


Demography of *Mythimna separata* (Lepidoptera: Noctuidae) at outdoor fluctuating temperatures

Bo-Liao Li^{1,2,*}, Mei-Mei Li^{1,2,*}, Tian-Tian Li^{1,2}, Jun-Xiang Wu^{1,2} 
and Xiang-Li Xu^{1,2}

Research Paper

*These two authors contributed equally to this study.

Cite this article: Li B-L, Li M-M, Li T-T, Wu J-X, Xu X-L (2021). Demography of *Mythimna separata* (Lepidoptera: Noctuidae) at outdoor fluctuating temperatures. *Bulletin of Entomological Research* **111**, 385–393. <https://doi.org/10.1017/S0007485321000110>

Received: 25 January 2019
Revised: 16 January 2021
Accepted: 5 February 2021
First published online: 14 May 2021

Keywords:

Adaptiveness; life table; migratory insect

Authors for correspondence: Jun-Xiang Wu,
Email: junxw@nwsuaf.edu.cn; Xiang-Li Xu,
Email: xuxiangli@nwsuaf.edu.cn

¹State Key Laboratory of Crop Stress Biology for Arid Areas, Northwest A&F University, No. 3 Taicheng Road, Yangling, Shaanxi 712100, China and ²College of Plant Protection, Northwest A&F University, No. 3 Taicheng Road, Yangling, Shaanxi 712100, China

Abstract

The oriental armyworm *Mythimna separata* (Walker) (Lepidoptera: Noctuidae) is a major migratory pest of cereal crops in East Asia, South Asia and Australia. To comprehensively understand the ecological tolerance of *M. separata*, we collected life table data of individuals from four consecutive generations reared under outdoor natural fluctuating temperatures from 15 April to 17 October 2018 in Yangling, Shaanxi, China. The results showed that the immature stage in early summer and summer were shorter than in spring and autumn. High mortality in late larval instar and pupal stages was observed in the summer generation. The adult pre-oviposition period in autumn was longer than the other seasons. The population in the earlier two seasons had heavier pupae and higher fecundity than the population in the latter two seasons. The intrinsic rate of increase and the finite rate of increase was the highest in early summer ($r = 0.1292 \text{ day}^{-1}$, $\lambda = 1.1391 \text{ day}^{-1}$), followed by spring ($r = 0.1102 \text{ day}^{-1}$, $\lambda = 1.1165 \text{ day}^{-1}$), and was the lowest in summer ($r = 0.0281 \text{ day}^{-1}$, $\lambda = 1.0293 \text{ day}^{-1}$). The results of this study would be useful to predict the population dynamics of *M. separata* and deepen our standing of the adaptiveness of this migratory pest in natural fluctuating ambient environments.

Introduction

The oriental armyworm *Mythimna separata* Walker (Lepidoptera: Noctuidae) is a major migratory pest in East Asia, South Asia and Australia (Chen and Bao, 1987; Chen *et al.*, 1989; Sharma *et al.*, 2002). It severely damages cereal crops and pasture grasses which yields great losses (Han and Gatehouse, 1991; Wang *et al.*, 2006). This pest has caused six nationwide outbreaks in 1970s in China (Wang *et al.*, 2006; Jiang *et al.*, 2011) and several local outbreaks in North China since 2010 (Jiang *et al.*, 2016; Xiao *et al.*, 2016). Its powerful flight capability (Chen *et al.*, 1989; Feng *et al.*, 2008), high fecundity (Li *et al.*, 1992, 2018) in the adult stage, and high feeding levels in the late larval stages (Lin, 1990) make outbreaks difficult to predict and prevent.

The oriental armyworm undertakes four large-scale long-distance-migrations in the east part of China: two northward displacements in spring and early summer, and two southward displacements in summer and autumn (Li *et al.*, 1964; Jiang *et al.*, 2011). Migration of insects requires mobilization of energy and synchronization with other life functions such as reproduction (Dingle, 2014). The substances and energy for migration in adults are accumulated in immature stages and are affected by biotic and abiotic factors during pre-adult developmental stage. Temperature is one of the most important abiotic factors that determines adaptive strategies of migratory insects (Dingle, 2014). For *M. separata*, temperature limits their geographic distribution, and they cannot overwinter in the northern part of China (north of 33°N). Escaping from high temperatures in South China in spring and summer, and from low temperatures in North China in autumn and winter, is considered to be an important pressure driver of the annual roundtrip migration of *M. separata* (Jiang *et al.*, 2011).

Life tables provide comprehensive information on the survival, development and reproduction of a population under various conditions (Yang and Chi, 2006). Previous laboratory experiments have studied the life history traits of *M. separata* under different temperatures (Li *et al.*, 1992, 2018; Jiang *et al.*, 2011). The insects showed the highest adult survival rate and fecundity at 24°C, and the fecundity decreased at 32°C (Li *et al.*, 1992). Life table and flight mill studies have suggested that moths have the highest flight potential at 27°C, but reproductive development and longevity declined compared with 24°C. Both flight potential and reproduction were suppressed at 30 and 33°C (Jiang *et al.*, 1998, 2000). The fecundity and population parameters decreased at 20 and 30°C before, after pupation, and through the

whole life cycle, compared with constant 25°C. Massive mortalities were observed in the pupal stage when eggs and larvae were reared at 30°C (Li et al., 2018). However, it was suggested that developmental times were distinct between those predicted from constant temperatures and those under alternating temperatures around the same mean or natural fluctuating temperatures (Mironidis and Savopoulou-Soultani, 2008; Carrington et al., 2013; Kjærsgaard et al., 2013); therefore, life table studies under constant temperature are not realistic enough to reflect physiology under natural fluctuating conditions. Although increasing attention has been paid to life history traits under diurnal fluctuating temperatures, rarely have outdoor experiments been undertaken due to the inherent difficulties of field experiments (Tuan et al., 2014; Chen et al., 2019).

In the current study, we collected life table data for *M. separata* reared outdoors from 15 April to 17 October 2018. We compared the demographic parameters of *M. separata* in four consecutive generations using the age-stage, two-sex life table program (Chi, 2018), which shows the stage overlaps governed by developmental rate among individuals and the contribution of males to the population. This research will provide supportive data for analyzing population fluctuations of *M. separata* under seasonally fluctuating abiotic conditions.

Materials and methods

Insect rearing

Larvae of the oriental armyworms were collected from maize fields in Xingping, Shaanxi Province, China in early July 2014. The population was successively reared in growth chambers (MGC-450HP-2, Shanghai Yiheng Science Instruments Ltd, Shanghai) at 25 ± 1°C, 75 ± 10% RH, and a photoperiod of 14:10 (L:D) (Li et al., 2018). The parent generations of larvae were reared on fresh wild oats (*Avena fatua* L.). The parent pupae were moved to outdoor in late March in 2018 in Yangling, Shaanxi, China. We collected the emerged adults, paired them, and provided them with 5% honey solution from 6 to 8 April. We used the eggs produced on 15 April for the life table studies.

Life table study

Fresh eggs laid within 24 h for life table studies were collected on 15 April, 7 June, 10 July, and 15 August in spring, early summer, summer, and autumn, respectively. Newly hatched larvae in different seasons were counted. A total of 49, 100, 98, and 89 larvae on 22 April, 10 June, 12 July, and 17 August, respectively, were selected for life table studies. The insects were reared in transparent plastic cups ($d_{bottom} = 5.0$ cm, $d_{top} = 6.5$ cm, and $h = 8.0$ cm). Cups were covered with a transparent plastic film with fine needle holes. Larval density was less than 10 per cup from first to fourth instars and less than 5 per cup for the fifth to sixth instars. All larvae were fed from 14:30 to 16:00, except for the sixth instar larvae that were additionally fed at 8:00 to ensure sufficient feeding. The mature larvae were transferred to new cups for pupation with peat soil covering the bottom. We distinguished the sex of 2 day old pupae and weighed them on a 1/10,000 analytical balance (AYU220, Shimadzu, Japan). Dark pupae that did not react to touch were considered dead. Adults were paired within 24 h after eclosion. Each pair was placed in a new plastic cup and covered with a plastic film with needle holes as were the larvae.

Cotton balls soaked in a 5% honey solution were supplied for food for the adults and folded paper for oviposition. Survival and fecundity were recorded daily until all individuals died. If a moth died after pairing, then another young adult in the same sex was recruited. The data of recruited individuals were not analyzed. Daily temperature was checked from <http://www.weather.com.cn/>.

Data analysis

The raw life data of *M. separata* were analyzed using the TWOSEX-MSChart program (Chi, 2018) based on the age-stage, two-sex life table theory (Chi and Liu, 1985; Chi, 1988). Following this program, the following parameters were calculated: age-stage-specific survival rate (s_{xj}) (where x is the age and j is the stage), age-stage-specific fecundity (f_{xj}), age-specific survival rate, age-specific fecundity (m_x), and demographic parameters including intrinsic rate of increase (r), finite rate of increase (λ), net reproduction rate (R_0), and mean generation time (T). l_x , which is the survival rate from age 0 to x , was calculated as:

$$l_x = \sum_{j=1}^{\beta} s_{xj} \quad (1)$$

where β is the number of stages. m_x , the average number of eggs produced by an individual at age x , was calculated as:

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

The net reproductive rate (R_0) was defined as the total number of offspring that an individual can produce during its lifetime and was calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (3)$$

The intrinsic rate of increase (r) was estimated using the iterative bisection method and the Euler-Lotka equation with the age indexed from 0 (Goodman, 1982):

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (4)$$

The finite rate (λ) was then calculated as:

$$\lambda = e^r \quad (5)$$

The mean generation time (T) is the length of time that a population needs to increase to R_0 -fold of its size approaching infinity and the population reaches to a stable age-stage distribution. Mean generation time was calculated as:

$$T = \frac{\ln R_0}{r} \quad (6)$$

Age-stage-specific life expectancy (e_{xj}) represents the time that an individual of age x and stage j is expected to live (Chi and Su, 2006), which was calculated as:

Table 1. Means and SE of the developmental durations, adult longevity, APOP, TPOP, fecundity, female proportion in cohort (N_f/N), and pupal weight of *M. separata* reared in four seasonal periods

Statistics	Season			
	Spring	Early summer	Middle summer	Autumn
Developmental duration (days)				
Egg	7.00 ± 0.00 a	3.00 ± 0.00 b	3.00 ± 0.00 b	3.00 ± 0.00 b
L1	2.98 ± 0.10 c	3.45 ± 0.05 b	2.83 ± 0.12 c	4.21 ± 0.12 a
L2–L4	8.44 ± 0.24 ab	6.80 ± 0.11 a	8.02 ± 0.14 b	8.75 ± 0.22 a
L5	4.55 ± 0.18 a	2.66 ± 0.10 c	2.85 ± 0.10 bc	3.25 ± 0.25 b
L6	6.52 ± 0.23 a	4.67 ± 0.09 c	5.37 ± 0.11 b	5.73 ± 0.21 b
Pre-pupa	1.64 ± 0.11 c	1.99 ± 0.02 b	2.24 ± 0.07 a	2.11 ± 0.05 a
Total larval stage	24.12 ± 0.18 a	19.41 ± 0.15 c	20.50 ± 0.22 b	23.85 ± 0.48 a
Pupa	12.69 ± 0.27 a	9.66 ± 0.14 b	7.50 ± 0.32 c	13.77 ± 0.42 a
Preadult survival rate (S_a)	0.6531 ± 0.0678 b	0.6500 ± 0.0500 a	0.1429 ± 0.0349 c	0.4944 ± 0.0532 b
Adult longevity (days)	8.59 ± 0.41 b	9.35 ± 0.34 b	4.54 ± 0.64 c	12.98 ± 0.6 a
Total longevity (days)	44.45 ± 1.78 a	33.56 ± 1.20 b	23.86 ± 0.83 c	34.24 ± 2.14 b
APOP (days)	5.43 ± 0.27 bc	5.86 ± 0.23 b	4.67 ± 0.31 c	8.39 ± 0.50 a
TPOP (days)	48.50 ± 0.29 a	37.62 ± 0.37 b	35.00 ± 0.54 c	46.58 ± 0.93 a
Fecundity (F) (eggs)	782.12 ± 94.56 a	578.91 ± 64.53 a	40.57 ± 24.98 c	294.68 ± 61.28 b
Oviposition days O_d	4.29 ± 0.28 b	5.14 ± 0.29 a	2.67 ± 0.62 c	5.89 ± 0.63 a
Female proportion (N_f/N)	0.3265 ± 0.0668 a	0.3200 ± 0.0466 a	0.0714 ± 0.0274 b	0.2472 ± 0.0459 a
N_f, N_{fr}, N_m, N_n	16, 14, 16, 17	32, 29, 33, 35	7, 3, 7, 84	22, 19, 22, 45
Pupae weight (mg)	342.5 ± 7.9 a	353.6 ± 10.9 a	238.8 ± 8.4 b	243.5 ± 6.2 b

APOP, adult pre-oviposition period; TPOP, total pre-oviposition period; L1–L6, larval instars 1–6. Means within a row followed by the same lowercase letter are not significantly different according to the paired bootstrap test at 5% level.

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{\beta} s'_{iy} \tag{7}$$

The contribution of an individual of age x and stage j to the future population (v_{xj}) (Tuan *et al.*, 2014) and was calculated as:

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-(i+1)} \sum_{y=j}^{\beta} s'_{iy} f_{iy} \tag{8}$$

The means and standard errors of stage means and demographic parameters were calculated by using the paired bootstrap method (*Bootstrap* = 100,000). Differences between treatments were calculated using the bootstrap test (Efron and Tibshirani, 1993). These procedures were carried out in the TWOSEXMSChart program (Chi, 2018).

Results

The duration in each stage of *M. separata* in four seasons is listed in table 1. The duration of the larval stage in spring and autumn was significantly longer than in the other two seasons. The duration of the pupal stage in early summer was significantly shorter than in spring and autumn, and longer than in summer (table 1). The temperature and duration of different stages of *M. separata* during outdoor life table studies are shown in fig. 1.

The age-stage-specific survival rate curves (s_{xj}) of *M. separata* reared in four consecutive seasons are shown in fig. 2. The s_{xj} represents the probability that a newly laid egg will survive to age x and stage j . Overlapping between stages was observed and resulted from variable developmental rates among individuals and stages. The curves for both sexes in spring and early summer were much higher than those in summer and autumn, reflecting the higher pre-adult survival rates in the former two seasons.

The stage-specific mortality is shown in table 2. The mortality of L1 in autumn was significantly higher than in the other seasons. From L2 to L4, the mortality in spring was significantly lower than that in the other seasons. The mortalities of L5 and L6 were extremely high in summer, over 8.5-fold and 5.2-fold greater than the mortalities of L5 and L6 in the other seasons, respectively. Pupal mortality was also the highest in summer, which was 4.4-fold, 2.1-fold, and 6.0-fold greater than that in spring, early summer and autumn, respectively. The survival rate of the total pre-adult stage was 65.31, 65.00, 14.29, and 49.44% in spring, early summer, summer, and autumn, respectively.

The longest adult longevity (13.0 days) and adult pre-oviposition period (APOP) (8.4 days) occurred in autumn, while the shortest adult longevity (4.5 days) and APOP (4.7 days) occurred in summer. The insects had the shortest total pre-oviposition period (TPOP) when reared in summer (35.0 days) and those had the longest TPOP when reared in spring (44.4 days) (table 1). Mean fecundity (F) of female adults (N_f)

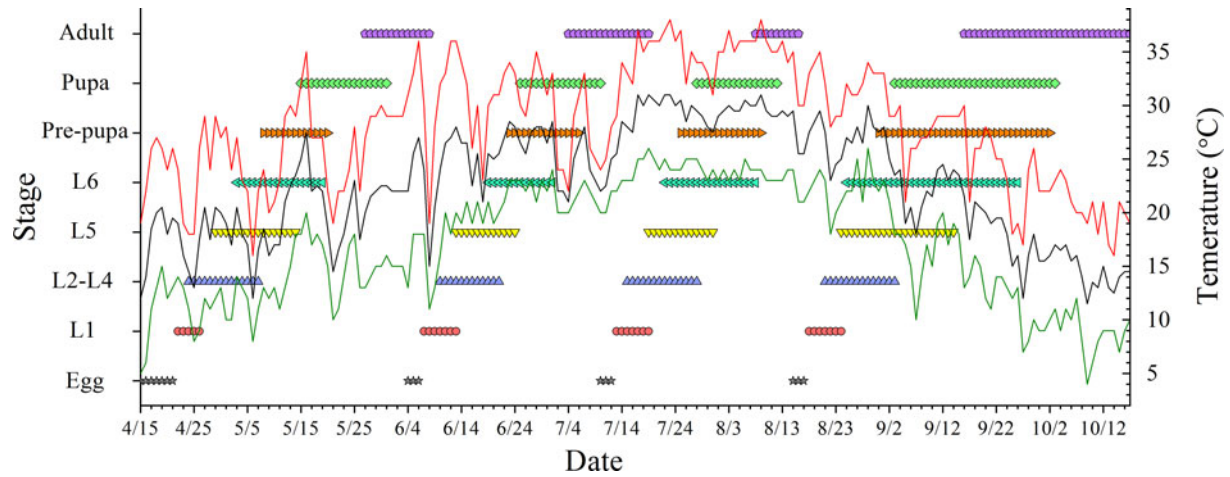


Figure 1. Temperature and different stages of *M. separata* during outdoor life table studies in 2018. The red line, black line, and dark green line represents the maximum temperature, the mean temperature, and the minimum temperature daily, respectively.

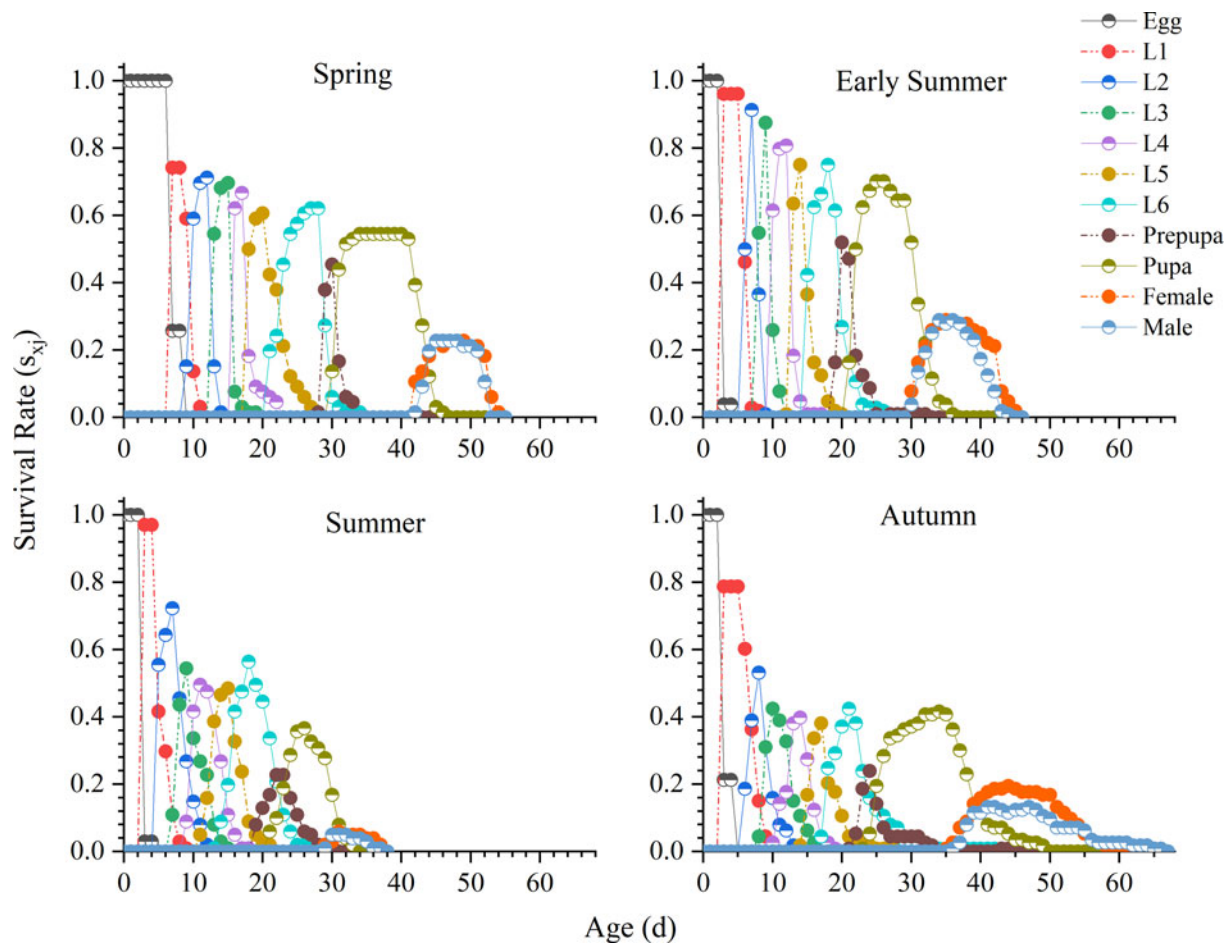


Figure 2. Age-stage-specific survival rate (s_{xj}) of *M. separata* in different seasons. L1–L6, larval instars 1–6.

was significantly different among the four generations. The lowest mean fecundity was observed in summer (40.6 eggs), and the greatest in spring (782.1 eggs). Oviposition days (O_d) in early summer (5.1 days) and autumn (5.9 days) were longer than those for the two other seasons. The mean number of eggs laid within each oviposition day (E_d) was also lowest in summer (6.5

eggs), which was only 4% of the number laid in spring (159.5 eggs). The pupae were heavier in spring (342.5 mg) and early summer (353.6 mg) than in summer (238.8 mg) and autumn (243.5 mg).

The demographic parameters are listed in table 3, including the net reproductive rate (R_0), the intrinsic rate of increase (r),

Table 2. Stage-specific mortality (\pm SE) of *M. separata* reared in four seasonal periods

Stage	Season			
	Spring	Early summer	Middle summer	Autumn
L1	0.0303 \pm 0.0210 b	0.0481 \pm 0.0209 b	0.0495 \pm 0.0215 b	0.1504 \pm 0.0337 a
L2–L4	0.0303 \pm 0.2111 b	0.1058 \pm 0.0302 a	0.1188 \pm 0.0321 a	0.1327 \pm 0.0319 a
L5	0.0151 \pm 0.0150 b	0.0096 \pm 0.0096 b	0.1287 \pm 0.0332 a	0.0176 \pm 0.0124 b
L6	0.0303 \pm 0.0211 b	0.0096 \pm 0.0096 b	0.1584 \pm 0.0363 a	0.0297 \pm 0.0151 b
Pre-pupa	0.0909 \pm 0.0355 a	0.03846 \pm 0.0188 a	0.1089 \pm 0.0310 a	0.0442 \pm 0.0193 a
Pupa	0.0606 \pm 0.0294 bc	0.1250 \pm 0.0325 b	0.2673 \pm 0.0440 a	0.0442 \pm 0.0151 c

L1–L6, first to sixth larval instars.

Means within a row followed by the same lowercase letter are not significantly different according to the paired bootstrap test at 5% significance level.

Table 3. Mean (\pm SE) of demographic parameters of *M. separata* reared in four seasonal periods: the reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ), and mean generation time (T)

Parameters	Season			
	Spring	Early summer	Middle summer	Autumn
R_0 (offspring)	255.39 \pm 60.31 a	185.25 \pm 35.92 a	2.90 \pm 1.95 c	72.84 \pm 20.14 b
r (day^{-1})	0.1102 \pm 0.0050 b	0.1292 \pm 0.0051 a	0.0281 \pm 0.0214 d	0.0888 \pm 0.0070 c
λ (day^{-1})	1.1165 \pm 0.0055 b	1.1391 \pm 0.0057 a	1.0293 \pm 0.0218 d	1.0929 \pm 0.0076 c
T (days)	50.29 \pm 0.18 a	40.10 \pm 0.36 b	36.77 \pm 0.38 c	48.29 \pm 1.18 a

Means within a row followed by the same lowercase letter are not significantly different according to the paired bootstrap test at 5% significance level.

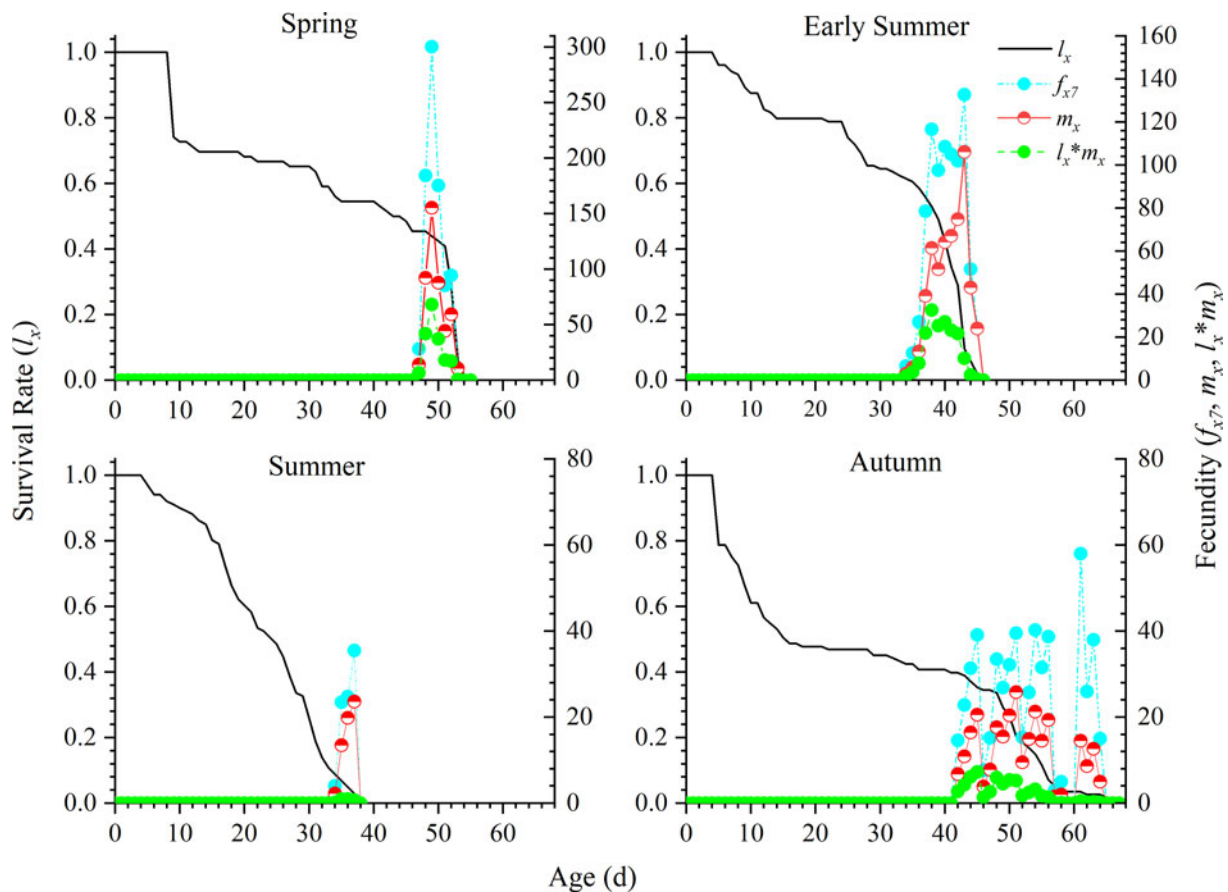


Figure 3. Age-specific survival rate (l_x), age-stage specific fecundity (f_{xT}), age-specific fecundity of total population (m_x), and age-specific maternity ($l_x m_x$) of *M. separata* in different seasons.

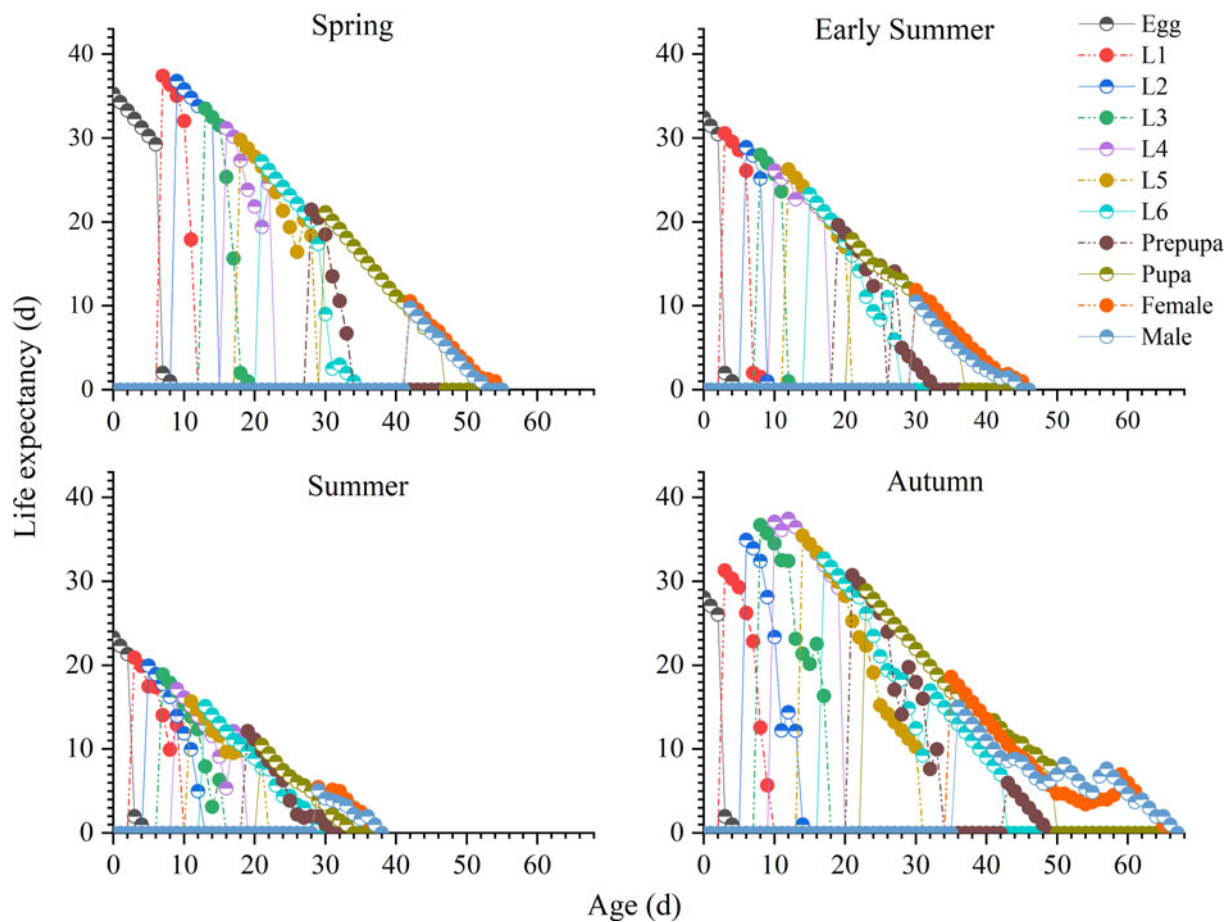


Figure 4. Life expectancy of each age-stage group of *M. separata* in different seasons. L1–L6, larval instars 1–6.

the finite rate of increase (λ), and the mean generation time (T). The R_0 values were significantly higher in spring and early summer than in the latter two seasons. The highest intrinsic rate of increase (r) and finite rate of increase (λ) appeared in early summer ($r = 0.1292 \text{ day}^{-1}$, $\lambda = 1.1391 \text{ day}^{-1}$), which was significantly higher than the other three seasons, while the lowest r and λ appeared in summer ($r = 0.0281 \text{ day}^{-1}$, $\lambda = 1.0293 \text{ day}^{-1}$). The mean generation time (T) was between the shortest (36.7 days) in summer and the longest (50.3 days) in spring.

The age-specific survival rate (l_x), female age-stage-specific fecundity (f_{x7}), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *M. separata* in the four seasons are shown in *fig. 3*. The l_x curve is a simplified version of all curves in *fig. 1*. The age-stage-specific fecundity of female adults (f_{x7}) represents the mean number of fertilized eggs laid by the female at age x (*fig. 2*). The peak f_{x7} values were 300.20, 132.75, 35.5, and 58.0 offspring in spring, early summer, summer and autumn, respectively. The highest age-specific maternity values ($l_x m_x$) were 91.9, 33.8, 1.0, and 10.0 offspring, respectively.

The age-stage specific life expectancy (e_{xj}) of *M. separata* reared in four seasons is shown in *fig. 3*, which gives the expected length of time that an individual of age x and stage j will survive. The life expectancy of a newborn egg (e_{01}) equals the mean longevity. e_{01} was 35.27, 33.56, 23.86, and 34.24 days in spring, early summer, summer, and autumn, respectively (*table 1*; *fig. 4*).

The reproductive value (v_{xj}) describes the expected contribution of an individual of age x and stage j to the future population

(Tuan *et al.*, 2014) (*fig. 5*). The reproductive curve peaks for individuals in the four seasons appeared at 49 days ($v_{49,7} = 691.8 \text{ day}^{-1}$), 37 days ($v_{37,7} = 427.4 \text{ day}^{-1}$), 35 days ($v_{35,7} = 64.3 \text{ day}^{-1}$), and 43 days ($v_{43,7} = 179.5 \text{ day}^{-1}$), respectively (*fig. 4*). The peak reproductive values were higher in spring and lowest in summer than the other seasons, whereas the peak values occurred earlier in early summer and summer than spring and autumn.

Discussion

As insects are ectothermal animals, their physiological progresses are highly sensitive to ambient temperature (Taylor, 1981; Beck, 1983). In our study, the duration of *M. separata* in the immature stage was the longest in spring when the average daily temperature was 18.8°C, and was the shortest in summer when the average daily temperature was 28.9°C. The results correspond to the trend of the developmental rates increasing with temperature within a certain temperature range. However, the duration in summer did not shorten compared with that in early summer, although the average temperature in summer (29.3°C) was much higher than the average temperature in early summer (24.9°C) during the larval stage. Similarly, a previous laboratory study showed that the larval development of *M. separata* at 33 and 35°C was slowed compared with 30°C (Jiang *et al.*, 1998). This may be attributed to the intolerance of this pest to daytime temperatures of mid-summer.

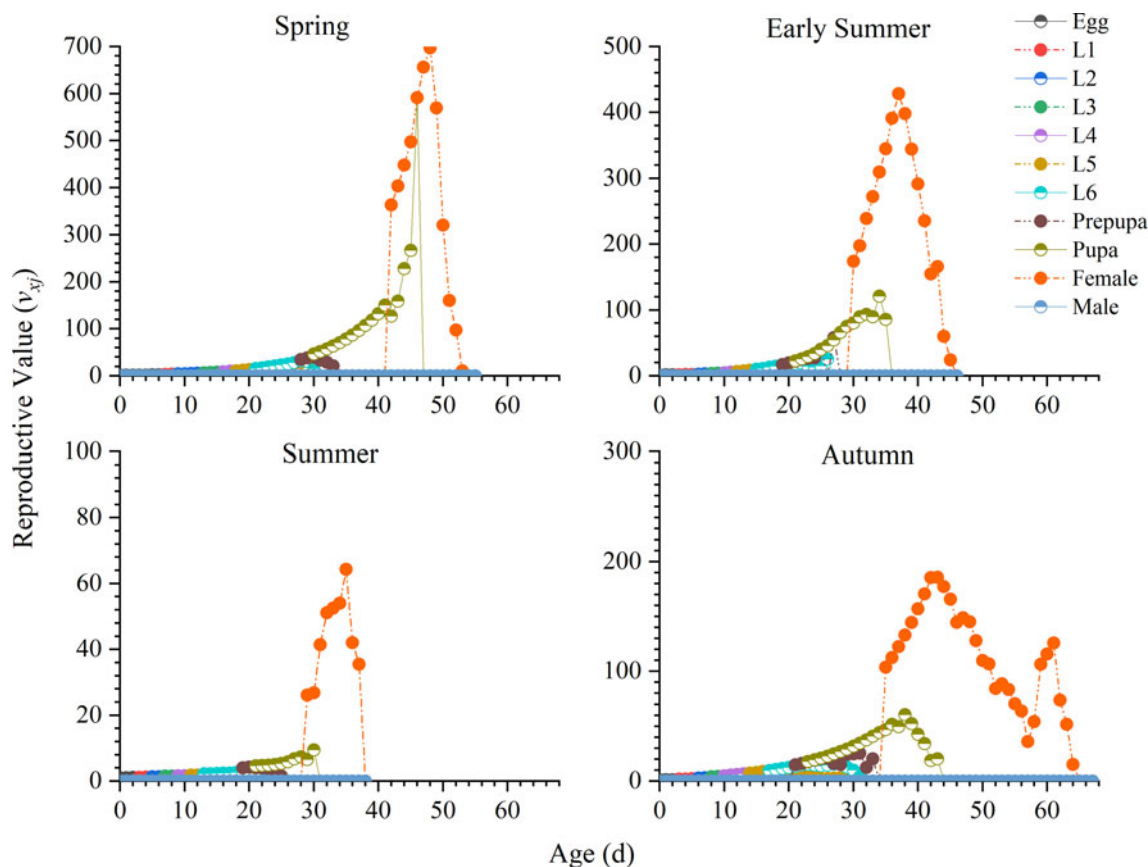


Figure 5. Reproductive value (v_{xj}) of each age-stage group of *M. separata* in different seasons. L1–L6, larval instars 1–6.

The s_{xj} curves (fig. 2) clearly characterized overlaps among stages induced by different developmental rates among individuals, which could not be observed in traditional l_x curves (fig. 2). High mortalities of *M. separata* were observed in 5th and 6th instars and the pupal stage in summer (table 2), largely owing to the high temperatures in this period. From 23 July to 9 August, the daily mean temperature was 29.6°C. In an earlier life table study of *M. separata* under different constant temperatures, the mortalities in L4–L6 instars, pre-pupal, and pupal stages at 32°C were much higher than those at 16–28°C (Li *et al.*, 1992). The results of the above two experiments indicated that high temperature has a detrimental effect on the survival of this migratory lepidopteran insect. The low survival associated with rapid development under high temperatures could be attributed to severe energy limitation, because high temperature increased the basal metabolic rate. This leaves lower resources and less energy for metamorphosis during the pupal stage when larval tissues degrade and adult tissues establish (Lee and Roh, 2010; Lemoine and Shantz, 2016).

The APOP of *M. separata* was longest in autumn due to low and decreasing ambient temperature from late September (table 1). Analogously, the APOP of *Mythimna convecta*, a closely related species in Australia, was inversely proportional to temperature (Smith, 1986). Pre-calling period of *M. (Pseudaletia) unipuncta* was extended for 11 days at 10°C compared with 25°C with a given photoperiod (Delisle and McNeil, 1987). Considering the lack of external phenotype differentiation between migratory and resident individuals in most lepidopteran migratory insects, APOP provides an indication of the

time available for migratory flight (Hill and Gatehouse, 1992; Colvin and Gatehouse, 1993). In this research, the long APOP of the autumn generation of *M. separata* reflected that these armyworms tended to delay maturation and probably undergo a long-distance migration, which coincides with the fact that this pest hardly causes damage during autumn in Shaanxi and the other Yellow-Huai river basin areas.

Pupal weight can be an indirect but easily measured index of fitness in Lepidoptera (Leuck and Perkins, 1972; Liu *et al.*, 2004; Chen *et al.*, 2019). Fecundity of insects is usually positively correlated with body size (Honěk, 1993; Nylin and Gotthard, 1998). In the current study, both the pupal mass and female fecundity in spring and early summer were significantly greater than those in summer and autumn (table 1). Smaller body size of organisms typically results from development at higher temperature (Atkinson, 1994; Kingsolver and Huey, 2008). For example, *Manduca sexta* larvae were smaller when reared at 30°C than those reared at 20 and 25°C (Davidowitz *et al.*, 2003). The wing length of *Drosophila subobscura* in the northwest USA was shortest in summer (Kari and Huey, 2000). The field captured females of *Asobara tabida*, a parasitoid of frugivorous *Drosophila* larvae, were larger at the start and at the end of the field season from early June to early October in the Netherlands (Ellers *et al.*, 2001). Although the growth rate and developmental rate were positively related to temperature, the thermal sensitivity of the development rate outperformed that of the growth rate for most ectothermal organisms (Walters and Hassall, 2006; Kingsolver and Huey, 2008). This could explain why *M. separata* pupae tended to be smaller in summer.

Three factors could determine the intrinsic rate of increase (r) according to equation 4: x , l_x , and m_x . These factors reflect the effects of the survival rate of individuals that successfully oviposited, the first reproductive age, the peak of reproduction, and the length of reproductive period (Akca et al., 2015; Liu et al., 2018). A large population increase requires a rapid development of immature stages, a high adult survival rate, and high female fecundity. In our study, although the immature stage of *M. separata* was the shortest, the extremely poor adult survival rate and fecundity resulted in the lowest r in summer. In contrast, the longest immature stage occurred in spring, but the high adult survival and fecundity resulted in the second highest r . From the above results, either one of these three factors, namely x , l_x , and m_x , could not solely, but could integrate to determine the intrinsic rate of increase. r could comprehensively reflect the effect of biotic and abiotic factors including temperature on the population fitness.

Various biotic and abiotic factors impact life tables of insect populations. Therefore, life tables based on naturally fluctuating environmental conditions are commonly more variable than those obtained from indoor controlled conditions (Tuan et al., 2014). Compared to our laboratory constant temperature life table studies (Li et al., 2018), the fitness at 25°C ($r = 0.1438 \text{ day}^{-1}$) was higher than that in early summer with almost the same mean daily temperature ($r = 0.1292 \text{ day}^{-1}$), probably because the insects under laboratory controlled conditions received better care (Tuan et al., 2014). The much lower r in summer (0.0281) than the population at 30°C (0.1024) was due to stressfully high daytime temperatures, although the summer population developed on a slightly lower mean daily temperature ($T_{\text{mean}} = 28.9^\circ\text{C}$). The maximum daily temperature reached or exceeded 35°C from 17 July to 25 July, and from 1 August to 13 August. Interestingly, the fitness of *M. separata* in spring was superior to that in autumn, when the T_{mean} of these two seasons was $\sim 20^\circ\text{C}$. It seems that temperature closer to adult stage had a more powerful effect on the reproduction of moths. This was supported by the experiment on *Plutella xylostella* under heat stress at different life stages (Zhang et al., 2015). In the current study, the spring generation experienced a stepwise warming environment, whereas the autumn generation experienced a stepwise cooling environment. The warm weather in early June was beneficial to the reproduction of *M. separata*, while the cool weather after late September delayed their maturation.

We concluded that the spring and early summer generation had a larger population growth potential, causing the larvae of early summer and summer generations to have a more serious damage potential in the Central Shaanxi Plain area. The autumn generation possessed a long APOP, which was beneficial to a long distance southward migration. This life table study under naturally fluctuating temperatures will be helpful to learn more about the population dynamics of *M. separata* in this region.

Acknowledgements. This study was supported by the National Key R&D Program of China (2017YFD0201807), and the Special Fund for Agro-scientific Research in the Public Interest of China (201403031).

References

Akca I, Ayvaz T, Yazici E, Smith CL and Chi H (2015) Demography and population projection of *Aphis fabae* (Hemiptera: Aphididae): with additional comments on life table research criteria. *Journal of Economic Entomology* **108**, 1466–1478.

- Atkinson D (1994) Temperature and organism size – a biological law for ectotherms? *Advances in Ecological Research* **3**, 1–58.
- Beck SD (1983) Insect thermoperiodism. *Annual Review of Entomology* **28**, 91–108.
- Carrington LB, Armijos MV, Lambrechts LC, Barker M and Scott TW (2013) Effects of fluctuating daily temperatures at critical thermal extremes on *Aedes aegypti* life-history traits. *PLoS One* **8**, e58824.
- Chen RL and Bao XZ (1987) Research on the migration of oriental armyworm in China and a discussion of management strategy. *International Journal of Tropical Insect Science* **8**, 571–572.
- Chen RL, Bao XZ, Drake VA, Farrow RA, Wang SY, Sun YJ and Zhai BP (1989) Radar observations of the spring migration into northeastern China of the oriental armyworm moth, *Mythimna separata*, and other insects. *Ecological Entomology* **14**, 149–162.
- Chen ZZ, Xu LX, Li LL, Wu HB and Xu YY (2019) Effects of constant and fluctuating temperature on the development of the oriental fruit moth, *Grapholita molesta* (Lepidoptera: Tortricidae). *Bulletin of Entomological Research* **109**, 212–220.
- Chi H (1988) Life-table analysis incorporating both sexes and variable development rates among individuals. *Environmental Entomology* **17**, 26–34.
- Chi H (2018) TWSEX-MSChart: a computer program for the age-stage, two-sex life table analysis. Available at <http://140.120.197.173/Ecology/Download/TWSEX.zip>
- Chi H and Liu H (1985) Two new methods for the study of insect population ecology. *Bulletin of the Institute of Zoology* **24**, 225–240.
- Chi H and Su HY (2006) Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. *Environmental Entomology* **35**, 10–21.
- Colvin J and Gatehouse AG (1993) Migration and the effect of three environmental factors on the pre-reproductive period of the cotton-bollworm moth, *Helicoverpa armigera*. *Physiological Entomology* **18**, 109–113.
- Davidowitz G, D'Amico LJ and Nijhout HF (2003) Critical weight in the development of insect body size. *Evolution & Development* **5**, 188–197.
- Delisle J and McNeil JN (1987) The combined effect of photoperiod and temperature on the calling behaviour of the true armyworm, *Pseudaletia unipuncta*. *Physiological Entomology* **12**, 157–164.
- Dingle H (2014) *Migration: The Biology of Life on the Move*. New York: Oxford University Press.
- Efron B and Tibshirani RJ (1993) *An Introduction to the Bootstrap*. New York, USA: Chapman and Hall, pp. 49–54.
- Ellers J, Bax M and van Alphen JJM (2001) Seasonal changes in female size and its relation to reproduction in the parasitoid *Asobara tabida*. *Oikos* **92**, 309–314.
- Feng HQ, Zhao XC, Wu XF, Wu B, Wu KM, Cheng DF and Guo YY (2008) Autumn migration of *Mythimna separata* (Lepidoptera: Noctuidae) over the Bohai Sea in Northern China. *Environmental Entomology* **37**, 774–781.
- Goodman D (1982) Optimal life histories, optimal notation, and the value of reproductive value. *The American Naturalist* **119**, 803–823.
- Han EN and Gatehouse AG (1991) Genetics of precalling period in the oriental armyworm, *Mythimna separata* (Walker) (Lepidoptera: Noctuidae), and implications for migration. *Evolution* **45**, 1502–1510.
- Hill JK and Gatehouse AG (1992) Effects of temperature and photoperiod on development and pre-reproductive period of the silver Y moth *Autographa gamma* (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* **82**, 335–341.
- Honěk A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* **66**, 483–492.
- Jiang XF, Liu YQ, Luo LZ and Hu Y (1998) Effects of high temperature on the immature stages of the oriental armyworm, *Mythimna separata* (Walker). *Journal of Beijing Agricultural College* **13**, 20–26.
- Jiang XF, Luo LZ and Hu Y (2000) Influences of rearing temperature on flight and reproductive capacity of adult oriental armyworm, *Mythimna separata* (Walker). *Acta Ecologica Sinica* **20**, 288–292.
- Jiang XF, Luo LZ, Zhang L, Sappington TW and Hu Y (2011) Regulation of migration in *Mythimna separata* (Walker) in China: a review integrating environmental, physiological, hormonal, genetic and molecular factors. *Environmental Entomology* **40**, 516–533.

- Jiang XF, Zhang L, Yang HX, Sappington TW, Cheng YX and Luo LZ (2016) Biocontrol of the oriental armyworm, *Mythimna separata*, by the tachinid fly *Exorista civilis* is synergized by Cry1Ab protoxin. *Scientific Reports* **6**, 26873.
- Kari JS and Huey RB (2000) Size and seasonal temperature in free-ranging *Drosophila subobscura*. *Journal of Thermal Biology* **25**, 267–272.
- Kingsolver JG and Huey RB (2008) Size, temperature, and fitness: three rules. *Evolutionary Ecology Research* **10**, 251–268.
- Kjærsgaard A, Pertoldi C, Loeschcke V and Blanckenhorn WU (2013) The effect of fluctuating temperatures during development on fitness-related traits of *Scatophaga stercoraria* (Diptera: Scathophagidae). *Environmental Entomology* **42**, 1069–1078.
- Lee KP and Roh C (2010) Temperature-by-nutrient interactions affecting growth rate in an insect ectotherm. *Entomologia Experimentalis et Applicata* **136**, 151–163.
- Lemoine NP and Shantz AA (2016) Increased temperature causes protein limitation by reducing the efficiency of nitrogen digestion in the ectothermic herbivore *Spodoptera exigua*. *Physiological Entomology* **41**, 143–151.
- Leuck DB and Perkins WD (1972) A method of estimating fall armyworm progeny reduction when evaluating control achieved by host-plant resistance. *Journal of Economic Entomology* **65**, 482–483.
- Li GB, Wang HX and Hu WX (1964) Route of the seasonal migration of the oriental armyworm moth in the eastern part of China as indicated by a three-year result of releasing and recapturing of marked moths. *Acta Phytophylacica Sinica* **3**, 101–110.
- Li XZ, Gong PY and Wu KJ (1992) Life tables of the armyworm, *Mythimna separata* (Walker), at different temperatures and its thermal requirement for development. *Acta Entomologica Sinica* **35**, 415–421.
- Li BL, Xu XL, Ji JY and Wu JX (2018) Effects of constant and stage-specific-alternating temperature on the survival, development and reproduction of the oriental armyworm, *Mythimna separata* (Walker) (Lepidoptera: Noctuidae). *Journal of Integrated Agriculture* **17**, 1545–1555.
- Liu ZD, Gong PY, Wu KJ and Li DM (2004) Effects of parental exposure to high temperature on offspring performance in the cotton bollworm, *Helicoverpa armigera* (Huebner) (Lepidoptera: Noctuidae): adaptive significance of the summer diapause. *Applied Entomology and Zoology* **39**, 373–379.
- Lin CS (1990) *Physiology and Ecology of The Oriental Armyworm Mythimna Separata* Beijing: Peking University Press.
- Liu YY, Li GY, Yang L, Chi H and Chen XS (2018) Demography and mass rearing of the medicinal blister beetle *Epicauta impressicornis* (Pic) (Coleoptera: Meloidae) at different temperatures. *Journal of Economic Entomology* **111**, 2364–2374.
- Mironidis GK and Savopoulou-Soultani M (2008) Development, survivorship, and reproduction of *Helicoverpa armigera* (Lepidoptera: Noctuidae) under constant and alternating temperatures. *Environmental Entomology* **37**, 16–28.
- Nylin S and Gotthard K (1998) Plasticity in life-history traits. *Annual Review of Entomology* **43**, 63–83.
- Sharma HC, Sullivan DJ and Bhatnagar VS (2002) Population dynamics and natural mortality factors of the oriental armyworm, *Mythimna separata* (Lepidoptera: Noctuidae), in South-Central India. *Crop Protection* **21**, 721–732.
- Smith AM (1986) Fecundity and survival of the common armyworm, *Mythimna convecta*. *Entomologia Experimentalis et Applicata* **42**, 31–37.
- Taylor F (1981) Ecology and evolution of physiological time in insects. *The American Naturalist* **117**, 1–23.
- Tuan SJ, Lee CC and Chi H (2014) Population and damage projection of *Spodoptera litura* (F.) on peanuts (*Arachis hypogaea* L.) under different conditions using the age-stage, two-sex life table. *Pest Management Science* **70**, 805–813, 1936.
- Walters RJ and Hassall M (2006) The temperature-size rule in ectotherms: may a general explanation exist after all? *The American Naturalist* **167**, 510–523.
- Wang GP, Zhang QW, Ye ZH and Luo LZ (2006) The role of nectar plants in severe outbreaks of armyworm *Mythimna separata* (Lepidoptera: Noctuidae) in China. *Bulletin of Entomological Research* **96**, 445–455.
- Xiao HJ, Fu XW, Liu YQ and Wu KM (2016) Synchronous vitellogenin expression and sexual maturation during migration are negatively correlated with juvenile hormone levels in *Mythimna separata*. *Scientific Reports* **6**, 33309.
- Yang TC and Chi H (2006) Life tables and development of *Bemisia argentifolii* (Homoptera: Aleyrodidae) at different temperatures. *Journal of Economic Entomology* **99**, 691–695.
- Zhang W, Chang XQ, Hoffmann A, Zhang S and Ma CS (2015) Impact of hot events at different developmental stages of a moth: the closer to adult stage, the less reproductive output. *Scientific Report* **5**, 10436.