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Comparative demography, population projection, functional response and host age preference behavior of the parasitoid *Goniozus legneri* on two lepidopterous insect hosts

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Abstract

Background This study was conducted to investigate life table characteristics of the parasitoid species, *Goniozus legneri* Gordh (Hymenoptera: Bethylidae), a major gregarious larval ecto-parasitoids of the carob moth, *Ectomyelois ceratoniae* Zeller (Lep.: Pyralidae). Demographic parameters of *G. legneri* reared on two hosts, the carob moth and the flour moth, *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae), were studied under laboratory conditions using age-stage, two-sex life table. Host stage preference and the functional response of this parasitoid were also determined.

Results The duration of the immature period, adult pre-ovipositional period and total pre-ovipositional period of *G. legneri* reared on *E. kuehniella* was significantly longer than that of those reared on *E. ceratoniae*, while fecundity and ovipositional days of the wasp were greater/longer in females reared on *E. ceratoniae*. There were also significant differences in intrinsic and finite rates of increase and mean generation time between wasp parasitoid reared on two hosts. Moreover, population projection indicated that the *G. legneri* population can grow swifter when reared on *E. ceratoniae* than on *E. kuehniella*. Based on the experiments conducted to determine the larval stage preferences of *G. legneri*, for both hosts, larger larvae were more preferred stages compared to smaller ones, thereby fulfilling the optimal oviposition theory. The functional responses of *G. legneri* to different population densities of *E. kuehniella* two last instar larvae were determined as type III at 25 °C and 60% RH.

Conclusion The results offer valuable information on some life history attributes of *G. legneri*. Although *G. legneri* performed better on *E. ceratoniae* larvae than on *E. kuehniella,* as the use of *E. ceratoniae* larvae as the main host in rearing of *G. legneri* might be a laborious process and can increase the production costs, *E. kuehniella* can be used as an alternative host. Further studies are required under greenhouse and field conditions for effective use of this biocontrol agent against the carob moth.

Keywords *Goniozus legneri*, *Ectomyelois ceratoniae*, Parasitism, Functional response, Biological parameters

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Background

Behavior of individual parasitoids in response to an increasing host density or the functional response is undeniably a salient feature, which is influential in parasitoid success (Tomasetto et al. 2018). Host stage might be another factor, which can affect the development and reproduction of a parasitoid at the time of parasitization and hence influence the parasitoid efficiency (Pandey and Singh 1999).

The carob moth, *Ectomyelois ceratoniae* (Zeller) (Lepidoptera: Pyralidae), is a polyphagous devastating pest throughout the world which invades various fruits both before and after harvest. Pomegranate, *Punica granatum* L. (Lythraceae), is one of the preferred hosts of this pest in nearly all pomegranate producing areas of the Middle East and its yield may be significantly reduced due to the attack of this species (Sobhani et al. 2015). Not only feeding of larvae from internal parts of fruits, but also contamination of fruits with saprophytic fungi cause the fruits become inedible and unsuitable for consumption in food processing industries (Shakeri 2004). Because larval feeding takes place inside the fruits, commercial insecticides are inefficacious and hence not applicable against this pest (Hosseini et al. 2017). Hence, development of integrated pest management programs aiming to decrease the damage caused by the pest below the economic injury level is of great priority and importance (Del Pino et al. 2015).

The genus *Goniozus* is one of the most important genera of bethylid parasitic wasps (Polaszek 1998). *Goniozus legneri* Gordh (Hymenoptera: Bethylidae) is a gregarious primary ecto-larval parasitoid of some lepidopterans, particularly members of the Pyralidae (Basha and Mandour 2006). This species firstly reported from pomegranate orchards of Iran in 2010, parasitizing larvae of carob moth (Ehteshami et al. 2013). The parasitoid is a high potential biological control agent in integrated management programs for the carob moth (Sarhan et al. 2004).

The Mediterranean flour moth, *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae), is an easily reared species, which hitherto has been widely utilized for mass rearing of various natural enemies including larval ectoparasitoids (Nakano et al. 2018). As rearing of the carob moth is tedious, *E. kuehniella* may be a suitable alternative host candidate for rearing of *G. legneri* (Shoeb et al. 2005).

Life tables, as the best way to project population growth and reveal the details of life history parameters such as survival, stage development and also reproduction, lubricate a full comprehension of insect population dynamics (Huang et al. 2018). They are considered as crucial instruments for prophesying anticipated damage from a pest population, implementing pest management programs and determining best timing of pest control practices (Huang et al. 2018). Comprehensive knowledge of life table and some behavioral responses (such as functional response) of a natural enemy lead to unerring description of growth, stage differentiation, and reproduction of the biocontrol agent in order to expound an efficacious mass-rearing procedure, which is an important factor for the success of biological control programs (Eliopoulos 2019).

In the present study, raw data on the life history of *G. legneri* and its functional response on two hosts, *E. ceratoniae* and *E. kuehniella* (as an alternative host) were collected and analyzed. The results from this study are expected to be beneficial in providing basic information on the utilization of *G. legneri* to control the population of *E. ceratoniae*.

Methods

Parasitoids

Infested fruits were collected from underneath and on the trees of pomegranate orchards of Shiraz and vicinity, Iran, and were transferred to the laboratory for dissection and removal of the carob moth larvae. The parasitized larvae were individually placed in plastic containers (10 cm height 20 cm width) until emergence of the adult parasitoids. Parasitoids were reared separately on two hosts, *E. kuehniella* and *E. ceratoniae* larvae, in the laboratory (26 ± 1 °C, 50 ± 5% RH and 14 L: 10 D) for three generations before using in the experiments. Honey solution (10%) was placed in the containers as adult food.

Host insects

Original carob moth colonies were obtained from adults emerged from infested pomegranate fruits collected from orchards in Shiraz vicinity, Iran. Emerged adults were transferred into mating cages (50 × 50 × 100 cm) and after 24 h. of exposure, each mated female was removed from the cage and placed separately in a plastic container (1 L volume). The container was inverted on a piece of rough filter paper. A 3-cm-diameter opening was cut on bottom of the plastic container and covered with a fine mesh for ventilation. During oviposition adult females were provided with cotton wool pieces which were soaked in 10% honey water solution for feeding. The hatched larvae were transferred on the artificial diet (wheat bran 300 g, sugar 80 g, yeast 9 g, multivitamin 1.4 g, tetracycline antibiotics 0.6 g, sterile distilled water 120 ml, and glycerin 130 ml) using a fine brush.

Life table analysis

The age-stage, two-sex life table approach was utilized to analyze the raw life-history data for *G. legneri* (Chi 1988) via the computer program TWOSEX-MSChart (Chi

2020a). The population parameters including age-stage-specific survival rate (s_{xj}), age-stage-specific fecundity (f_{xj}), age-specific fecundity of total population (m_x), age-specific survival rate (l_x), age-specific maternity (l_xm_x), intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), mean generation time (T), age-stage life expectancy (e_{xj}) and reproductive value (v_{xj}) were calculated. In order to estimate the variances and standard errors of population parameters, the bootstrap technique with 100,000 resampling was applied (Wei et al. 2020). Quick paired bootstrapping (paired 1 by 1) function was used for estimating the significant differences between means. Sigma plot v. 12.5 was used to create graphs.

Population projection

Using the computer program TIMING (Chi 2020b), the population growth of *G. legneri* after 100 days was projected through the method of Chi (1990) and Huang et al. (2018) as follows:

$$N_t \xrightarrow{G,D,F} N_{T+1}$$

where G, D and F are growth, development and fecundity matrices produced via using TWOSEX-MSChart.

Host stage preference

To determine the host larval stage preferences of *G. legneri*, a non- and a choice experiment were designed based on the size of larvae of each host, i.e., small (L_1 and L_2) and large (L_4 and L_5). Experiments were conducted separately for each host species. In the non-choice experiment, a female and male of *G. legneri* were confined in a Petri dish (8 cm) and provided with 10% honey solution for food. The insects were 2–3 days old, and the females were naïve. A total of 60 larvae, in batches of 30 for each group (L_1+L_2 and L_4+L_5), were placed separately in Petri dishes. The larvae were exposed to the parasitoids for 24 h in an incubator at 25° C and a 14:10 (L:D) photoperiod. After exposure, the parasitoids were removed from the Petri dishes, and the parasitized larvae were counted. In choice experiment, the procedures were the same as above, except that in each Petri dish, a mixture of larvae belonging to two groups, i.e., 15 small larvae (L_1+L_2) and 15 large larvae (L_4+L_5), were provided. Each experiment was replicated 10 times.

Comparisons of host larval stage preferences in non- and a choice experiment were done by independent t test ($P<0.05$). Data were normalized using arcsine transformation. All analyses were done with SPSS software version 19 (SPSS Inc., Chicago, USA).

Parasitoid's preference for the host stage was evaluated by calculating a preference index according to Manly (1974). This index is as follows:

$$\beta_i = \frac{\log\left[\frac{e_i}{A_i}\right]}{\sum_{s=1}^{k}\log\left[\frac{e_s}{A_s}\right]}$$

where β_i is the preference for prey group i, e_i are the numbers of hosts remaining after the experiment; A_i and A_s are the number of prey groups i and s offered, respectively. This index provides a value between 0 and 1. With two-prey choices, as in our experiment, the value 0.5 for β_i shows that the predator has no preference for any of prey groups, whereas values greater and lower than 0.5 indicate a preference for prey group i and prey groups, respectively (Meyling et al. 2004). To assess if the estimates deviated from 0.5, a two-tailed t test ($P<0.05$) SPSS 19 software was utilized.

Parasitoid's preference for the host stage was also assessed by calculating a preference index according to Jervis and Kidd (1996) using the following equation:

$$\frac{E_1}{E_2} = c\left(\frac{N_1}{N_2}\right)$$

where the N_1 and N_2 are the number of small and large larvae, and E_1 and E_2 are the number of small and large parasitized larvae, respectively. The value $c<1$ indicates preference for prey 2 (group 2), whereas $c>1$ depicts preference for prey 1.

Functional response

Since in nature, only one larva in each pomegranate fruit is exposed to *G. legneri* females for being parasitized, so the functional response with *E. ceratonia* larvae seemed to be meaningless. Therefore, only the flour moth larvae were included in the experiment. The 4th and 5th instar larvae of *E. kuehniella* were placed within the Petri dishes in different densities of 4, 6, 10, 20, 30, 50 and 60. One mated 10-day-old female parasitoid (fed on drop of 20% honey/water) was introduced into each Petri dish. Ten replicates for each host density were utilized. The parasitoids were removed after 24 h, and the parasitized larvae were counted. In order to determine the shape (type) of functional response, the logistic regression of the proportion of parasitized hosts (Na/N_0) as a function of host density (N_0) is used. For doing this, a polynomial function (Eq. 1) is fitted:

$$\frac{N_a}{N_t} = \frac{\left[\exp\left(P_0 + P_1N_t + P_2N_t^2 + P_3N_t^3\right)\right]}{1 + \exp\left(P_0 + P_1N_t + P_2N_t^2 + P_3N_t^3\right)} \tag{1}$$

where N_a/N_t is the proportion of parasitized hosts, N_t is the initial host density, P_0, P_1, P_2 and P_3 are the intercept, linear, quadratic, and cubic coefficients estimated through the CATMOD procedure in SAS, respectively. If the signs of the linear parameter (P_1) and the quadratic parameter (P_2) are both negative, the proportion of parasitized host decreases monotonically with host density (De Clercq et al. 2000) implying type II functional response. If P_1 and P_2 are positive and negative, respectively, the proportion of parasitized host is positively density-dependent depicting type III functional response (Juliano 2001).

After determination of the type of functional response, to estimate the parameters associated with functional response models, a nonlinear least square regression (SAS Institute 2014) was utilized. As our data fit a type III functional response, the type III equation for parasitoids was utilized as follows (Eq. 2):

$$N_a = N_t\left[1 - \exp\left(-\frac{bTN_t p_t}{1 + cN_t + bT_h N_t^2}\right)\right] \tag{2}$$

where N_a is the number of parasitized hosts, N_t is the initial number of hosts, P_t is the number of the parasitoid, T is the total time of the experiment (24 h in our study), T_h is the handling time, b and c are constants, (24 h). The coefficient of determination (R^2) was calculated using the following equation: $R^2 = 1 -$ (residual sum of squares/corrected total sum of squares).

Results

Developmental time, survival, longevity and fecundity

The mean developmental durations of each pre-adult stage and the adult longevities of females and males as well as reproductive features of females are given in (Table 1). The total immature stages of *G. legneri* reared on *E. ceratoniae* were significantly shorter than the equivalent durations on *E. kuehniella*. Female wasps lived an average of 76.33 and 53.79 d on flour moth and carob moth, respectively. The adult pre-ovipositional period (APOP) of *Goniozus* wasps was significantly shorter on the carob moth. In other words, the mated females of *G. legneri* began oviposition, on average, 0.62 and 0.77 d after emergence when reared on *E. ceratoniae* and *E. kuehniella*, respectively. There were also significant differences between total pre-ovipositional periods (TPOP) of parasitoid wasps on two hosts (Table 1). The mean fecundity per *Goniozus* female was (101.17) on flour moth which was remarkably lesser compared to (118.04) eggs on carob moth (Table 1). The number of ovipositional days of parasitoids reared on *E. kuehniella* (13.53 d) was significantly lesser than those reared on *E. ceratoniae* (14.74 d).

Life table

The age-stage survival rates (s_{xj}) of *G. legneri* on two hosts are depicted in (Fig. 1). These curves show the likelihood that a newly deposited egg will survive to age *x* and stage *j*. The overlap of stages in the survival curves

Table 1 Comparative duration of immature and adult stages development in days (mean ± SE) and reproductive features (APOP, TPOP, fecundity, and oviposition days) of *Goniozus legneri* reared on *Ectomyelois ceratoniae* and *Ephestia kuehniella*

Basic statistic	**Hosts**				***P* values (Based on bootstrap samples)**
	n[a]	***E. kuehniella***	**n**	***E. ceratoniae***	
Developmental duration (d)					
Egg	50	1.06 ± 0.03 a	50	1.06 ± 0.03 a	1
Larva	50	3 ± 0 b	50	3.12 ± 0.04 a	0.007
Pupa	50	10.92 ± 0.009 a	50	8.4 ± 0.18 b	< 0.0001
Adult longevity	50	56.6 ± 2.19 a	50	37.41 ± 1.41 b	< 0.0001
Male longevity	5	28.80 ± 2.58 a	7	26.71 ± 0.68 a	0.421
Female longevity	45	76.33 ± 1.14 a	43	53.79 ± 0.69 b	< 0.0001
Preadult Duration	50	14.98 ± 0.10 a	50	12.58 ± 0.18 b	< 0.0001
total developmental time	50	71.58 ± 2.24 a	50	50 ± 1.49 b	< 0.0001
Adult pre-ovipositional period (Apop) (d)	45	0.77 ± 0.06 a	43	0.62 ± 0.07 a	0.119
Total pre-ovipositional periods (Tpop) (d)	45	15.87 ± 0.12 a	43	13.26 ± 0.22 b	< 0.0001
Fecundity (eggs/female)	45	101.17 ± 4.28 b	43	118.04 ± 3.45 a	0.005
Oviposition days (d)	45	13.53 ± 0.27 b	43	14.74 ± 0.34 a	0.006

n: number of individuals of *G. legneri* completed a stage

The estimation of standard errors was conducted by using 100,000 bootstraps. Means within a row followed by different letters are significantly different using the paired bootstrap test based on the confidence interval of 100,000 differences ($P < 0.05$)

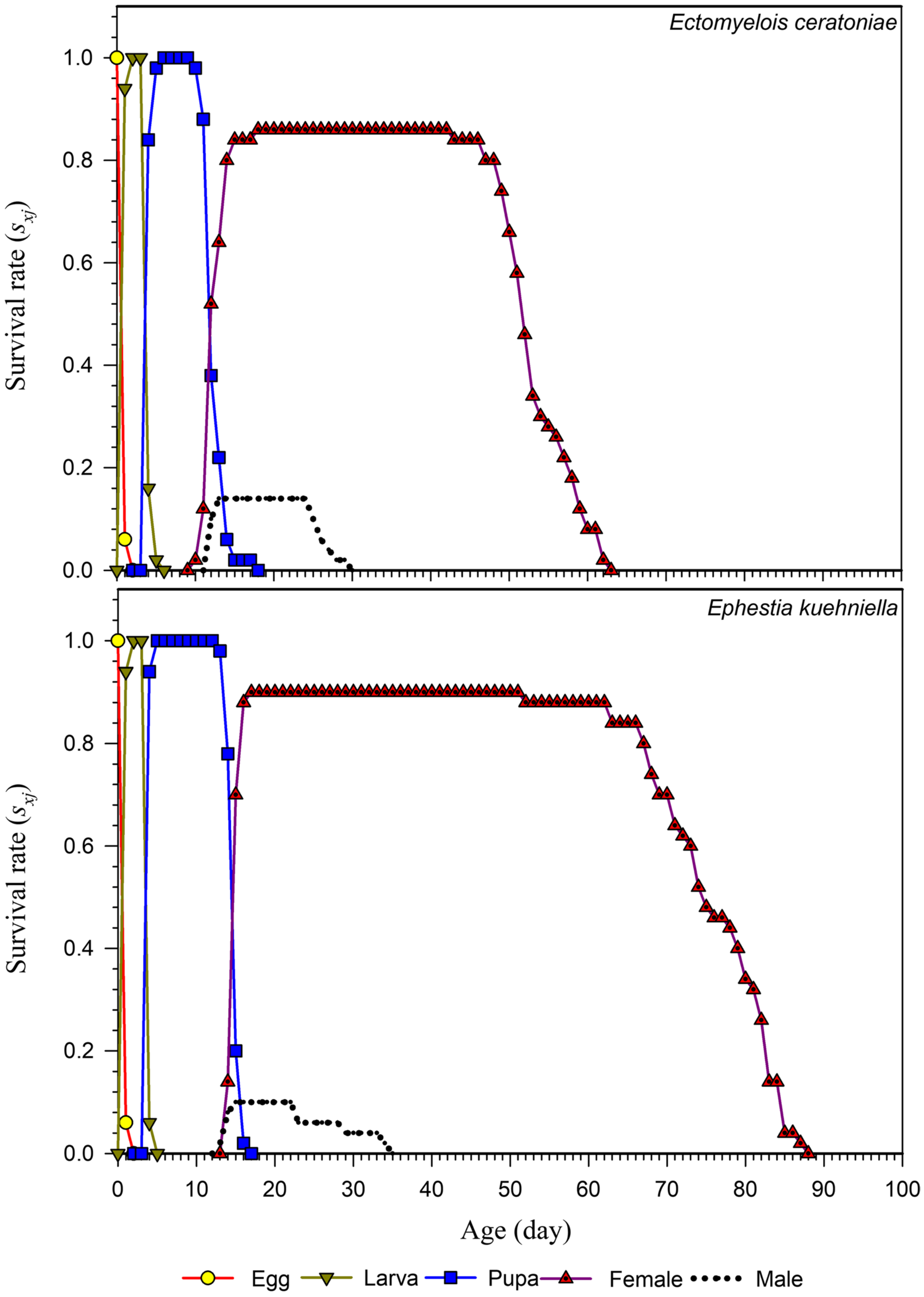

Fig. 1 Age-stage survival rate (s_{xj}) of *Goniozus legneri* fed on *Ephestia kuehniella* and *Ectomyelois ceratoniae* larvae at 25 ± 1 °C and 75 ± 5% RH

is due to variable developmental rates among individuals (Yu et al. 2013).

The age-stage specific survival rate (l_x), age-specific fecundity (m_x) and age-specific maternity ($l_x m_x$) of parasitoid wasps on two lepidopteran hosts are plotted in Fig. 2. Because only female wasps reproduce, there was just a single curve, f_{x4}, representing the number of hatched eggs produced by each female (fourth life

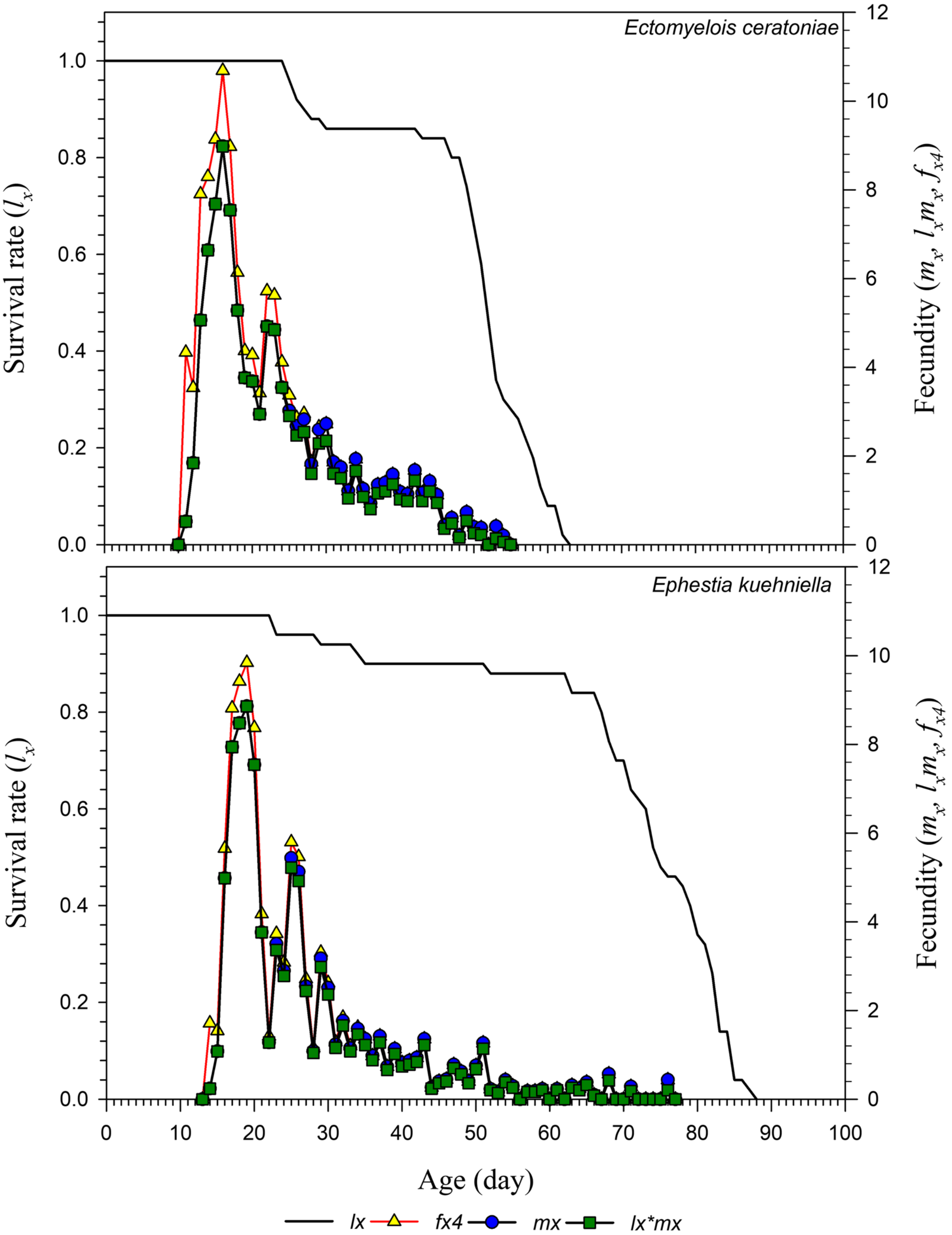

Fig. 2 Age-specific survival rate (l_x), age-specific fecundity (m_x), age-specific maternity (l_xm_x) and age-stage specific fecundity (f_x) of *Goniozus legneri* fed on *Ephestia kuehniella* and *Ectomyelois ceratoniae* larvae at 25 ± 1 °C and 75 ± 5% RH

stage) at age x. Age-specific fecundity (m_x) depicts the mean number of hatched eggs produced by each individual (regardless of sex or stages) on age x. As shown in Fig. 2, on both hosts, the cure f_{x4} is higher than the representative m_x curve. The cohorts began the production of offspring on days 11 and 14, reached a peak for 16 d and 19 d and ended on days 55 and 78, on carob moth and flour moth, respectively.

The age-stage life expectancy (e_{xj}), as one of the major outputs of life table analysis, defines the number of days that an individual at age x and stage j is anticipated to survive after age x (Chi and Su 2006). The life expectancy

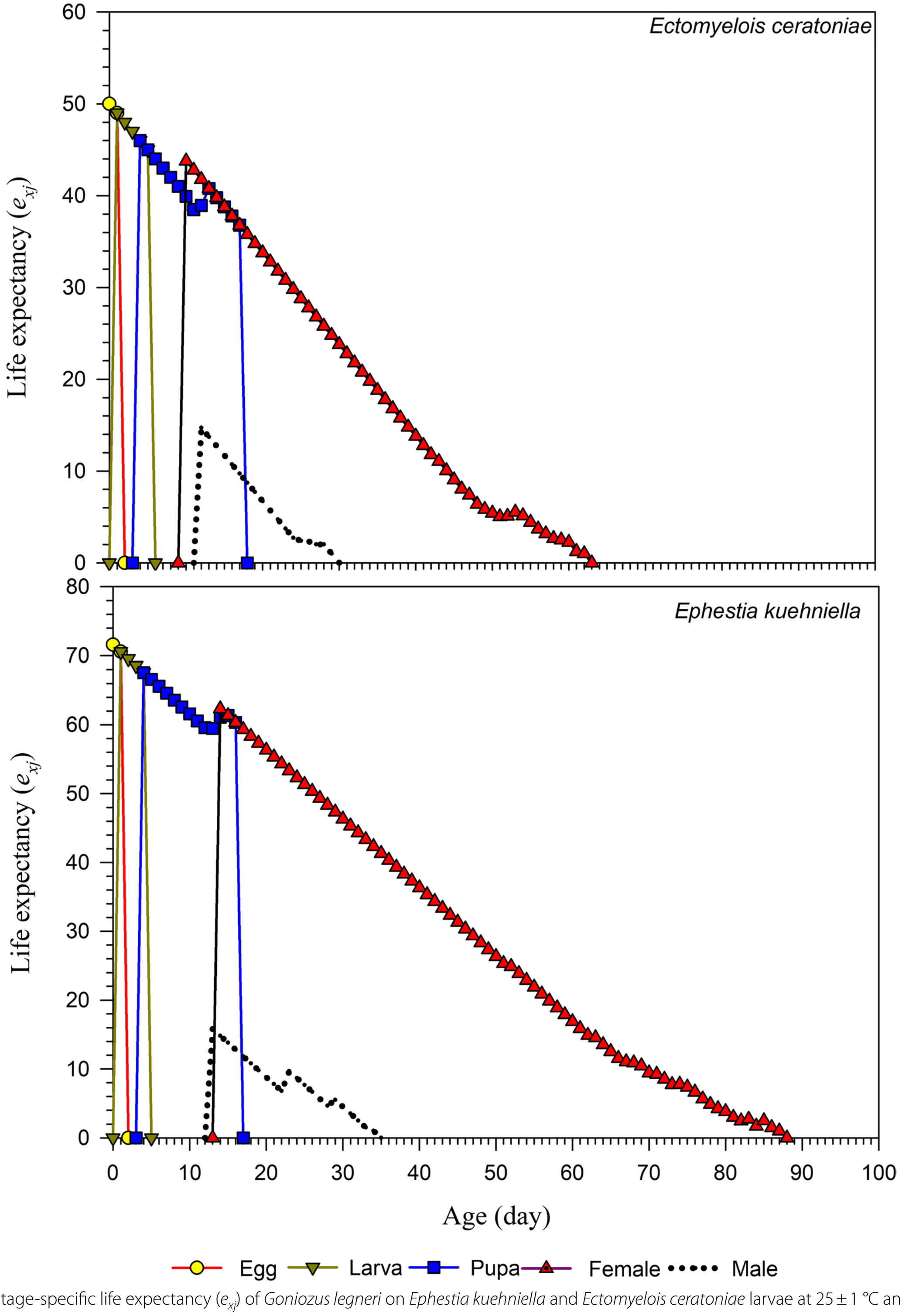

Fig. 3 Age-stage-specific life expectancy (e_{xj}) of *Goniozus legneri* on *Ephestia kuehniella* and *Ectomyelois ceratoniae* larvae at 25 ± 1 °C and 75 ± 5% RH

of each age-stage of *G. legneri* is depicted in Fig. 3. With increasing time intervals, the expectancy of different life stages of *G. legneri* decreased (Fig. 3). A newly deposited egg (e_{01}) was anticipated to live and develop through succeeding stages until an age of (71.5 and 50 d) on flour moth and carob moth larvae, respectively, which was quite equal to the mean longevity in Table 1. As shown in Fig. 3, the e_{xj} curves showed a gentle linear decreasing trend due to the lack of notable high mortality throughout life history of the wasp.

The age-stage reproductive value (v_{xj}) of *G. legneri* expounds the contribution of an individual wasp of age *x* and stage *j* to the upcoming offspring. In other words, the v_{xj} curves distinctly depicted the impact of age on the reproductive value. The results of the current study displayed that the reproductive value sharply raised when females started egg laying. The highest reproductive values were recorded at the age of 17 and 13 days on flour moth and carob moth hosts, respectively (Fig. 4). After emergence of all female wasps and when all of them began depositing eggs (after TPOP), the greatest contribution value of female parasitoids was 17 at age (35.08 d) when reared on *E. kuehniella*, while the highest v_{xj} of wasps, which were reared on *E. ceratoniae* was 14 at age (34.12 d) (Fig. 4). As the contribution of males to the subsequent populations was not described by Fisher (1930), there was not any curve for males.

Life table parameters including intrinsic rate of increase (*r*), net reproductive rate (R_0), mean generation time (*T*) and finite rate of increase (λ) calculated using the age-stage, two-sex life table method are shown in (Table 2). Except for net reproductive rate, all other population parameters were significantly different on *E. kuehniella* from those gained on *E. ceratoniae.* According to the results, if the population reaches the stable age-stage distribution and if the physiological factors are the only mortality factors, the population of *G. legneri* reared on *E. kuehniella* can increase 1.2270-fold per day or at an exponential rate of 0.2046 per day, and it can multiply 91.06 times every 22.05 d. By comparison, when reared on *E. ceratonia*, the wasp population had the capability to grow 1.2767-fold per day or at an exponential rate of 0.2442 per day, and it was capable to increase 101.52 times every 18.91 d.

Population projection

The population growth projections of *G. legneri* utilizing the life table data are shown in Fig. 5. The parasitoid population grew much faster on *E. ceratoniae* than on *E. kuehniella* (Fig. 5). After 100 days, there were 227,553,267 individuals in various pre-adult stages, 81,422,480 female and 9,457,624 male adult wasps (reared on *E. kuehniella*), while on *E. ceratoniae*, there were 111,142,980,734 individuals in pre-adult stages, and 4,476,203,151 female and 731,806,109 male adults (Fig. 5). With an increase in time, the growth rate of all stages of *Goniozus* wasps on both hosts in natural logarithmic scale approaches the intrinsic rate of increase (Fig. 5 c, d).

Host stage preference

When different stages (L_1+L_2 as small larvae and L_4+L_5 as large larvae) of the Mediterranean flour moth and carob moth larvae were offered to the parasitoids under no-choice conditions, there were non-significant differences among the larval stages in the number of hosts parasitized ($P=0.26$, $df=18$) (Table 3). Nonetheless, *Goniozus* wasps significantly preferred larger larvae of *E. ceratoniae* for egg laying ($P<0.01$, $df=18$) (Table 3). When the Mediterranean flour moth larvae of various developmental stages were offered together to *G. legneri*, there were significant differences among the larval stages in the number of hosts parasitized ($P<0.0001$, $df=18$). Smaller larval stages (L_1 and L_2) were less preferred by *G. legneri* than larger ones (L_4 and L_5) (Table 3). Similar results were obtained for *Goniozus* wasps on carob moth larvae ($P<0.0001$, $df=18$) and the parasitoid wasps preferred larger larvae over smaller ones (Table 3). The values of Manly's preference index for two groups of larvae of each host (*E. kuehniella* and *E. ceratoniae*) are presented in (Table 4). This index was higher than 0.5 for larger larvae for both the flour moth (0.64) and the carob moth (0.70) meaning that the parasitoid wasp showed a distinct preference for laying eggs on larger larvae.

The value of Jervis and Kidd preference index between zero and one indicated a preference for smaller larvae and the value between 1 and infinity indicated a preference for larger larvae. These parameters were 1.37 and 1.44 for the flour moth and the carob moth, respectively, which indicated preference for larger larvae (Table 4).

Functional response

Functional responses of *G. legneri* determined as type III by a logistic regression (Table 5). The results of logistic regression analysis (Table 5) indicating the linear and cubic coefficients were positive for parasitism which is an indication of a type III functional response. The parasitization rate first rose at lower host density and then decreased at a higher host density resulting a sigmoid curve. The attack coefficients *b* and the handling time T_h for *E. kuehniella* larvae were (0.0176 ± 0.0058) and (0.8950 ± 0.0342), respectively (Table 6).

Discussion

Adequate information about a biocontrol agent is prerequisite for implementing any decision to use it in any pest management program. The intrinsic rate of increase, survival rate, developmental rate and fecundity, as basic elements representing the life history and stage differentiation, can be utilized in population ecology research, forecasting population growth and the stage structure of a population in both short- and long-term intervals. The

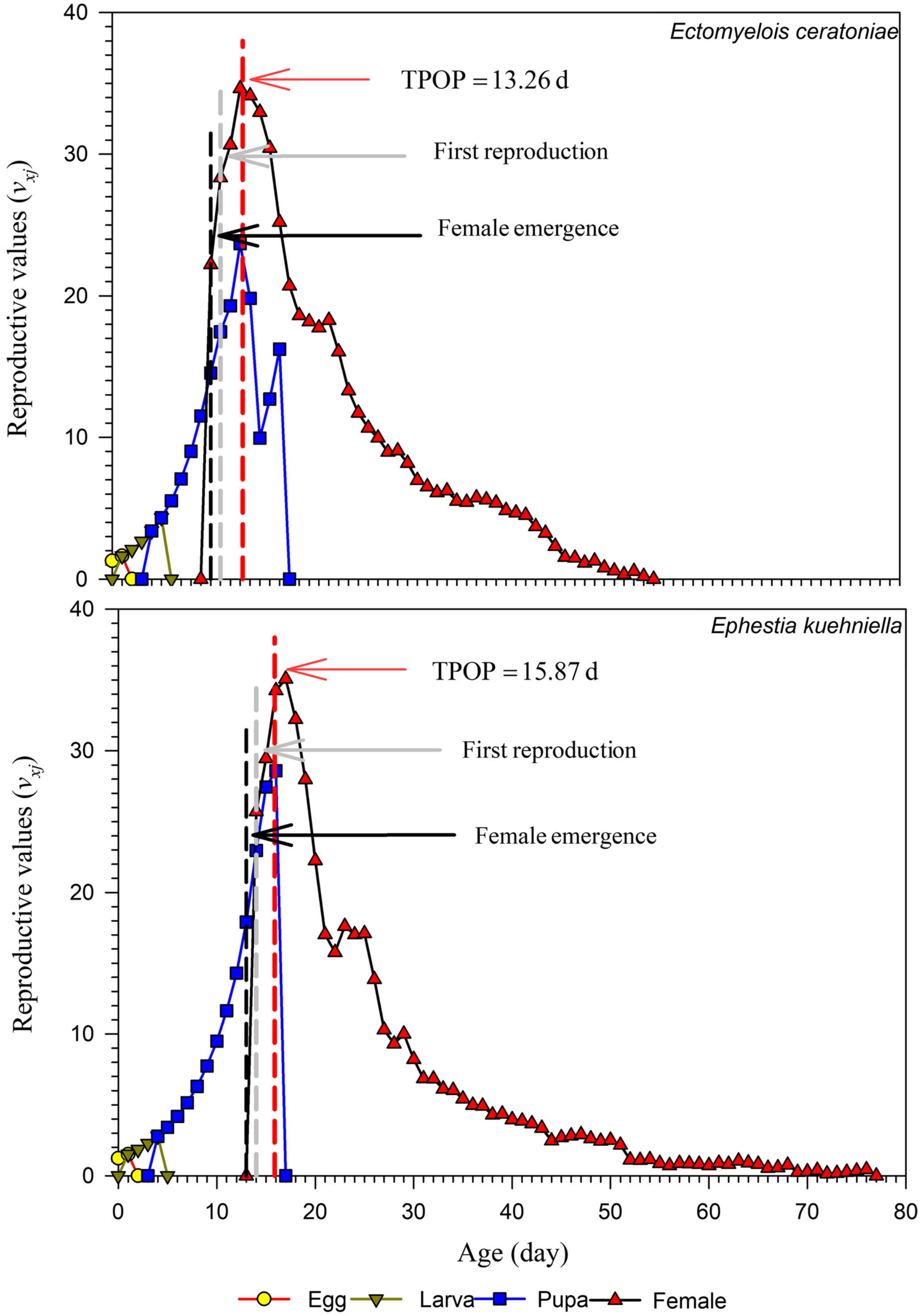

Fig. 4 Reproductive value (v_{xj}) of each stage of female *Goniozus legneri* on *Ephestia kuehniella* and *Ectomyelois ceratoniae* larvae at 25 ± 1 °C and 75 ± 5% RH

life table data should be taken into account as the foundation of any release program of a biocontrol agent, including *G. legneri*, to achieve accurate timing and coincident with susceptible stages of the host (Getu et al. 2004). Moreover, information on the biological parameters of a parasitoid contributes mightily to prognosticating the

Table 2 Population parameters (means ± SE) of *Goniozus legneri* reared on *Ectomyelois ceratoniae* and *Ephestia kuehniella* estimated in this research

Parameters	**Hosts**		***P* values (Based on bootstrap samples)**
	E. kuehniella	***E. ceratoniae***	
Net reproductive rate (R_0) (offspring/individual)	91.06 ± 4.68 a	101.52 ± 6.42 a	0.1890
Intrinsic rate of increase (r) (d^{-1})	0.2046 ± 0.0028 b	0.2442 ± 0.0004 a	< 0.0001
Finite rate of increase (λ) (d^{-1})	1.2270 ± 0.0035 b	1.2767 ± 0.0006 a	< 0.0001
Mean generation time (T) (days)	22.05 ± 0.14 a	18.91 ± 0.25 b	< 0.0001

The estimation of standard errors was conducted by using 100,000 bootstraps. Means within a row followed by different letters are significantly different using the paired bootstrap test based on the confidence interval of 100,000 differences ($P < 0.05$)

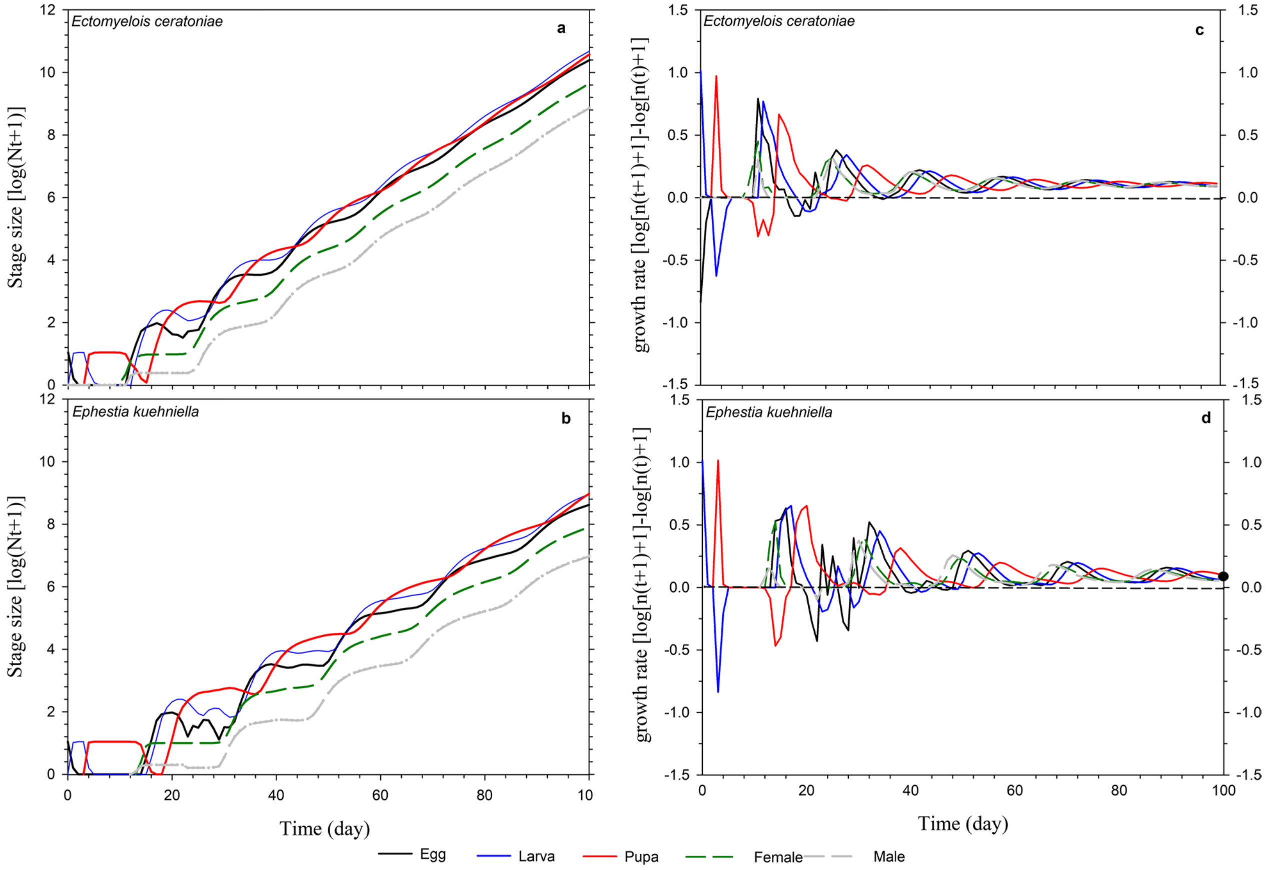

Fig. 5 Population growth projection of *Goniozus legneri* on *Ephestia kuehniella* (**a**, **b**) and *Ectomyelois ceratoniae* (**c**, **d**); a, b: stage curves, c, d: stage growth rates

generation time and preparing a reference for mass-rearing of it (Chen et al. 2021).

Based on obtained results, total pre-adult developmental period of *Goniozus* wasps reared on *E. kuehniella* was significantly lengthier than those reared on *E. ceratoniae*. Nonetheless, the larval development of wasps was fairly shorter when reared on *E. kuehniella*. The present findings showed that adult females began egg laying nearly immediately or in less than 1 day after emergence on both hosts, a pattern which has been observed in many parasitoids (Ebrahimi et al. 2013). The total pre-ovipositional period (TPOP) was 15.87 d and 13.26 d on *E. kuehniella* and *E. ceratoniae,* which were both close to the age of peak reproductive value at age 17 and 13 D on these two hosts, respectively (Fig. 4). Similar results have been reported in some other studies based on the two-sex life table (Amir-Maafi and Chi 2006). Although female wasps lived remarkably longer

Table 3 Number of parasitized larvae of two hosts by *Goniozus legneri* on no-choice and choice tests

Experiment	Hosts		Number of parasitized (mean ± SE)	P value (independent t test)
No choice test	*Ephestia kuehniella*	Small larvae	23.50 ± 0.98	$T=0.61$ $P=0.26$
		Large larvae	24.50 ± 1.3	
	Ectomyelois ceratoniae	Small larvae	24.40 ± 0.95	$T=2.95$ $P<0.01$
		Large larvae	27.40 ± 0.37	
Choice test	*Ephestia kuehniella*	Small larvae	9.80 ± 0.38	$T=5.40$ $P<0.0001$
		Large larvae	13.40 ± 0.54	
	Ectomyelois ceratoniae	Small larvae	9.70 ± 0.58	$T=6.79$ $P<0.0001$
		Large larvae	14 ± 0.26	

Table 4 Manly's and Jervis and Kidd's preference indices of *Goniozus legneri* on small and large larvae of *Ephestia kuehniella* and *Ectomyelois ceratoniae*

Experiment	Host		Manley's preference index ± SE		Jervis and Kidd's index
1	*E. kuehniella*	Small larvae	0.36 ± 0.03	$T=4.23$ ($df=5$)	1.367
		large larvae	0.64 ± 0.03	$P<0.01$	
2	*E. ceratoniae*	Small larvae	0.30 ± 0.02	$T=6.85$ ($df=6$)	1.443
		large larvae	0.70 ± 0.02	$P<0.0001$	

Table 5 Maximum-likelihood estimates from logistic regressions of the proportion of *Ephestia kuehniella* larvae parasitized by *Goniozus legneri*

Host	Parameters	Estimate	Standard error	Chi-square*	P value
E. kuehniella	Constant	2.2219	0.4311	26.57	< 0.0001
	Linear	0.0257	0.0461	0.31	0.5768
	Quadratic	− 0.00242	0.00144	2.82	0.0933
	Cubic	0.000021	0.000013	2.54	0.1111

*Chi-square is the value of the likelihood ratio test to determine whether equation coefficients differed significantly from zero

Table 6 Estimated attack coefficients (b), handling times (T_h), and maximum attack rates (T/T_h) of the *Goniozus legneri* to different densities of *Ephestia kuehniella* larvae

Parameters	Estimate	Approximate SE	Approximate 95% lower	Approximate 95% upper	T/T_h (h)	R^2
b (h^{-1})	0.0176	0.0058	0.00589	0.0292	27	0.94
T_h (h)	0.8950	0.0342	0.8270	0.9631		

when reared on *E. kuehniella*, the mean fecundities and number of oviposition days of them were significantly greater/longer when reared on *E. ceratoniae* (Table 1). There were non-significant differences on male longevities between the wasps reared on two hosts. There were also non-significant differences in immature survival rates (s_{xj}) between the two hosts.

In the present study, the sex ratio was in favor of females, which was in line with some previous studies (Khidr et al. 2012). The sex ratios of most bethylid species, including *G. legneri*, were female biased with low variances (Khidr et al. 2012). The reproductive biology of *G. legneri* conformed closely to the assumptions of the model of sex ratio evolution under local mate competition theory (LMC). In this species, each host was stung and paralyzed by an adult female, which protects it against utilization by other females (Lize et al. 2012). Because of brood guarding and conspecific infanticide, all offspring developing on the same host are the offspring of a mother (Khidr et al. 2012). Moreover, in *G. legneri*, sibling mating was greatly prevalent before dispersal and brood sex ratios are mainly female biased (9–19% of offspring are male) and had a low variance (Hardy and Mayhew 1998) qualitatively conforming to expectation under single founders LMC (Krackow et al. 2002).

If a parasitoid has an equal or greater population growth rate compared to that of its host, it will probably capable of regulating its host population. The intrinsic rate of increase of *G. legneri* on *E. kuehniella* and *E. ceratoniae* were 0.2046 and 0.2442, respectively, whereas it ranged from 0.107 to 0.018 in case of (the carob moth) (Norouzi et al. 2008); the intrinsic rate of increase in G. legneri was much higher than those of its host. Hence, *G. legneri* had the potential to be used in integration with other compatible control methods to achieve an efficacious control of carob moth.

The population growth rates (r and λ) of *G. legneri* wasps were significantly higher on *E. ceratoniae* than those on *E. kuehniella*. It should be noted that both r and λ are efficacious parameters for evaluating population fitness (Chi et al. 2020). Overall, all these results demonstrated that varying hosts may result in considerable changes in various population traits of a parasitoid species which is in line with some the results of previous studies (Saadat et al. 2014).

Although parasitoids may have the ability to develop successfully in various larval instars of the same host, either the costs of parasitism or the suitability may vary among different instars (Fellowes et al. 2005). According to the results of the present study, the parasitoid parasitized all larval stages of both *E. kuehniella* and *E. ceratoniae*; nevertheless, there were significant differences in the parasitism rates on the different larval instars. A preference for the last two stages ($L_4 + L_5$) compared to two first instars ($L_1 + L_2$) was observed for both hosts. Based on the optimal foraging theory (Charnov 1976), which our results agreed with it, when given a choice, female parasitoids prefer larger host larvae than smaller ones for oviposition.

According to the various conducted studies on functional response of insect parasitoids, more than three-quarters of functional responses were type II and less than one-fifth were type III (Fernández-Arhex and Corley 2003). Nonetheless, our study depicted that the functional response of *G. legneri* followed Type III model. For *G. legneri*, we do not know on which behavioral mechanism the type III functional response was based. Nonetheless, this response resulted in an increasing percentage of host parasitized at a certain range of host densities, and that over this range the response may act as a stabilizing factor. It is noteworthy to mention that each species of natural enemy can show different types of functional responses depending on various elements such as the age of the natural enemy and its hunger status, the species of a host, host size and distribution, availability of alternative hosts, the temperature and also conditions of the experiment (Van Lenteren et al. 2016). As type III functional response represents a density-dependent relationship between the proportion of parasitism and host density (Holling 1959), it seems that *G. legneri* probably was efficient at high density of its host. However, it should be noted that interpretation of functional response results is mostly strenuous and their meaning for evaluating the control capability of a biocontrol agent is restricted (Van Lenteren et al. 2016).

Conclusions

Overall, obtained results offered valuable information on some life history attributes of *G. legneri* which can be useful for using it as a biological control agent. The findings theoretically verified that *G. legneri* is a promising biocontrol agent against *E. ceratoniae* by showing that the parasitoid is intrinsically has the capability to suppress its host as revealed by the intrinsic rate of increase (r) comparisons. From present results it can also be concluded that different hosts had a significant effect on life history traits and also performance of *G. legneri*. Although *G. legneri* could be reared on both *E. ceratoniae* and *E. kuehniella* larvae, this parasitoid wasp performed better on carob moth. Nonetheless, as rearing of the flour moth is more cost-efficient and less strenuous compared to carob moth, this species could be a suitable alternative candidate host for mass-rearing of this parasitoid. It is noteworthy to mention that if hosts other than those studied here are considered for rearing, it is required to evaluate the performance of the parasitoid wasp on those hosts.

Abbreviations

s_{xj}	Age-stage-specific survival rate
v_{xj}	Age-stage reproductive value
e_{xj}	Age-stage life expectancy
l_x	Age-specific survival rate
f_{xj}	Age-stage-specific fecundity
m_x	Age-specific fecundity
$l_x m_x$	Age-specific maternity
R_0	Net reproductive rate
r	Intrinsic rate of increase

λ	Finite rate of increase
T	Mean generation time
APOP	Adult preoviposition period
TPOP	Total preoviposition periods
β_i	Preference for prey group *i*
e_i	The numbers of hosts remaining after the experiment
A_i	The number of prey groups *i* offered
A_s	The number of prey groups *s* offered
N_1	The number of small larvae
N_2	The number of large larvae
E_1	The number of small parasitized larvae
E_2	The number of large parasitized larvae
N_a/N_t	The proportion of parasitized hosts
N_t	The initial host density
N_a	The number of parasitized hosts
N_t	The initial number of hosts
P_0	Intercept coefficients
P_1	Linear coefficients
P_2	Quadratic coefficients
P_3	Cubic coefficients
P_t	Number of the parasitoid
T_h	Handling time
T	Total time of the experiment (24 h)
a	The attack rate
R^2	Coefficient of determination

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Author contributions
Dr. MA and Dr. HA conceived research, Dr. MA and FE conducted experiments, Dr. MA, Dr. LF and Dr. AK analyzed data and conducted statistical analyses, and Dr. LF and Dr. MA wrote the paper. All authors read and approved the manuscript.

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