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Influence of *Aphis gossypii* Glover (Hemiptera: Aphididae) density on life table parameters of *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) under laboratory conditions

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Abstract: Life table gives the most comprehensive explanation of the survivorship, development, and reproduction of a population. The life table parameters of an aphidophagous midge, *Aphidoletes aphidimyza* were studied on different densities (5, 10, 20, 40, 60, 80) of third instar nymphs of *Aphis gossypii* as prey in a growth chamber (25 ± 1 °C, 70 ± 5% RH and a photoperiod of 16L: 8D h). The pre-ovipositional period of female *A. aphidimyza* was reduced as prey density increased with no significant difference. The oviposition periods were 3.833 ± 0.401 and 5.5 ± 0.463 days in lowest and highest prey density, respectively. Fecundity increased significantly with increasing prey density. The lowest fecundity was obtained at density of 5 preys/day (49.667 ± 6.053 eggs) and the highest was at density of 80 preys/day (104.25 ± 7.78 eggs). Intrinsic rate of increase (r_m) ranged from 0.110 ± 0.016 to 0.166 ± 0.014 d^{-1} with increasing prey density. Net reproductive rate (R_0) was positively dependent on prey density. The peak reproductive values showed that female aphidophagous midge at ages of 17, 18, 19, 22 and 25 days made the highest contribution to the population when reared on 5 to 80 preys in a day, respectively. However, mean generation time (T) ranged from 22.42 ± 0.55 to 24.47 ± 1.04 days. It was concluded that the increase in the density of third instar nymphs of *A. gossypii* significantly affected the demographic parameters of *A. aphidimyza* and it had a better reproductive performance in higher prey densities.

Keywords: *Aphis gossypii*, intrinsic rate, prey density, reproductive values, *Aphidoletes aphidimyza*

Introduction

The cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae), is a cosmopolitan, polyphagous species widely distributed in tropical, subtropical and temperate regions (Kersting *et al.,* 1999; Isikber, 2005). It is a major pest of cotton, cucurbits and citrus, and principally attacks vegetables in fields and greenhouses (Leclant and Deguine, 1994; Parrella *et al.*, 1999; Baniameri and Nasrollahi, 2003). It can also infest other economically important crops such as melon, zucchini, coffee, vegetables (eggplant, okra, sweet pepper, etc.) as well as ornamental plants (*Lantana*, *Hibiscus*, and *Chrysanthemum*) (Razmjou *et al.,* 2006). The cotton aphid not only reduces fruit quantity and quality through direct feeding and honeydew production but also transmits more than 50 plant viruses (Roistacher *et al.,* 1984; Blackman and Eastop, 2000). The population of *A. gossypii* has

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strongly increased in main cotton growing areas of Iran, especially in northern regions (Mojeni and Rezvani, 1997; Razmjou *et al.,* 2002). Outbreaks of this insect have been attributed to the development of resistance to insecticides which are known to have injurious effects on populations of insect's natural enemies as well as changes in nutritional and bioclimatic factors in host plants (Isikber, 2005). Biological control of aphids is being increasingly applied on the greenhouse crops (van Lenteren and Woets, 1988; Parrella *et al.,* 1999). However, studies are needed for evaluating more aphidophagous insects because the availability of additional natural enemies of aphids would lead to an increase in successful biological control of aphids under various situations.

The predacious gall midge, *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae), is a specialist effective predator of many aphid species worldwide in greenhouses, on field crops, and fruit trees (Morse, 1981; Markkula and Tittanen, 1985; Malais and Ravensberg, 1992) and has a wide geographical distribution (Xie *et al.,* 2000). Since 1973, this gall midge has been commercially used in many countries as one of the most effective biological control agents against aphids, particularly on greenhouse crops, and has proven effective (e.g., Asyakin, 1973; Markkula *et al.,* 1979; Adams and Prokopy, 1980; Havelka, 1980, 1982; Meadow *et al.,* 1985; Morse and Croft, 1987; Nijveldt, 1988; Kulp *et al.,* 1989; Solarska, 2004). It shows great promise as a biological control agent because of its high degree of density-dependency (El-Titi, 1973; Stewart and Walde, 1997), its inclination to kill more aphids than it consumes (Uygun, 1971), and its compatibility with many pesticides (Warner and Croft, 1982; Meadow *et al.*, 1985). Larvae of this species feed on a wide variety of aphids, at least 80 species have been recorded as its hosts (Yukawa *et al.,* 1998), e. g. *A. pomi* DeGeer (Adams and Prokopy, 1980; Jokinen, 1980; Morse and Croft 1987); *A. spiraecola* Patch (Brown, 2004), *Dysaphis plantaginea* Pass. (Wyss *et al.,* 1999); *Myzus persicae* Schultzer (Meadow *et al.,* 1985; Choi *et al.,* 2001), *Diuraphis noxia* Kurdjumov (Tóth *et al.,* 2009); *Brevicoryne brassicae* L. (Raworth *et al.,* 1984), as well as the cereal aphids, *Rhopalosiphum padi* Linnaeus, *Sitobion avenae* Fabricius and *Metopolophium dirhodum* Walker (Dixon, 1997; Schmidt *et al.,* 2004).

Among the life table parameters, intrinsic rate of increase (r_m) is a key demographic parameter useful to predict the population growth potential of an animal under a given environmental condition (Ricklefs and Miller, 1999; Southwood and Henderson, 2000) and may help predict the outcomes of pest–natural enemy interactions (Roy *et al.,* 2003). Besides being a measure of population growth, r_m has been widely used to estimate the insect response to resistant plants (Ruggle and Gutierrez, 1995), and in comparison of different food types that predators consume (Engel, 1990). Furthermore, construction of life fertility tables may help improve pest management (Toapanta *et al.,* 2005). Chi and Liu (1985) and Chi (1988) developed an age-stage two-sex life table theory. Age-stage two-sex life table theory has been applied to insect pests (Gabre *et al.,* 2005; Silva *et al.,* 2006; Yin *et al.,* 2009; Bailey *et al.,* 2010; Huang and Chi, 2011); and predator life table and predation rate studies (Chi and Yang, 2003; Yu *et al.,* 2005; Mo and Liu, 2006).

The main objective of this study was to assemble, describe, and analyze life table parameters for *A. aphidimyza* population exposed to different densities of third instar nymphs of *A. gossypii*. We analyzed the data to find out the effect of prey density on life table parameters such as age-stage specific survival and fecundity, reproductive value, expected remaining life time, net reproductive value (R_0), intrinsic rate of increase (r_m), mean generation time (T), and finite rate of increase (λ). These parameters can be used to estimate the rate of increase of a natural or released population (El Hag and Zaitoon, 1996).

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Materials and Methods

Rearing prey and predator

Third instar nymphs of *A. gossypii* were collected from cucumber fields in Rasht and Pir-bazaar region, Guilan Province (Northern Iran) and reared on cucumber (cultivar: Super dominus) in a greenhouse at University of Guilan. Larvae of *A. aphidimyza* were collected from the colony of *A. gossypii* in an infested cucumber field. The predators were reared for one generation on different nymphal instars of *A. gossypii* 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 h. (L: D).

Life table study

Tests were undertaken after rearing the population under constant laboratory conditions as mentioned above for one generation. To obtain eggs of the predator, a stock culture of *A. aphidimyza* were kept in laboratory and visited frequently in a day. Newly hatched 1st instar larvae of *A. aphidimyza* were transferred and placed individually in experimental transparent plastic containers (15 × 13 × 3 cm) and offered densities of 5, 10, 20, 40, 60 and 80 third instar nymphs of *A. gossypii* every day to study their life table parameters. The duration of the successive developmental 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 consumed (from 1st instar larva to pupa). Prior to pupation, mature larvae were individually transferred to larger transparent plastic containers (19 × 16 × 6 cm) to change into pupa in a 2-3 cm layer of moist fine sand which had been sterilized in an autoclave (20 minutes at 120 °C). The pupae were left in the 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 pupal stage. Adults were fed on few strips of paper (1 × 7 cm) soaked in sucrose solution placed on the corners of containers. Then, they were provided with the same densities of prey similar to their immature stages. The *A. aphidimyza* adult females and male mortality and number of eggs laid were recorded daily until all adults died. The number of replicates was 20 for each prey density.

Statistical analysis

Data were analyzed using 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). 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). The Jackknife method (Meyer *et al.,* 1986; Sokal and Rohlf 1995) was used to calculate the means and standard errors of the life table parameters. We used Duncan procedure to compare the differences among treatments following the description of Sokal and Rohlf (1995).

Results

The adult pre-ovipositional periods (APOP), that is the duration from adult emergence to first oviposition, was higher in females fed on 5 preys per day during their larval stage than those fed on higher prey densities but without any significant differences. The total pre-ovipositional periods (TPOP) in different prey densities, that are the duration from egg to first oviposition, did not differ significantly (F = 1.85; df = 5, 40; *P* = 0.129). There were also no significant differences in oviposition periods of the female predator on different prey densities per day (F = 1.91; df = 5, 40; P = 0.117). The density provided to immature stages and adults had also no significant effect on female longevity (F = 1.17; df = 5, 40; P = 0.343). However, the fecundity was affected positively by prey density (Fig. 1). Total fecundity of females fed on 5 preys per day during their larval stage, was significantly lower than those fed on other prey densities per day. Similarly, the highest fecundity was observed in females fed on 80 prey per day during their larval stage (F = 9.61; df = 5, 40; $P < 0.0001$) (Table 1).

Results showed that increasing prey density affected the intrinsic rate of increase (r_m), the finite rate of increase (λ) and the net reproduction rate (R_0). The intrinsic rate of increase (r_m) increased significantly with increasing prey density (F = 5.34; df = 5, 119; P = 0.045). There was no significant difference in finite rates of increase (λ) with increasing prey density (F = 1.68; df = 5, 119; P = 0.144). The net reproductive rate (R_0) of females increased positively by increasing prey density (Fig. 2). The net reproductive rate of females fed on 5 preys per day during their larval stage, was significantly lower than those fed on other prey densities per day. Likewise, females fed on 60 and 80 preys per day during their larval stage had significantly higher net reproductive rate than those fed on other prey densities per day (F = 9.51; df = 5, 119; $P < 0.0001$). Increasing prey density had no significant effect on mean generation time (T) (F = 1.64; df = 5, 119; P = 0.155) (Table 2).

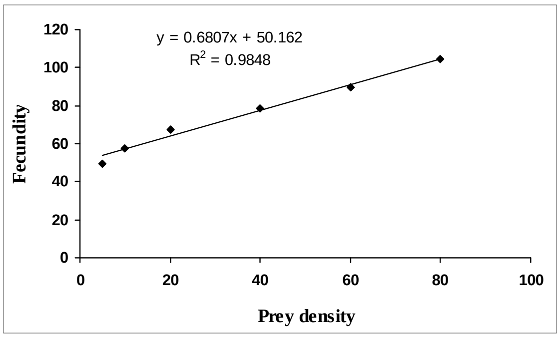

Figure 1 Effect of different densities of *Aphis gossypii* on *Aphidoletes aphidimyza* fecundity at 25 ± 1 °C, 70% ± 5% relative humidity, photoperiod 16: 8h (L: D).

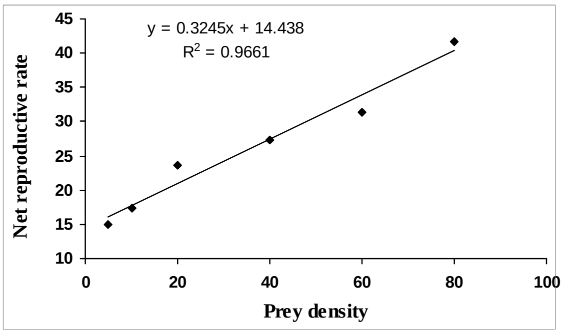

Figure 2 The relationship between net reproductive rate of *Aphidoletes aphidimyza* and different densities of *Aphis gossypii* at 25 ± 1 °C, 70% ± 5% relative humidity, photoperiod 16: 8h (L: D).

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. 3). However, the peak reproductive value appeared at ages of 25 days on 5 preys/day, 22 days on 10 preys/day, 19 days on 20 preys/day, 18 days on 40 preys/day, 17 days on 60 preys/day and 18 days on 80 preys/day. It showed that female aphidophagous midge at ages of 17, 18, 19, 22 and 25 days made the highest contribution to the population when reared on 60, 40 and 80, 20, 10 and 5 prey densities per day, respectively. There was also a positive relationship between the peak reproductive values and prey density (R^2 = 0.995) (Fig. 4). The age-specific survival rate (l_x) and fecundity rate (m_x) are shown in Fig. 5. 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.

Table 1 Biological parameters, longevity and fecundity of *Aphidoletes aphidimyza* adults reared on different densities of *Aphis gossypii* (Mean ± SE).

Prey density	APOP*	TPOP*	Oviposition (day)	Female longevity (day)	Fecundity (eggs/female)
5	1.33 ± 0.211 a	21.83 ± 0.792 a	3.833 ± 0.401 a	5.167 ± 0.307 a	49.667 ± 6.053 a
10	1.17 ± 0.167 a	21.5 ± 0.764 a	4.667 ± 0.333 a	5.833 ± 0.401 a	57.833 ± 5.043 ab
20	1 ± 0 a	21.29 ± 0.421 a	5 ± 0.378 a	6 ± 0.378 a	67.428 ± 53.554 bc
40	1 ± 0 a	21.14 ± 0.705 a	5.143 ± 0.404 a	6.143 ± 0.404 a	78.276 ± 6.875 bc
60	1 ± 0 a	19.71 ± 1.017 a	5.143 ± 0.404 a	6.285 ± 0.474 a	89.857 ± 7.035 cd
80	1 ± 0 a	19.5 ± 0.534 a	5.5 ± 0.463 a	6.5 ± 0.463 a	104.25 ± 7.782 d

APOP, adult pre-ovipositional period; TPOP, total pre-ovipositional period (from egg to first oviposition). Within columns, values followed by the same letter do not differ significantly ($P < 0.05$) using Duncan procedure.

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

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	0.110 ± 0.016 a	1.117 ± 0.018 a	14.9 ± 5.49 a	24.47 ± 1.04 a	43.9 ± 20.39 a
10	0.116 ± 0.015 a	1.123 ± 0.017 a	17.35 ± 6.24 ab	24.53 ± 0.78 a	40.43 ± 13.52 a
20	0.129 ± 0.014 b	1.138 ± 0.016 a	23.6 ± 7.61 bc	24.37 ± 0.48 a	53.10 ± 15.57 b
40	0.138 ± 0.015 b	1.148 ± 0.017 a	27.4 ± 8.87 cd	24.04 ± 0.72 a	65.15 ± 18.59 c
60	0.154 ± 0.016 c	1.166 ± 0.018 a	31.45 ± 10.11 d	22.44 ± 1.06 a	91.6 ± 45.62 d
80	0.166 ± 0.014 c	1.181 ± 0.017 a	41.70 ± 12.09 d	22.42 ± 0.55 a	89.25 ± 45.91 d

Within columns, values followed by the same letter do not differ significantly ($P < 0.05$) using Duncan procedure.

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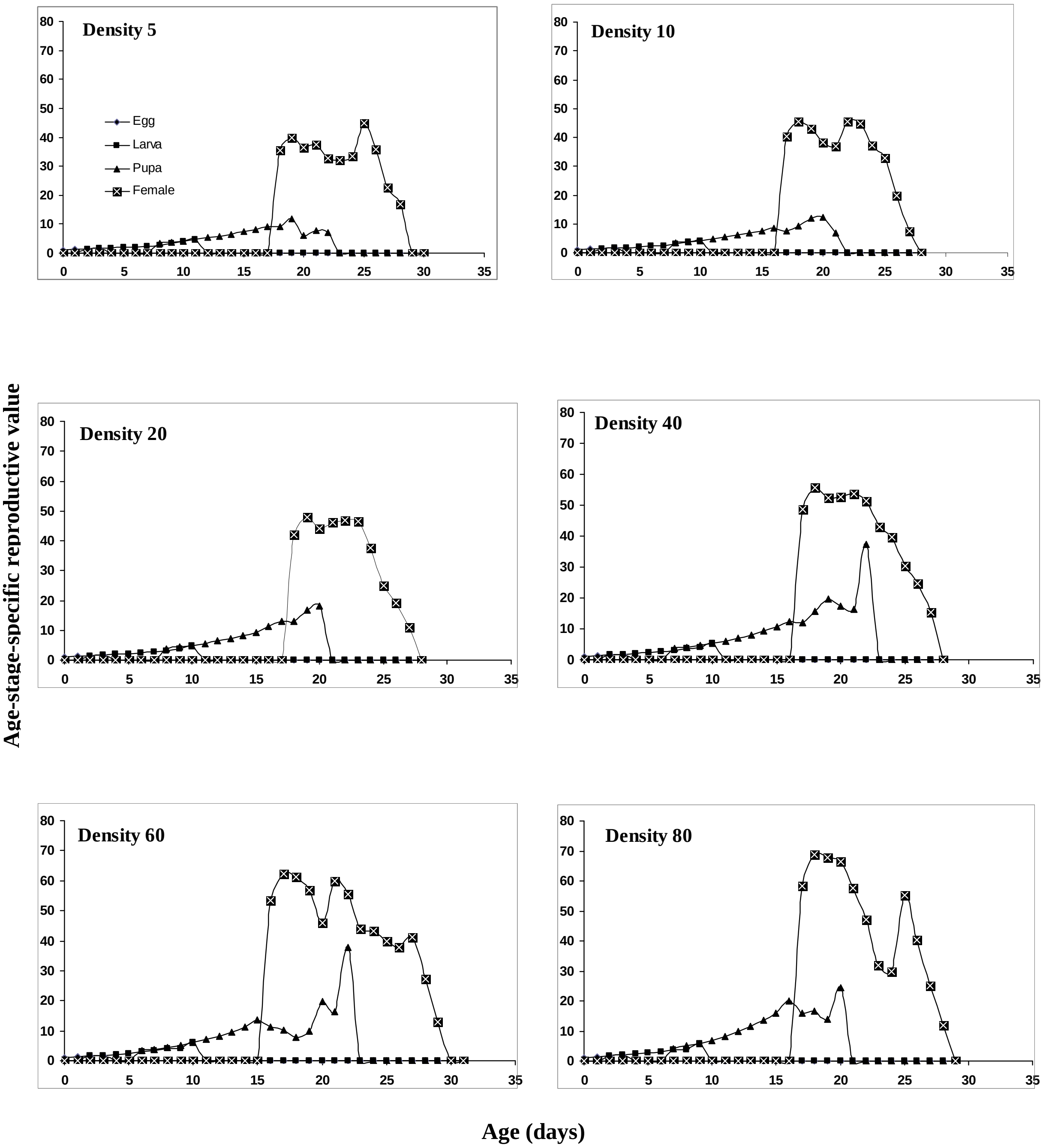

Figure 3. Age-stage-specific reproductive value of *Aphidoletes aphidimyza* fed on different densities of *Aphis gossypii* at 25 ± 1 °C, 70% ± 5% relative humidity, photoperiod 16: 8h (L: D).

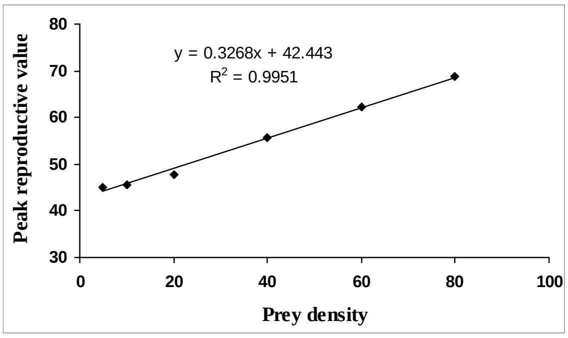

Figure 4 The effect of different densities of *Aphis gossypii* on peak reproductive value of *Aphidoletes aphidimyza* at 25 ± 1 °C, 70% ± 5% relative humidity, photoperiod 16: 8h (L: D).

Discussion

In this study, the pre-ovipositional periods (APOP) reduced insignificantly with an increase in prey density. There were also no significant differences in the total pre-ovipositional period (TPOP) of the female predator with increasing prey density. However, Yaşar and Özger (2005) found that increasing prey density resulted in shorter adult pre-ovipositional and 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*. The prey density had no significant effect on *A. aphidimyza* oviposition period. Feeding on different prey densities during larval stage had no effects on adults' longevity, but influenced the females fecundity positively. Similar studies showed the effect of prey density on fecundity of predators which are in agreement with the results obtained here (Atlihan and Guldal, 2009, Yaşar and Özger, 2005, Agarwala *et al.,* 2008). The same prey density was offered to *A. aphidimyza* 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; Havelka and Ruzicka, 1984). The lowest fecundity was obtained at lower prey densities per day, and a rapid increase was found at higher prey density levels. The fecundity ranged between 49.667 to 104.25 eggs at different prey densities and it was nearly close to those reported by Havelka and Zemek (1999) that 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 higher reproduction rate. 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 dependent on larval nutrition too. The peak reproductive value of female predator midge was positively density dependent and appeared at ages of 17, 18, 19, 22 and 25 days. It made the highest contribution to the population when reared on 5 preys per day to 80 preys in a day.

The intrinsic rate of increase (r_m), the finite rate of increase (λ) and the net reproduction rate (R_0) were also increased with increasing prey density per day. Atlihan and Guldal (2009) obtained similar trends in demographic parameters of *S. subvillosus* fed on different densities of *H. pruni*. As it was reported by Havelka and Zemek (1999), the values of r_m differed statistically among different populations and ranged between 0.095 and 0.212 d^{-1}, while it ranged from 0.110 to 0.166 at different prey densities in this study. The range of net reproductive rate (R_0) in this study (14.9-41.70 female offspring/female/generation) was somewhat the same as those reported by Havelka and Zemek (1999) (8.57-65.04 offspring). The mean generation time (T) ranged from 22.42 to 24.47 days which was very close to those (18.48 to 23.38 days) found by Havelka and Zemek (1999) on different geographic populations of *A. aphidimyza*.

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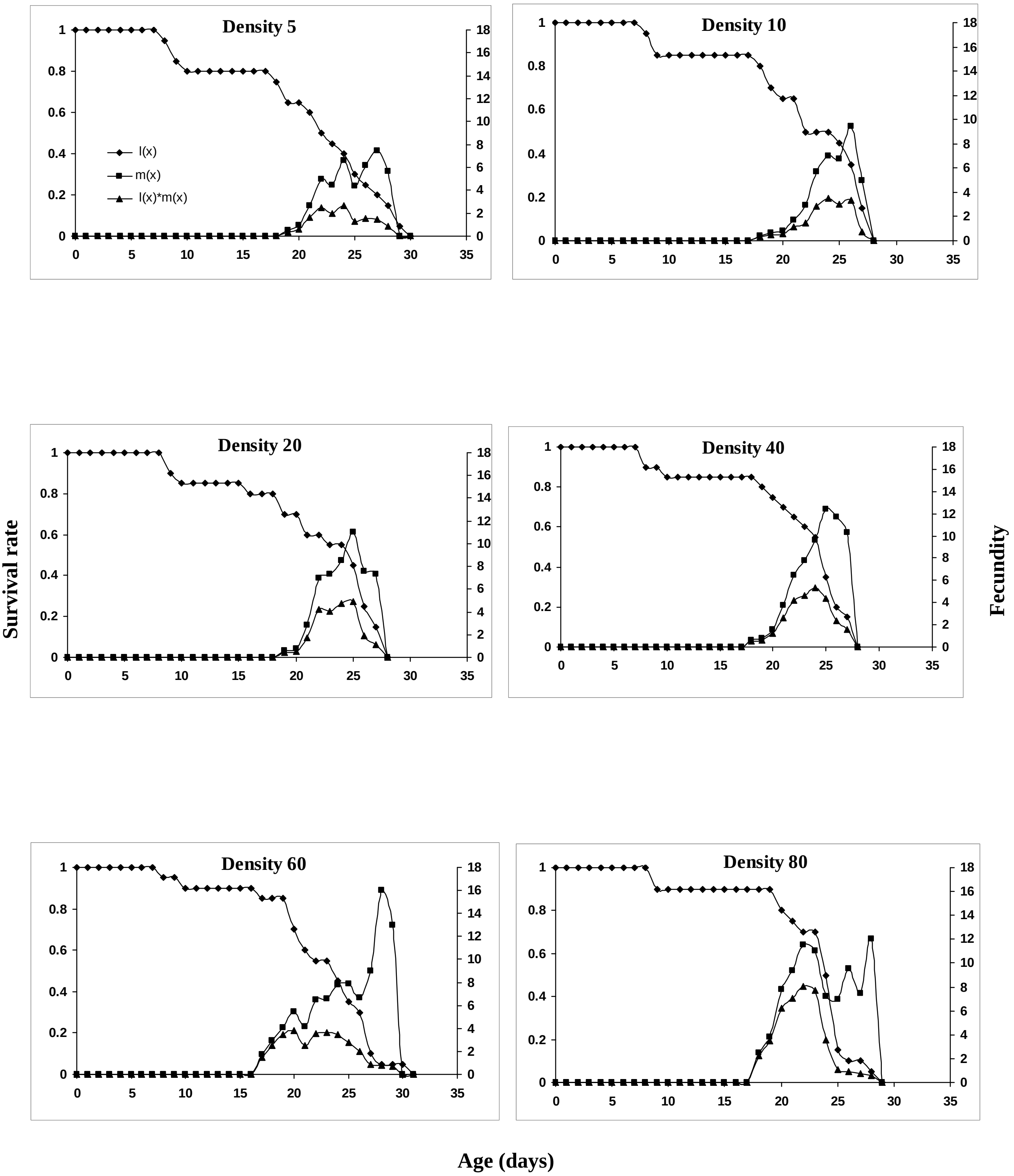

Figure 5 Age-specific survival rate (l_x), age-specific fecundity (m_x) and age-specific maternity (l_xm_x) of *Aphidoletes aphidimyza* fed on different densities of *Aphis gossypii* at 25 ± 1 °C, 70% ± 5% relative humidity, photoperiod 16: 8h (L: D).

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Chi (1988) found 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 is the total number of individuals used at the beginning of the life table study and N_f is the number of female adults emerging from these N eggs. It also means $N_f * F = R_0 * N$. In other words, the total number of offspring produced by all females of *A. aphidimyza* equals the net reproductive rate by the cohort size. In our results, the average of $N_f * F$ was 521.321 and $R_0 * N = 521.333$ at different prey densities. This minor difference was due to rounding-off. This relationship showed that the precision is obtainable in the age-stage, two-sex life table analysis (Farhadi *et al.,* 2011). It has also been found some other kind of relationships among life table parameters as Yu *et al.,* (2005) proved a relationship among gross reproduction rate, net reproduction rate, and pre-adult survivorship of *Lemnia biplagiata* (Coleoptera: Coccinellidae) feeding on *A. gossypii*.

Based on the results obtained here, the aphidophagous midge, *A. aphidimyza* can be considered as an effective biological control agent of *A. gossypii*, as it develops successfully to adult stage at all prey densities. However, it is clear that higher prey densities are more favorable than lower ones to rear this predator. It can also be concluded that *A. aphidimyza* is a beneficial natural enemy in the population dynamics of its prey, *A. gossypii*. This study might result in the development of management tactics for the control of aphid pests.

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تأثیر تراکم *Aphis gossypii* Glover (Hemiptera: Aphididae) بر پارامترهای جدول زندگی *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) در شرایط آزمایشگاه

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چکیده: جدول زندگی جامع‌ترین توضیح بقا، رشد و نمو و تولید مثل یک جمعیت را ارایه می‌دهد. در این بررسی پارامترهای جدول زندگی پشه شته‌خوار *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) روی تراکم‌های مختلف (۵، ۱۰، ۲۰، ۴۰، ۶۰ و ۸۰) پوره‌های سن‌سوم شته *Aphis gossypii* Glover به‌عنوان طعمه در یک اتاقک رشد (۱ ± ۲۵ درجه سلسیوس، رطوبت نسبی ۵ ± ۷۰ درصد و دوره نوری ۱۶ ساعت روشنایی و ۸ ساعت تاریکی) مطالعه شد. داده‌های مربوط به رشد و نمو، بقا، باروری و نرخ شکارگری با استفاده از جدول زندگی سن- مرحله دو جنسی تجزیه و تحلیل شدند. دوره پیش از تخم‌ریزی ماده *A. aphidimyza* بدون تفاوت معنی‌دار با افزایش تراکم طعمه کاهش پیدا کرد. دوره تخم‌ریزی به‌ترتیب ۰/۴۰۱ ± ۳/۸۳۳ و۰/۴۶۳ ± ۵/۵ روز در پایین‌ترین و بالاترین تراکم طعمه بود. باروری به‌طور معنی‌داری با افزایش تراکم طعمه افزایش پیدا کرد. پایین‌ترین باروری در تراکم ۵ طعمه (۶/۰۵۳ ± ۴۹/۶۶۷ تخم) و بالاترین آن در تراکم ۸۰ طعمه (۷/۷۸ ± ۱۰۴/۲۵ تخم) به‌دست آمد. نرخ ذاتی افزایش جمعیت (r_m) با افزایش تراکم طعمه از ۰/۰۱۶ ± ۰/۱۱۰ تا ۰/۰۱۴ ± ۰/۱۶۶ بر روز در نوسان بود. نرخ خالص تولید مثل (R_0) به‌طور مثبت وابسته به تراکم طعمه بود. اوج مقادیر تولید مثل نشان داد که ماده پشه شته‌خوار هنگامی‌که روی ۵ تا ۸۰ طعمه در روز پرورش یافت به‌ترتیب در سنین ۱۷، ۱۸، ۱۹، ۲۲، و ۲۵ روزگی بالاترین نقش را در جمعیت ایفا کرد. به هرحال، متوسط مدت زمان نسل (T) از ۵۵/. ±۲۲/۴۲ تا ۱/۰۴ ± ۲۴/۴۷روز در نوسان بود. نتیجه‌گیری شد که افزایش تراکم پوره‌های سن سوم *A. gossypii* اثرات معنی‌داری بر پارامترهای دموگرافی *A. aphidimyza* داشتند و این شکارگر عملکرد تولید مثلی بهتری در تراکم‌های بالاتر طعمه نشان داد.

واژگان کلیدی: *Aphis gossypii* نرخ ذاتی افزایش جمعیت، تراکم طعمه، مقادیر تولیدمثل، *Aphidoletes aphidimyza*

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