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Research Article

Temperature-dependent life table parameters of *Galleria mellonella* (L.) (Lepidoptera: Pyralidae)

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Abstract: The effect of temperature on demographic parameters of the greater wax moth, *Galleria mellonella* (L.) was studied at 23, 25, 27, and 30 °C, 50 ± 10% RH and a photoperiod of 16:8 (L: D) h. The life table parameters were estimated according to the age-stage, two-sex life table procedure. In addition, the bootstrap technique was employed for estimating the means, variances, and standard errors of the population parameters at all studied temperatures. All estimated parameters were affected considerably by temperature. Among examined temperatures, the highest values of net reproductive rate (R_0), intrinsic rate of increase (r_m) and finite rate of increase (λ) were 223.04 egg, 0.096 day^{-1}, and 1.101day^{-1}, respectively at 27 °C. The lowest mean generation time was 50.31 day at 30 °C. Moreover, the highest reproductive value was observed at 27 °C. According to the results, temperature can affect all life table parameters of *G. mellonella*, and according to our investigation, 27 °C is the best temperature for its mass rearing in laboratory condition among the evaluated temperatures.

Keywords: *Galleria mellonella*, Life history, temperature

Introduction

The greater wax moth (GWM), *Galleria mellonella* (L.) (Lepidoptera: Pyralidae) is an important pest of the honeybee *Apis mellifera* L. It is found in most of the world, including Europe and adjacent Eurasia, its presumed native range, and as an introduced species in other continents, including North America and Australia (Grabe, 1942).

The larvae can be used as food for the rearing of captive animals in terrarium, such as geckos or predatory insects (Grabe, 1942; Harding *et al*., 2013). One of invertebrate models is GWM that is valuable tool in the study of fungal pathogenesis. Within its natural environment, it undoubtedly encounters various microbes to which it has evolved immune responses. Its amenability to infection as well as its ability to mount a defense response makes *G. mellonella* an interesting host in the study of microbial pathogenesis. The larval stage of GWM has been employed to study a wide range of microbial infections including mammalian fungi (Cotter *et al*., 2000; Bergin *et al*., 2003; Scully and Bidochka, 2005; Mylonakis, 2005) and bacterial pathogens (Purves *et al*., 2010; Chandwick *et al*., 1990; Jander *et al*., 2000; Ramarao *et al*., 2012). The larvae of GWM present several technical advantages in bacterial and fungal studies: they are relatively large,

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thus enabling the injection of defined doses of bacteria; they can be reared at various temperatures (20 °C to 30 °C) and infection studies can be conducted between 15 °C to above 37 °C (Jones *et al.,* 2010). Its ability to support interactions with human pathogens at 37 °C (the physiological temperature in mammals) is important because microbial pathogenesis depends on the temperature-sensitive expression of virulence factors. Similar temperature-regulated virulence factors are involved when pathogens infect *G. mellonella* and humans. Another advantage is that larval diets can be supplemented with defined microbial inoculums, allowing the quantitative analysis of immune responses and intestinal homeostasis (Mukherjee *et al*., 2012; Vilcinskas, 2011).

Temperature is a critical abiotic factor influencing insect population dynamics, developmental rates and seasonality occurrence of mite and insect pests and their natural enemies (Campbell *et al*., 1974; Huffaker *et al*., 1999). Different life history adaptations are favored under conditions of high and low population density relative to the carrying capacity of the environment (Cody, 1966). It is confirmed that the life history studies were a great impetus to the development of modern evolutionary ecology (Ricklefs and Miller, 2000; Kasap and Alten, 2006). Life table analysis is a standard ecological method for estimating demographic parameters related to population dynamics (Carey, 1993; Legaspi, 2004). Calculation of vital statistics such as intrinsic rate of increase, generation time, finite rate of increase, and doubling time help explain oscillations in population density and provide a better understanding of the population dynamics of a species (Southwood and Henderson, 2000; Carey, 2001).

Considering the effect of temperature on insect population dynamics, current study was conducted to examine the effect of different temperatures on life table parameters of GWM. The obtained results can be used not only to improve GWM rearing in laboratory conditions but also to better understanding of different environmental conditions on GWM population dynamics in apicultures.

Materials and Methods

Laboratory rearing

Applied laboratory colony of GWM was obtained originally from its established laboratory culture in Biological Control Research Department (BCRD), Iranian Research Institute of Plant Protection (IRIPP). Larvae were reared on modified artificial diet prepared as follows: wheat flour (1200 g), yeast powder (300 g), glycerine (492 ml), honey (600 g) and wax (120 g), which had been thoroughly mixed together (Marstone *et al*., 1975). Finally, the diet was poured into a plastic container and allowed to cool. The colony was maintained in a growth chamber set at temperature 27 ± 1 °C, 50 ± 10% relative humidity and a photoperiod of 16: 8 (L: D) h.

The GWM larvae were reared in plastic containers (with 17 × 24 × 9 cm in size) until pupation. Newly emerged adult moths (age < 24 h) were transferred to plastic jars (17cm in diameter and 25cm in height) for mating and oviposition. The open end of jars was covered with a fine mesh net for ventilation. Moreover, a paper sheet was put on the net cover to provide an appropriate oviposition substrate. Egg mass were collected daily and adult moths were paired in a new container.

Experimental Conditions

Study was conducted at four constant temperatures (23, 25, 27 and 30 ± 1 °C), 50 ± 10% RH and a photoperiod of 16: 8 (L: D) h in growth chambers. The fluctuations of environmental condition were monitored by a temperature and %RH data logger (Germany, Testo, 175-H2) during the study.

Life table study

Ten egg masses laid on the same day from different oviposition jars were collected for the life table study at different temperatures. Each egg mass was placed in a larval rearing container (mentioned size) with a piece of

artificial diet. Egg masses were checked daily and depending on the hatching rate, about 6-10 newly hatched first instar larvae form each egg mass were randomly picked and then transferred to a new container and reared individually. The numbers of individuals as cohort (age < 24h) were 92, 79, 82, and 85 at temperatures, 23, 25, 27, and 30 °C, respectively, in the starting of the experiment. Artificial diet was supplied as needed until pupation occurred. Male and female moths were separated by isolating pupae just before adult emergence. Then newly emerged moths were transferred to mating and oviposition jars. Survival and fecundity were recorded daily for each studied individual until death. Egg masses laid at different times were kept separately until hatching to estimate the hatch rate of eggs. In current study, hatched eggs were used to determine age-specific female fecundity.

Life table data analysis

The raw data were analyzed according to the age-stage, two-sex life table theory (Chi and Liu, 1985) and the method (Chi, 1988) by using the TWOSEX-MSChart program (Chi, 2013). The age-stage survival rate (s_{xj}; where x= age and j= stage), which is the probability that a newly laid egg will survive to age x and stage j, and the age-stage fecundity (f_{xj}), which is the number of hatched eggs produced by female adult at age x were calculated. The age-specific survival rate (l_x), and the age- specific fecundity (m_x), as well as the population parameters, the intrinsic rate of increase (r), the finite rate of increase (λ, $\lambda = e^r$), the net reproductive rate (R_0), and the mean generation time (T), were estimated in sequence.

Age-specific survival rate (l_x) was calculated by:

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

where m is the number of stages.

Age-specific fecundity (m_x) was calculated as:

$$m_x = \frac{\sum_{j=1}^{m} s_{xj} f_{xj}}{\sum_{j=1}^{m} s_{xj}}$$

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

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

The net reproductive rate represents the mean number of offspring that an individual can produce during its lifetime and was calculated as:

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

The mean generation time is defined as the period that a population needs to increase to R_0-fold of its size when time approaches infinity and the population reaches a stable age-stage distribution, and is calculated as

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

Age-stage-specific life expectancy (e_{xy}) is the time that an individual of age x and stage y is expected to live. This parameter was calculated according to the method described by Chi and Su (2006) as:

$$e_{xy} = \sum_{i=x}^{n} \sum_{j=y}^{m} s'_{tj}$$

Where s'_{ij} is the probability that an individual of age x and stage y will survive to age i and stage j. Fisher (1930) defined the reproductive value as the contribution of individuals of age x and stage y to the future population. According to Tuan *et al.* (2014) reproductive value in the age-stage, two-sex life table is calculated as:

$$v_{xy} = \frac{e^{-r(x+1)}}{s_{xy}} \sum_{i=x}^{n} e^{-r(i+1)} \sum_{j=u}^{m} s'_{ij} f_{if}$$

All the life table parameters were estimated by using TWOSEX-MSChart software (Chi, 2013).

The bootstrap (Efron and Tibshirani, 1993; Yu *et al*., 2013) technique was used to estimate the mean, variances, and standard errors of the population parameters. Because bootstrapping uses random sampling, a small number of replications will generate variable means and standard errors. To generate less variable results, we used 10,000 replications in this study. The paired bootstrap test based on confidence interval (Efron and Tibshirani, 1993; Akca *et al.*, 2015; Reddy and Chi, 2015) was used to compare the difference in developmental time, adult longevity, adult preoviposition period (APOP), total preoviposition period (TPOP), oviposition period, and fecundity among treatments. The population parameters (r, λ, R_0, and T) among treatments were also compared by using the paired bootstrap test (Reddy and Chi, 2015).

Results

Development Time and Fecundity

Developmental times of all GWM life stages decreased with increasing temperature from 23 ˚C to 30 ˚C. Accordingly, the longest developmental time of egg, larva, pupa, and preadult stages were 13.96, 57.31, 13.54, and 84.84 days at 23 °C. On the other hand, the shortest developmental times were 7.31, 29.92, 9.81, and 47.05 days for the mentioned developmental stages, respectively, at 30 °C (Table 1).

TPOP was affected significantly by temperature. At 23 ºC, GWM began oviposition at age 87.01 day (TPOP). However, at 30 °C, Oviposition started at age 47.75 day, which was the shortest in comparison with the other examined temperatures (Table 1).

Oviposition period of GWM was not significantly different, at temperatures 23, 25, and 30 °C. While, at 27 °C, with the value 5.84 day was the longest among all temperatures (Table 1).

Table 1 Developmental time and fecundity of *Galleria mellonella* at four constant temperatures.

Entries	Mean ± SE[1, 2]			
	23 °C	25 °C	27 °C	30 °C
Development time (day)				
Egg	13.96 ± 0.14a	11.55 ± 0.20b	8.29 ± 0.07c	7.31 ± 0.06d
Larva	57.31 ± 0.69a	43.72 ± 0.78b	33.90 ± 0.54c	29.92 ± 0.38d
Pupa	13.54 ± 0.40a	12.62 ± 0.21b	11.18 ± 0.29c	9.81 ± 0.17d
Preadult	84.84 ± 0.39a	67.90 ± 0.80b	53.37 ± 0.66c	47.05 ± 0.40d
APOP (day)[3]	2.27 ± 0.37a	1.58 ± 0.30a	0.62 ± 0.17b	0.58 ± 0.19b
TPOP (day)[4]	87.01 ± 0.56a	68.57 ± 1.08b	54.88 ± 0.86c	47.75 ± 0.51d
Longevity (day)	78.56 ± 2.15a	60.13 ± 3.75b	54.38 ± 2.60b	45.10 ± 1.90c
Oviposition period (day)	2.60 ± 0.41a	3.68 ± 0.39a	5.84 ± 0.40b	3.46 ± 0.27a
Fecundity (eggs/female)	242.48 ± 50.91c	487.89 ± 50.68b	675.74 ± 61.71a	351.43 ± 31.91c

[1] Means of followed by different letters within each row are significantly different according to the paired bootstrap test at 95% confidence interval.
[2] The SEs were estimated by 10,000 bootstraps.
[3] APOP: Adult preoviposition period.
[4] TPOP: Total preoviposition period.

The highest mean fecundity (F) was 675.74 eggs/female at 27 °C and the lowest *F* was 242.48 eggs/female at 23 °C. There was no significant difference between *F* values at temperatures 23 and 30 °C (Table 1).

Female adult longevity was 7.11, 7.95, 9.15, and 6.17 days at 23, 25, 27, and 30 °C, respectively. While, male adult longevity was 11.94, 19.35, 14.18, and 10.36 days at the mentioned temperatures, respectively.

Life Table and population Parameters

Age-stage survival rates (s_{xj}) of GWM at different evaluated temperatures are shown in Figure 1. Due to variation in developmental rates of individuals at each temperature, there were overlapping in the final ages of each life stage and starting of the next life stage (Fig. 1). According to the obtained results, the highest values of age-stage survival rate of egg stage were the same among all examined temperatures. While, in larval stage, highest value of the survival rate was estimated at 23 °C. In pupa, female and male life stages, the maximum values of the mentioned parameter were 0.7439, 0.2439, and 0.3902 at 27 °C, respectively.

The age-stage life expectancy (e_{xj}) of GWM at all studied temperatures are presented in Figure 2. Based on the results, it was confirmed that the age-stage life expectancy of GWM steadily decreased with aging (Figure 2). The highest value of the life expectancy for egg stage was 78.55 days at temperature 23˚C. Life expectancy of larva and pupa stages was the highest at 25 °C. Similarly, the highest values of the life expectancy for larva and pupa stages were 72.40, and 34.95 days, respectively at 25 °C. While, the life expectancy of the female moths was highest (14.34 days) at temperature 27 °C. The life expectancy of the male moth of GWM was the highest (24.38 days) at 25 °C (Fig. 2).

The number of offspring produced by an individual of GWM in age x and stage j is shown in figure 3. Moreover, age-specific survival rate (l_x), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) show periodic peaks in reproduction (Figure 3). Based on the estimated data for these curves, the highest values for m_x and f_x were 40.64 and 321 eggs per female at temperature 25 °C. While, the highest value of age-specific maternity was 25.87 eggs per female at temperature 27 °C.

Age-stage specific reproductive values (v_{ij}) of *G. mellonella* at four studied temperatures are presented in Figure 4. Based on the results, it cleared that the reproductive value of GWM is affected considerably by temperature, and the highest reproductive value was 1011.96 at temperature 27 °C. At 23 °C, an increase in reproductive value occurred at age 82nd day with the value 215.66, and reached a peak of 241.10 at age 85th day. Increasing reproductive value at temperatures 25, 27, and 30 °C were observed at the ages 61, 48, and 41 days, respectively. The highest reproductive values at temperatures 25, 27, and 30˚C were in 83, 49, and 46days.

The net reproductive rate (R_0), intrinsic rate of increase (r_m), finite rate of increase (λ), and mean generation time (*T*) are presented in Table 2. The net reproductive rate (R_0) of GWM increased with increasing temperature from 23 to 27 °C, then decreased severely at 30 °C. The highest value for the net reproductive rate was observed at 27 °C and the lowest at 23 °C (Table 2). The order of R_0 was similar to that of the mean fecundity (*F*) (Table 1).

The lowest intrinsic rate of increase (r_m) of GWM was 0.0429 day^{-1} at 23 °C. The highest value for the mentioned parameter was 0.0965 day^{-1} at 27 °C (Table 2).

The estimated values for the finite rate of increase (λ) of GWM indicated the same trend as intrinsic rate of increase, among examined temperatures. The highest value for λ was 1.101day^{-1} at 27 °C and the lowest was 1.044 day^{-1} at 23 °C (Table 2).

As opposed to r_m, λ, and R_0, the mean generation time (*T*) decreased with increasing temperatures, reaching a lowest value at 30 °C (Table 2).

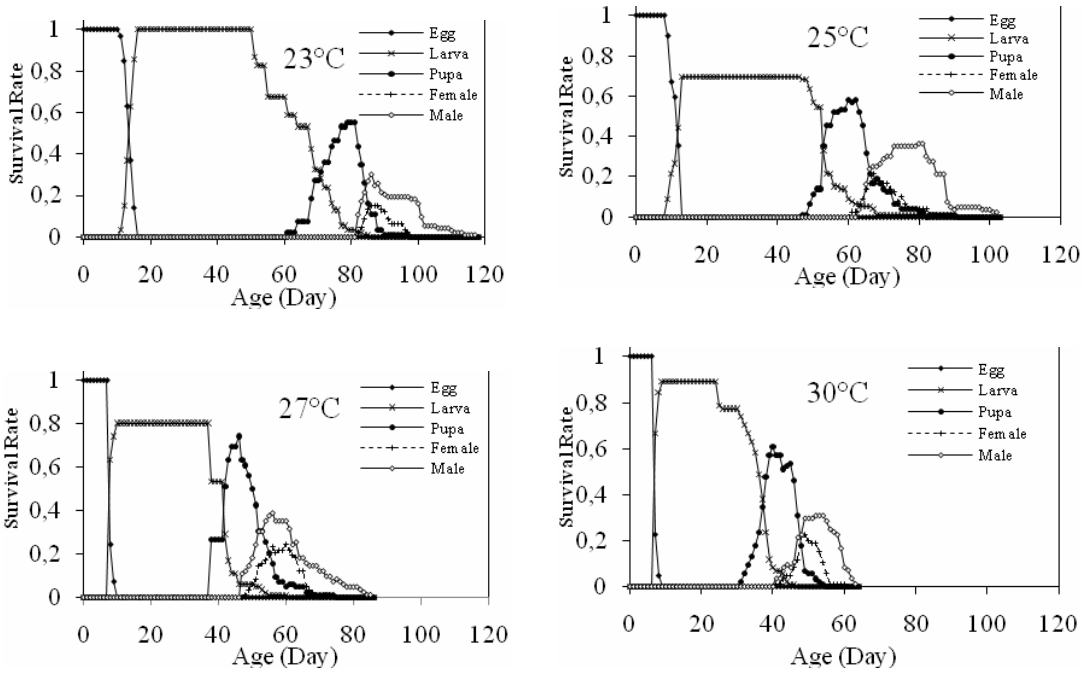

Figure 1 Age-stage specific survival rate of *Galleria mellonella* at four constant temperatures.

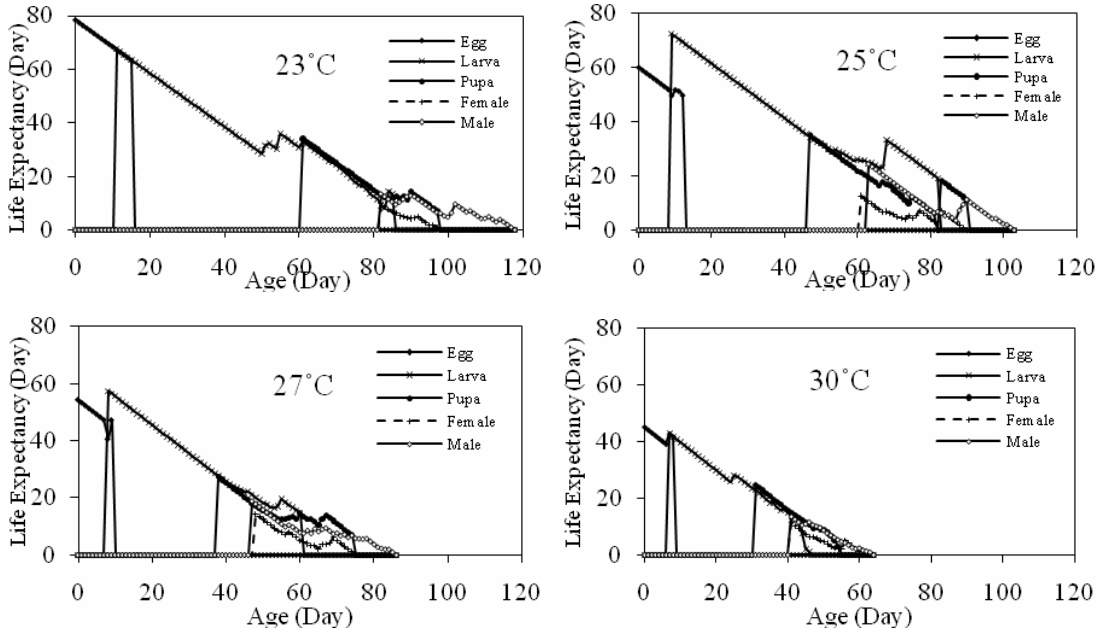

Figure 2 Age-stage specific life expectancy of *Galleria mellonella* at four constant temperatures.

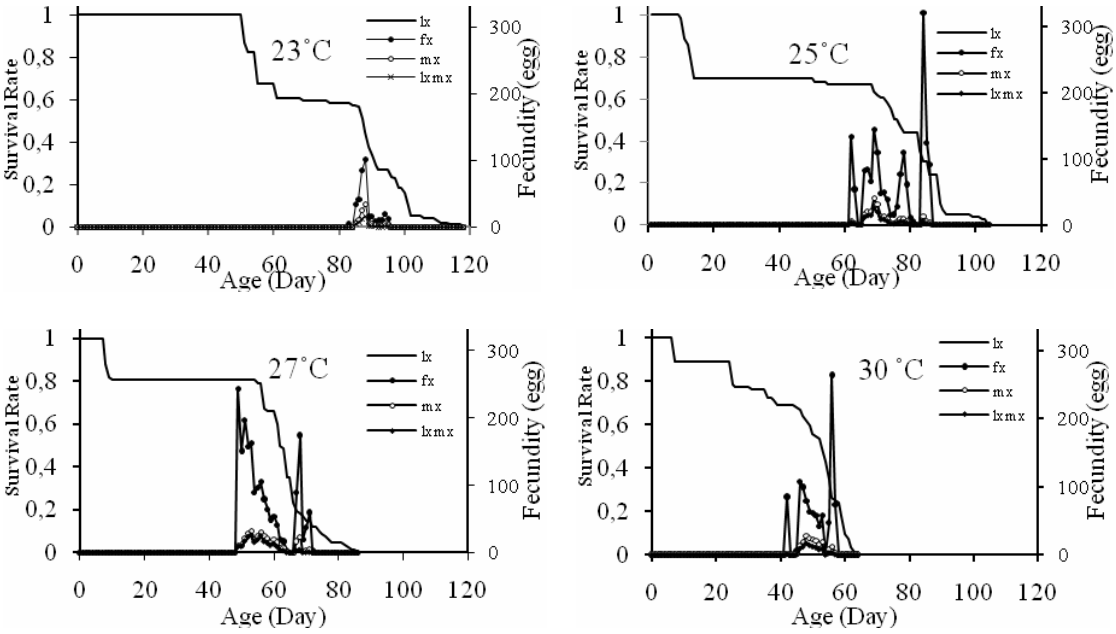

Figure 3 Age specific survival rate (l_x), fecundity (m_x), maternity ($l_x m_x$) and age-stage specific fecundity (f_x) of *Galleria mellonella* at four constant temperatures.

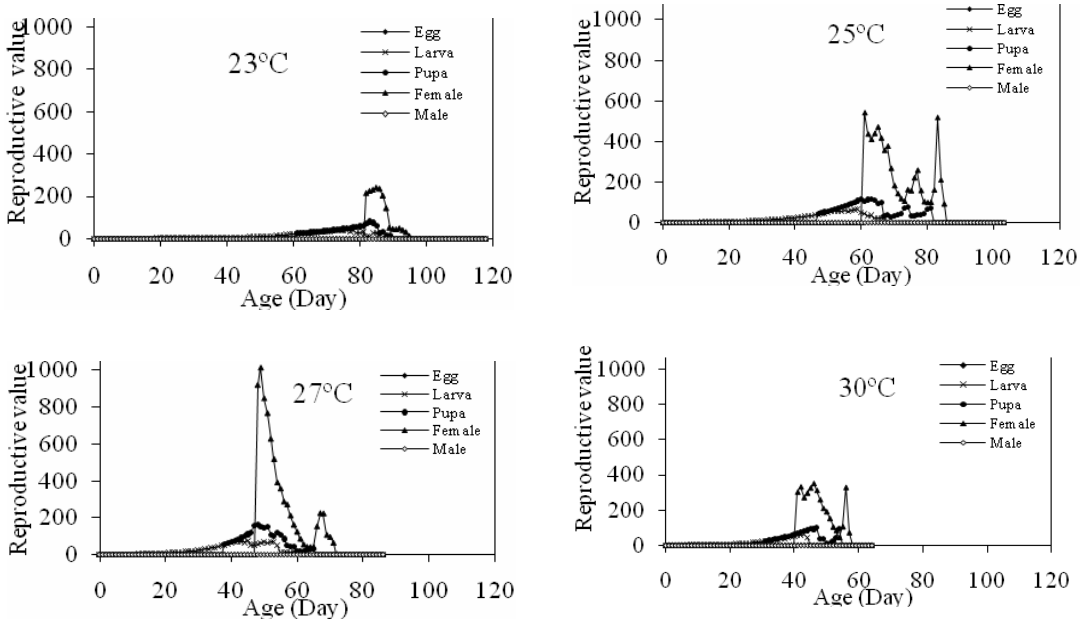

Figure 4 Age-stage specific reproductive value (v_{ij}) of *Galleria mellonella* at four constant temperatures.

Table 2 Comparison of estimated life table parameters of *Galleria mellonella* at four constant temperatures.

Temperature (˚C)	Life table parameters (Mean ± SE)[1, 2, 3]			
	r_m (day^{-1})	λ (day^{-1})	R_0 (eggs / female)	T (day)
23	0.0429 ± 0.0035c	1.0439 ± 0.0037c	47.17 ± 13.75c	88.69 ± 0.44a
25	0.0699 ± 0.0032b	1.0724 ± 0.0034b	136.18 ± 28.16b	69.95 ± 0.80b
27	0.0965 ± 0.0038a	1.1013 ± 0.0042a	223.04 ± 40.68a	55.86 ± 0.73c
30	0.0912 ± 0.0040a	1.0955 ± 0.0043a	100.38 ± 19.72b	50.31 ± 0.55d

[1] Means followed by different letters within each column are significantly different according to the paired bootstrap test at 95% confidence interval.
[2] The SEs were estimated by 10,000 bootstraps.
[3] Abbreviations: r_m: Intrinsic rate of increase, λ: Finite rate of increase, R_0: Net reproductive rate, T: Generation time.

Discussions

Temperature determines the physiological state of poikilothermic organisms, therefore is the key variable regulating their development, survival, mortality, reproduction, and population growth (Logan *et al.*, 1976; Diaz and Fereres, 2005; Tuan *et al.,* 2014). There is much literature regarding study of the effect of temperature on different aspects of insect life history (e.g. Rodriguez-Del-Basque *et* al., 1989; Roy *et al.,* 2003; Kontodimas *et al.,* 2007; Ranjbar Aghdam *et al.*, 2009b; Sandhu *et al.*, 2013). According to the obtained results here, developmental time of egg, larva, pupa, and preadult stages of GWM were affected considerably by temperature and increasing temperature from 23 to 30 °C tend to decrease developmental time of all immature stages. Inverse relationship between developmental time and temperature was reported in the same temperature range previously for the codling moth, *Cydia pomonella* L. (Ranjbar Aghdam *et al.* 2009a), *Chrysoperla cannea* Stephen (Nemati, 2013) and *Sesamia cretica* Led. (Soltani *et al.* 2014). Moreover, according to the results, APOP, TPOP and total longevity of GWM dramatically declined as temperature increased from 23 to 30 °C. While, the longest and shortest oviposition periods were 5.84 and 2.60 days, at 27 and 23 °C, respectively. Similar trend was shown regarding the value of GWM fecundity and the highest fecundity was recorded at 27 °C (Table 1). This investigation showed different trend of developmental time in comparison with reproduction at different temperatures. On the other hand, although, both F and R_0 had a similar trend at different temperatures, the trends of r_m and λ were different. The estimated R_0 values were different at all tested temperatures, and was significantly highest at 27 °C. According to Akca *et al.* (2015), because the intrinsic rate of increase (r_m) is calculated by using x, l_x, and m_x, it reflects the effects of the first reproductive age, the peak of reproduction, the length of reproductive period, and survival rate on the population growth rate; thus it is a good parameter to represent the growth potential of a population under different conditions (Birch, 1948; Andrewartha and Birch, 1954). While, the R_0 is calculated using only l_x, and m_x, and is the total offspring that an individual can produce during its life time (Akca *et al.* 2015). In this research, r_m increased as temperature increased from 23 to 27 °C and was consistent with the trend of developmental rate. At 30°, fecundity significantly decreased and the value of r_m dropped to 0.0912 day^{-1}. Consequently, the optimum temperature for the highest population growth potential of GWM among treatments occurred at 27 °C (0.0965 day^{-1}). Sandhu *et al.* (2013) have studied the effect of temperature on life table parameters of *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae) on Sugarcane. According to Sandhu

et al. (2013), the highest value of r_m was 0.1229 day^{-1} at 30 °C. While, the highest value of R_0 was obtained at 27 °C.

Legaspi and Legaspi (2007) studied the effect of five constant temperatures from 18 to 34 ºC on life table parameters of *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae). According to Legaspi and Legaspi (2007), the highest reproduction was 0.0562 day^{-1} at 30 °C, which indicates an approximate optimal temperature.

In conclusion, temperature significantly affects developmental time, survivorship, reproduction, and longevity of *G. mellonella*. Based on current comparative study on life table parameters of GWM, ambient temperature of 27 °C appeared to be most suitable for population growth among those tested (23, 25, 27, and 30 °C). The life table data can be used to predict population growth (Chi, 1990) and to plan mass rearing of GWM for biological control (Chi and Getz, 1988) and as a suitable model organism for *in vivo* toxicology and pathogenicity testing (Harding *et al*., 2013).

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تأثیر دما روی فراسنجه‌های جدول زندگی پروانه‌ی موم‌خوار گالریا (L.) *Galleria mellonella* (Lepidoptera: Pyralidae)

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چکیده: تأثیر دما روی فراسنجه‌های دموگرافیک پروانه‌ی موم‌خوار گالریا، *Galleria mellonella* (L.) در چهار دمای ۲۳، ۲۵، ۲۷ و ۳۰ درجه‌ی سلسیوس، رطوبت نسبی ۱۰ ± ۵۰ درصد و دوره‌ی نوری ۱۶ ساعت روشنایی و ۸ ساعت تاریکی بررسی شد. فراسنجه‌های جدول زیستی با استفاده از روش تشکیل جدول زندگی مرحله سنی دو جنسی برآورد شد. علاوه بر این، به‌منظور برآورد میانگین‌ها، واریانس و انحراف استاندارد فراسنجه‌های جمعیت از روش بوت استرپ استفاده شد. براساس نتایج به‌دست آمده مشخص شد تمام فراسنجه‌های برآورد شده به‌طور محسوسی تحت تأثیر دما قرار گرفتند. بالاترین مقدار نرخ خالص تولید مثل (R_0)، نرخ ذاتی افزایش جمعیت (r_m) و نرخ متناهی افزایش جمعیت (λ) به‌ترتیب، ۲۲۳/۰۴ تخم، ۰/۰۹۶ در روز و ۱/۱۰۱ در روز در دمای ۲۷ درجه‌ی سلسیوس بود. کم‌ترین مقدار میانگین طول یک نسل نیز در دمای ۳۰ درجه‌ی سلسیوس با مقدار ۵۰/۳۱ روز بود. علاوه بر موارد یاد شده بیش‌ترین مقدار برآورد شده برای فراسنجه‌ی ارزش تولید مثلی در دمای ۲۷ درجه‌ی سلسیوس مشاهده شد. براساس نتایج به‌دست آمده مشخص شد دما روی تمام فراسنجه‌های جدول زندگی پروانه‌ی موم خوار گالریا تأثیر داشته و دمای ۲۷ درجه‌ی سلسیوس از میان دماهای مورد بررسی به‌عنوان بهترین دما برای پرورش انبوه این حشره در شرایط آزمایشگاهی می‌باشد.

واژگان کلیدی: *Galleria mellonella*، جدول زندگی، دما