Age Preference and Fitness of Microplitis manilae (Hymenoptera: Braconidae) Reared on Spodoptera exigua (Lepidoptera: Noctuidae)

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AGE PREFERENCE AND FITNESS OF *MICROPLITIS MANILAE* (HYMENOPTERA: BRACONIDAE) REARED ON *SPODOPTERA EXIGUA* (LEPIDOPTERA: NOCTUIDAE)

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Abstract

The larval parasitoid *Microplitis manilae* Ashmead (Hymenoptera: Braconidae) is a potential biological control agent of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae). To understand the preference and fitness of *M. manilae* on larval instars of *S. exigua*, we compared host choice, development, and life table parameters when different larval instars of *S. exigua* were supplied in the laboratory. Results showed that parasitism of 2nd or 3rd instar larvae was significantly higher compared with other instars. The intrinsic rate of increase (r), finite rate of increase (λ), net reproduction rate (R_0) and mean length of a generation (T) were significantly affected by which larval instars were attacked. The maximum values of r, λ, R_0 and T were observed when *M. manilae* parasitized 2nd instar *S. exigua* larvae. Therefore, we conclude that the 2nd larval instar of *S. exigua* represents the optimum host stage and suggest that 2nd larval instar of *S. exigua* will be the most suitable host stage for mass production of *M. manilae* as well as the best instar to target for biological control in the field.

Key Words: braconid, beet armyworm, endoparasite, age, development, life table

Resumen

El parasitoide larval *Microplitis manilae* Ashmead (Hymenoptera: Braconidae) es un agente de control biológico potencial de *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae). Para entender la preferencia y desempeño de *M. manilae* en los instares larvales de *S. exigua*, comparamos la selección de hospedero, el desarrollo, y los parámetros de tablas de vida en diferentes instares larvales de *S. exigua* provistos en el laboratorio. Los resultados mostraron que el parasitismo en el segundo y tercer instar larval fueron significativamente más altos que en los demás instares. La tasa intrínseca de aumento de una población (r), la tasa finita de incremento natural (λ), la tasa reproductiva neta (R_0) y el tiempo medio de una generación (T) fueron afectados significativamente por el instar larval atacado. Los valores mayores de r, λ, R_0 y T fueron observados cuando *M. manilae* parasitó larvas de segundo instar de *S. exigua*. Concluimos que las larvas de segundo instar de *S. exigua* representan el estadio óptimo del hospedero, y sugerimos que el 2 do instar de *S. exigua* es el más apropiado para producción masiva de *M. manilae,* y también el mejor instar para utilizar como blanco de control biológico en campo.

Palabras Clave: bracónido, gusano cogollero, endoparasito, edad, desarrollo, tablas de vida

The beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) originated in Southeast Asia, and is an important pest that defoliates crops causing crop losses (Lara et al. 2000; Bajpaiet al. 2006; Deshmukhe et al. 2010). Female moths lay eggs on crop leaves on which newly emerged larvae feed (Wilson 1932). The larva is the only stage that can injure crop leaves, and this stage has 5 instars (Wilson 1932). Crop plants were completely destroyed by the larvae when populations reached or exceeded a critical density (Luo et al. 2000; Bajpai et al. 2006). Pesticides have been extensively used for controlling this pest, but many negative impacts have been

widely observed and associated with this control method (Elzen et al. 1989; Foster 1989; All et al. 1996; Yeh et al. 1997; Kranthi et al. 2002).

Microplitis manilae Ashmead (Hymenoptera: Braconidae) is one of the major larval endoparasitoids of *Spodoptera* species (Rajapakse et al. 1985), and it has served as a potent biological control agent of *S. exigua* (Sun & Huang 2010; Qiu et al. 2012). It can also parasitize *S. litura* (F.) and *S. frugiperda* (Smith) larvae in the field (Rajapakse et al. 1985, 1992; Ando et al. 2006; Qiu et al. 2012). The biology, ecology and interspecific competition between *M. manilae* and other parasitoid species (e.g. *Chelonus insularis* Cresson) have been investigated (Rajapakse et al. 1985, 1992; Ando et al. 2006; Sun & Huang 2010; Qiu et al. 2012). The female parasitoid can lay an average of more than 300 eggs during her lifespan under optimum conditions (Ando et al. 2006; Qiu et al. 2012).

Previous studies suggested that the development and fecundity of parasitoids were closely related to the age of their hosts, and thus when given a choice of different host ages, female parasitoids can choose their preferred host ages (Li et al. 2006; Kant et al. 2012). The differences in host quality are often very significant among various host ages, which can influence the choice of a host based on age by the parasitoid and the subsequent development of parasitoid larvae in bodies of hosts (Li et al. 2006). A suitable host can provide enough nutrition for the development of the parasitoid offspring (Salt 1938). The selection by the parasitoid of suitable hosts is critical to the development of the parasitoid (Vinson 1990; Godfray 1994; Beckage & Gelman 2004). Fitness of the parasitoid is often assessed by survival, fecundity, development duration and sex ratio (Godfray 1994; Roitberg et al. 2001). Therefore, hosts of the optimum age can significantly facilitate mass rearing of a parasitoid. Life table parameters have been applied to evaluate the population development and fitness of an insect (Tanigoshi & McMurtry 1977; Chi & Liu 1985; Chi 1988; Zhou et al. 2010).

The present experiment focused on the choice of different *S. exigua* instars by *M. manilae* and the differences in fitness of its progeny depending on the host instar that was parasitized in laboratory bioassays. The results could offer valuable information on the best age to use for rearing *M. manilae* and for controlling *S. exigua* in the field.

Materials and Methods

Host and Parasitoid Cultures

Spodoptera exigua larvae were collected from a vegetable field in the suburb of Guangzhou City, Guangdong Province and reared on a standard artificial diet developed for Lepidotpera (Raulston & Lingren 1972) at constant temperature (26 ± 1 °C), 65 ± 5% RH and at 14:10 h L:D in the laboratory of the Department of Entomol-ogy, South China Agricultural University, Guangzhou, Guangdong Province. First through fifth *S. exigua* instars were used for these experiments.

Spodoptera exigua larvae parasitized by *M. manilae* were collected from a vegetable field in the suburb of Guangzhou City, Guangdong Province. Newly emerged female and male *M. manilae* adults were paired, and each pair was provided with *S. exigua* larvae for oviposition. For these experiments, newly emerged adult parasitoids were individually maintained in glass vials (7 × 2 cm diam) when they emerged from pupae under the same laboratory conditions as above. *Microplitis manilae* adults from the culture described above were fed 10% fresh honey solution and then paired for a 2-day mating period prior to being exposed to *S. exigua* larvae.

Preferences of *M. manilae* Adult Females for Different *S. exigua* Instars

To determine the preferences of *M. manilae* adult females for different larval instars of *S. exigua*, 2-day-old mated female parasitoids were exposed to larvae in a cage (30 × 30× 25 cm) containing 10% honey water for 24 h. This experiment was replicated 10 times. Each cage contained 10 mated female parasitoids and 150 larvae (ca. 30 of each of the 5 instars). After a 24h exposure period, the different host instars were separated and placed in a clean transparent plastic box (15.5 × 11 × 5 cm) covered with organdy cloth and provided the standard artificial diet for host larvae under the laboratory conditions. The host larvae were checked daily until they pupated or died. The host larvae that died prior to pupation were dissected to ascertain if they had been parasitized. Parasitism was confirmed by the presence in the cadaver of an egg or immature parastoid. The date and the numbers of different *S. exigua* instars parasitized were recorded.

Development of *M. manilae* Immature Stages Parasitized on Different *S. exigua* Instars

Since the parasitoid did not accept 5th *S. exigua* instars in the age preference experiment, only 1st to 4th host instars were provided for developmental studies. Each treatment included 30 mated female parasitoids, and each female was provided with 40 *S. exigua* larvae of each stadium from the 1st to the 4th instar. Host larvae and adult parasitoids were kept together for 24 h in a clean transparent plastic box covered with mesh as above, and subsequently the exposed host larvae were transferred to separate boxes and provided with artificial diet and randomly placed in environmental chambers (PQX-330A-12WM; Ningbo Laifu Experimental Equipment, Zhejiang, China) set at 25 ± 1 °C, 65 ± 5% RH and 14:10 h L:

D. The development of the *M. manilae* eggs was assessed by dissecting a batch of 30 parasitized larvae of each larval stage on each consecutive day. Another batch of 40 *S. exigua* larvae at each larval stage exposed to *M. manilae* was left intact until the parasitoid larvae had fully developed. The parasitized host larvae were collected 24 h after parasitism and each was held individually in an unsealed cuvette covered with organdy until the *M. manilae* larva crawled out of the *S. exigua* larva and pupated. The *M. manilae* pupae were monitored daily until the adults emerged. The next cohort of *S. exigua* larvae was exposed to parasitoids when all parasitoid larvae in the previous treatment had become pupae. Duration of parasitoid development and pupal weights were recorded. The experiment was repeated 10 times.

Longevities and Fecundities of *M. manilae* Adults Derived from *S. exigua* Parasitized in Different Instars

Microplitis manilae adult cohorts, derived from *S. exigua* parasitized in different instars as described above, were paired and fed 10% fresh honey solution. Two days after mating, *M. manilae* mated females were used for the experiment. Each female was provided 40 second instars of *S. exigua* from the culture described, and these 2nd instars were fed artificial diet in clean transparent mesh-covered plastic boxes held in the environmental chambers. The number of parasitoid pupae from each box were then recorded as female's fecundity. Dead parasitoids and dead host larvae were discarded.

Data Analysis

Data were checked for normality and homoscedasticity and, if needed, were arcsine, square-root or log-transformed. The developmental durations were first transformed by $log10(x+1)$, and the survival rates were first transformed by arcsine square-root when the data did not fit a normal distribution. A one-way analysis of variance (ANOVA) was conducted in comparing the overall differences of the data among treatments when significant treatment differences were indicated by a significant F-test at $P < 0.05$. The Fisher protected least significant difference (LSD) test was used as an one way-ANOVA test in comparing the means between treatments (SAS Institute 2004).

We used life table parameters to evaluate the population development of the parasitoid derived from different host instars. The computational formulas of life table parameters were described as:

$$R_0 = \Sigma \, l_x m_x \qquad (1)$$

$$\sum_{x=0} e^{-rm(x+1)} l_x m_x = 1 \qquad (2)$$

$$T = \frac{\ln R_0}{r} \qquad (3)$$

$$\lambda = \exp(r) \qquad (4)$$

where x is the age in days of parasitoid; l_x is the age-specific survival rate; m_x is age-specific fecundity; T is the mean generation time; R_0 is the net reproductive rate; r is the intrinsic rate of increase estimated by using the Euler-Lotka formula (Eq. 2) with age indexed from 0 (Goodman 1982; Chi & Liu 1985; Chi 1988); λ is the finite rate of increase. The computer program TWOSEXMSChart was used to analyze the life history raw data (Chi & Liu 1985; Chi 2005).

RESULTS

Preferences of *M. manilae* Adult Females for Different *S. exigua* Instars

There were significant differences in the *M. manilae* parasitization rates among the various *S. exigua* instars when 1st to 5th instars were exposed simultaneously to the parasitoid ($F_{4,45} = 201.82$, $P < 0.0001$). The parasitization rates of female parasitoids on 2nd and 3rd instar larvae were significantly higher than those of any other instars, and the rates on these 2 instars did not differ from each other. No parasitism was recorded in 5th instars (Fig. 1).

Development of *M. manilae* Immature Stages Parasitized on Different *S. exigua* Instars

Host larval instars affected significantly the parasitoid's development (egg: $F_{3,36} = 80.78$, $P <$
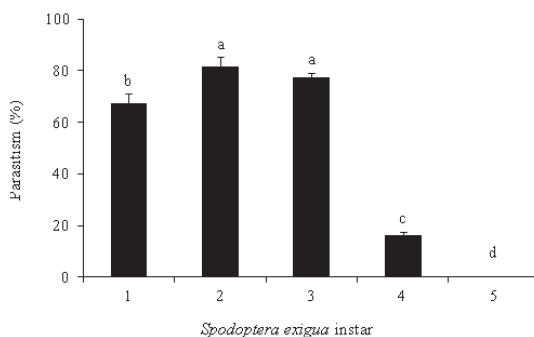

Fig. 1. Preferences of *Microplitis manilae* adult females for the different *Spodoptera exigua* instars. Shown are the average percent parasitization (± SE) by female parasitoids of 1st through 5th host larval instars when given 40 host larvae of each instar. Letters above the bars represent significant differences between treatments of the different host instars (LSD, $P < 0.05$).

Table 1. Durations of the developmental periods of immature stages of *Microplitus manilae* parasitized on different instars of *Spodoptera exigua*.

| Host instars | Developmental period (days)[a] | | | |
	Egg	Larva	Pupa	All immature stages[b]
1st instar	2.3 ± 0.1 b	4.7 ± 0.1 c	5.6 ± 0.1 b	12.6 ± 0.2 ab
2nd instar	2.7 ± 0.2 a	5.3 ± 0.1 b	5.1 ± 0.1 c	13.1 ± 0.1 a
3rd instar	1.2 ± 0.1 c	5.8 ± 0.1 a	6.1 ± 0.1 a	13.1 ± 0.1 a
4th instar	0.8 ± 0.1 d	6.0 ± 0.1 a	5.3 ± 0.1 bc	12.1 ± 0.1 b

[a]Mean ± SE. Means within the same column followed by the different letters are significantly different at $P < 0.05$ level according to ANOVA: LSD test.
[b]All immature stages refers to the developmental period of *M. manilae* from egg until adult emergence.

0.0001), (larva: $F_{3,36} = 20.68$, $P < 0.0001$), (pupa: $F_{3,36} = 11.95$, $P < 0.0001$) and (all immature stages: $F_{3,36} = 6.16$, $P = 0.0017$). The developmental duration for the entire immature stage parasitized on 4th instar host larvae was the shortest (Table 1). The particular larval instars that were parasitized also affected significantly the pupal weight of *M. manilae* ($F_{3,36} = 2.90$, $P = 0.0481$). The parasitoid achieved the lowest pupal weight when it developed in larvae that had been parasitized as 1st instars (Fig. 2).

Life Table Parameters of *M. manilae* Parasitized on Different Instars of *S. exigua*

The intrinsic rate of increase (r) ($F_{3,36} = 6.79$, $P = 0.0036$), finite rate of increase (λ) ($F_{3,36} = 6.62$, $P = 0.0041$), net reproduction rate (R_0) ($F_{3,36} = 1117.82$, $P < 0.0001$) and mean length of a generation (T) ($F_{3,36} = 4.94$, $P = 0.0129$) of *M. manilae* were significantly affected by which of the instars had been parasitized. The maximum values of r, λ, R_0 and T were achieved when 2nd instars were
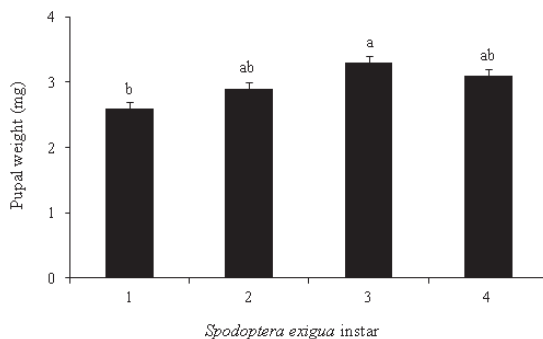

Fig. 2. The weights of *Microplitis manilae* pupae that developed on different larval instars of *Spodoptera exigua*. Shown are the average percent parasitization rates (± SE) by female parasitoids of 1st through 4th host larval instars when given 40 host larvae of each instar. Letters above the bars represent significant differences between treatments of the different host instars (LSD, $P < 0.05$).

parasitized. However, r, λ, R_0 and T of *M. manilae* all reached their minimum values when 4th instars of *S. exigua* were parasitized (Table 2).

Age-Stage Survival Rates, Age-Specific Survival Rates and Age-Specific Fecundities of *M. manilae* Parasitized on Different *S. exigua* Instars

The trend in age-stage survival rate (S_{xj}) of *M. manilae* reflected developmental rates and survivorship of the parasitoid during various stages of its life cycle in different *S. exigua* instars. The overall developmental rate of the parasitoid was the fastest when it was parasitized on the 4th instar larvae (Fig. 3).

The maximum daily fecundities of female parasitoids were 11.3, 16.0, 11.5 and 4.4 eggs per female when they parasitized the 1st, 2nd, 3rd and 4th instar larvae, respectively. The longest ovipositional period was observed when they parasitized 2nd instar larvae. The age-specific survival rate (l_x) of *M. manilae* was maintained at a high level (≥ 80%) during 25 days after adult emergence when *M. manilae* was parasitized the 2nd instars, and thereafter it decreased precipitously. Decreasing trends in age-specific survival rate were significant within 20 days after adult emergence when *M. manilae* parasitized the first through the fourth instars (Fig. 4).

Discussion

In general, host evaluation and selection of parasitoids are very important because a high-quality host can promote the fitness of the parasitoid (e.g., development and fecundity) (Vinson 1990; Godfray 1994; Beckage & Gelman 2004; Li et al. 2006; Murillo et al. 2013). In nature, most parasitoid species can accept or reject hosts for oviposition based on assessment of host qualities (Strand & Pech 1995; Harvey & Strand 2002; Li et al. 2006; Murillo et al. 2013). Therefore, a parasitoid can often select the optimum host age for improving the population quality of the offspring (Wang et al. 1984; Li et al. 2006; Murillo et al. 2013). For example, the early 2nd instar of *Tricho-*

TABLE 2. EFFECTS OF THE HOST (*SPODOPTERA EXIGUA*) INSTAR ON THE LIFE TABLE PARAMETERS OF *MICROPLITIS MANILAE*.

Host instars	Intrinsic rate of increase (r)[a] days^{-1}	Net reproduction rate (R_o)[a]	Generation time (T) (days)[a]	Finite rate of increase (λ)[a] days^{-1}
1st instar	0.238 ± 0.024 a	56.9 ± 0.4 c	17.0 ± 0.9 a	1.268 ± 0.030 a
2nd instar	0.263 ± 0.021 a	123.9 ± 1.8 a	18.4 ± 0.9 a	1.300 ± 0.028 a
3rd instar	0.236 ± 0.018 a	62.5 ± 2.1 b	17.5 ± 0.4 a	1.267 ± 0.019 a
4th instar	0.152 ± 0.008 c	9.3 ± 0.42 d	14.7 ± 0.4 c	1.164 ± 0.010 c

[a]Mean ± SE. Means followed the same letters are not statistically different (LSD, $P < 0.05$) between treatments.

plusia ni (Hübner) was considered to be the most suitable host age for the development of the larval endoparasitoid *Campoletis sonorensis* (Cameron), because this host age resulted in more parasitized larvae, a higher emergence rate, a higher female ratio of adult parasitoids, and a higher survival rate of immature parasitoids (Murillo et al. 2013). Another study (Li et al. 2006) revealed that 2nd and 3rd instars of *M. separate* provide the optimum environmental and nutritional conditions for the development of a related species, *Microplitis mediator* (Haliday). Therefore the percent parasitism and the development of the parasitoid

could be optimized when *M. separate* chose to parasitize 2nd and 3rd host instars (Li et al. 2006).

A earlier study found that *M. manilae* preferred parasitizing the 49-72 h-old larvae of *S. frugiperda*, but did not accept larvae older than 130 h (Rajapakse et al. 1985). The results of our study suggested that *M. manilae* females preferred to parasitize earlier instars of *S. exigua*, i.e., 2nd or 3rd instars, but never 5th instars. Based on our study and the study of Rajapakse et al. (1985), acceptance of *M. manilae* to hosts – except that of newly-hatched larvae – decreased with host age. Although the developmental dura-
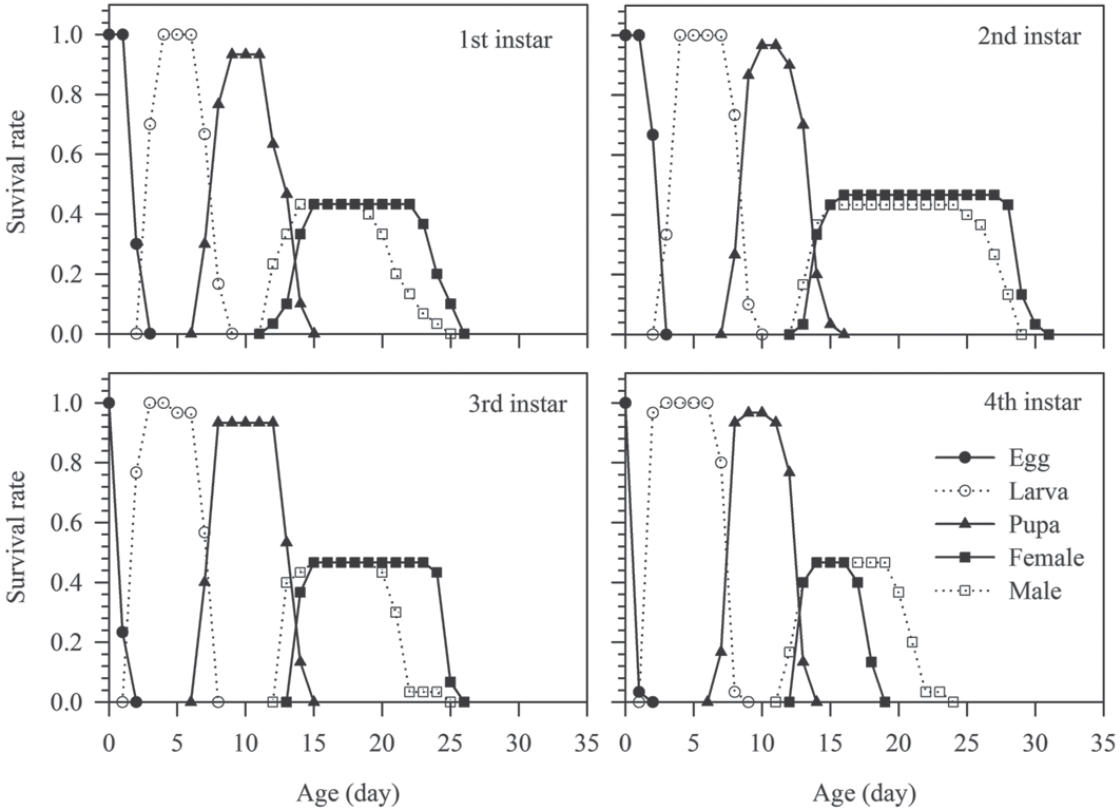

Fig. 3. Age-stage survival rate (S_{ij}) of *Microplitis manilae* that developed on different larval instars of *Spodoptera exigua*.
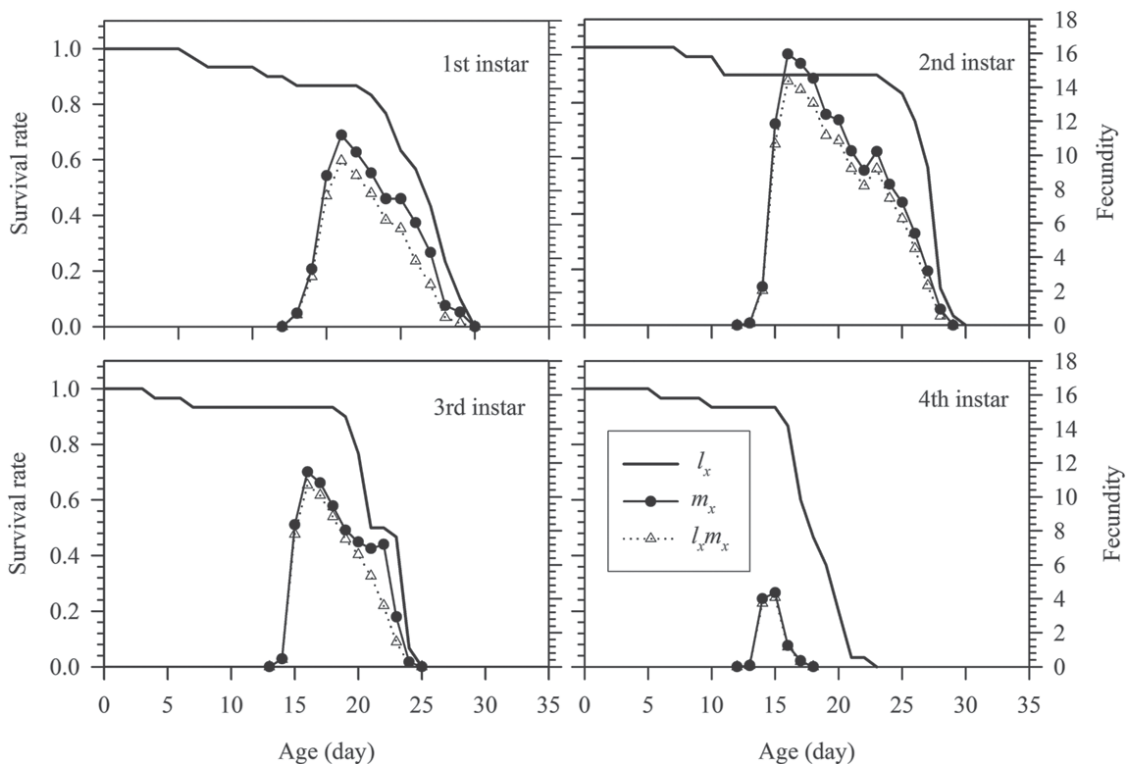
Fig. 4. Age-specific survival rate (l_x) and age-specific fecundity (m_x) of *Microplitis manilae* that developed on different larval instars of *Spodoptera exigua*.

tion for the entire immature stage of *M. manilae* parasitized on 2nd or 3rd larval *S. exigua* instars was longer than that on 1st or 4th host instars, the 2nd instar represented the most suitable host stage for high fitness of the parasitoid because on this instar the parasitoid exhibited the longer ovipositional period, the greater age-specific survival rate, and the greater pupal weight.

A previous study suggested that a larger host larva might be the best nutritional source for *M. mediator* because the highest pupal weight of the parasitoid was attained on the 4th instar (Li et al. 2006). Other studies reported that preferences for larger hosts had been observed in several parasitoid species (Elzinga et al. 2003; Harvey et al. 2004; Sandanayaka et al. 2009; Kant et al. 2012). Do larger hosts really provide better nutrition for parasitoids? In fact, the optimal host acceptance of a parasitoid may be based on a combination of host qualities, e.g., quality and quantity of nutrition, host defenses and host endocrine changes (Lawrence 1990; Li et al. 2006; Kant et al. 2012; Murillo et al. 2013). Therefore, the host age preference of parasitoid species seems consistent with the theory of optimal host stage (Vinson & Iwantsch 1980; Charnov 1982; Stephens & Krebs 1986; Islam & Copland 1997; Bennett

& Hoffmann 1998; Jervis et al. 2008). Several previous studies focused on life table parameters such as intrinsic rate of increase (r), finite rate of increase (λ), and net reproduction rate (R_0) have revealed that the population development of an insect natural enemy depends on the nature and quality of its hosts (Tanigoshi & McMurtry 1977; Mo & Liu 2006; McClay & Hughes 2007; Farhadiet al. 2011). In this study, we found that the values of r, λ, and R_0 of *M. manilae* were highest when it parasitized 2nd instars and that r, λ and R_0 values were lowest when it parasitized 4th instars. Therefore, we concluded that 2nd instar larvae are the most suitable for the development of *M. manilae*. This also implies that 2nd larval instar of *S. exigua* have the best nutritional and endocrine conditions and levels available for the parasitoid.

The selection of the optimal host instar is essential for mass rearing and field release of a parasitoid (Pu 1978; Li et al. 2006). Based on the present study, the 2nd instar of *S. exigua* is optimal for mass rearing *M. manilae* because it assures optimum selection, development and fecundity for the parasitoid reared in an insectary. In addition, if biological control of *S. exigua* relies on field release of *M. manilae*, the parasitoid

should be released when 2nd instars of the host are prevalent in the field.

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