *et al.* (2005) pointed out that total pre-oviposition period is a more appropriate statistic from the point of view of demography, because it represents the effect of the first reproduction on the population parameters. TPOP (the total pre-ovipositional period) of the female predator was reduced as prey density increased. Yaşar and Özger (2005) also observed that an increased prey density resulted in shorter total pre-ovipositional periods in *Adalia fasciatopunctata revelierei* (Mulsant). Atlihan and Guldal (2009) also obtained similar results in the study of *Scymnus subvillosus* (Goeze) fed on *Hyalopterus pruni* (Geoffroy). The oviposition period increased as prey density increased. Feeding on different prey densities during the larval stage had a positive effect on fecundity of female *A. aphidimyza*. Studies on the effect of prey density on fecundity of predators are in agreement with our results (Yaşar and Özger 2005; Atlihan and Guldal 2009; Agarwala *et al.* 2008).

Although only the larvae of aphidophagous midge are predaceous (Hoffmann and Frodsham 1993), we offered the same prey density for females as in their larval stage, because females strongly prefer to oviposit on plants with high prey density (Messelink *et al.* 2011). In addition, in previous studies it has been discussed that the variation in fecundity of *A. aphidimyza* might be related to variation in aphid density, host plant, genetic makeup, larval nutrition, and honeydew intake by females (El-Titi 1973; Mansour 1975; Kuo 1982; Havelka and Ruzicka 1984; Sell and Kuo 1987). The lowest fecundity was observed at 5 prey/ day, but a rapid increase was found at higher density levels with no significant difference between 20 and 40 prey per day and 60 and 80 prey per day during the larval stage. The fecundity for all different densities ranged between 52.5 (5 prey per day) and 121.375 eggs (80 prey per day) and it was close to those reported by Havelka and Zemek (1999) which ranged between 48 and 148 eggs for different populations. According to these results, it can be concluded, that an increase in prey density will result in longer longevity which in turn will lead to higher reproduction rates. Our results are similar to those of El-Titi (1973); Stewart and Walde (1997) and Lucas and Brodeur (1999), where fecundity of *A. aphidimyza* females increased as a function of aphid density and it was also dependent on larval nutrition.

The intrinsic rate of increase (r), the finite rate of increase (λ), and the net reproduction rate (R_0) also increased as prey density increased – up to density of 80 individuals per day. Atlihan and Guldal (2009) obtained similar trends in demographic parameters of *S. subvillosus* fed on different densities of *H. pruni*. Havelka and Zemek (1999) found that the values of *r* were significantly different among different populations; it ranged between 0.095 and 0.212 h^{-1}. In our study, it was very close to their results as it ranged from 0.122 to 0.193 h^{-1} for different prey densities. The range of the net reproductive rate (R_0) (15.75–48.55 offspring) was somehow the same as that reported by Havelka and Zemek (1999) (8.57–65.04) for this predator. Values of mean generation time (T) ranged from 20.28 to 23.13 days. This value also ranged from 18.48 to

23.38 days in the study of Havelka and Zemek (1999) on different populations of *A. aphidimyza*.

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

$$R_0 = F * \frac{N_f}{N}$$

where:
N – the total number of individuals used at the beginning of the life table study,
N_f – the number of female adults emerging from these N eggs.

Our results for *A. aphidimyza* at different prey densities, were consistent with the relationships given by this equation. Researchers have also found some other kinds of relationships among life table parameters. Yu *et al.* (2005) proved a relationship among gross reproduction rate, net reproduction rate, and pre-adult survivorship of *Lemnia biplagiata* Schwartz (Col., Coccinellidae) feeding on *A. gossypii*.

According to the results obtained here, the gall midge, *A. aphidimyza,* can be considered as an effective biological control agent of *A. craccivora*, as it develops successfully to adult stage at all prey densities and reproduces even at lower prey densities. However, it is obvious that higher prey densities are more suitable than lower ones for rearing this predator. Based on the results of this study, it can be concluded that *A. aphidimyza* is a useful natural enemy in the population dynamics of its prey, especially *A. craccivora*. This study might result in the development of management tactics for the control of aphid pests, as these kinds of controlled laboratory studies provide better insights into the management development and population dynamics of insects.

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