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Abstract

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Keywords

Mythimna loreyi, life table, temperature, developmental threshold, effective accumulated temperature

Disciplines

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Population Projection and Development of the *Mythimna loreyi* (Lepidoptera: Noctuidae) as Affected by Temperature: Application of an Age-Stage, Two-Sex Life Table

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Abstract

The *Mythimna* (= *Leucania*) *loreyi* (Duponchel) has recently emerged as a major pest of grain crops in China. Little is known about its basic biology and ecology, making it difficult to predict its population dynamics. An age-stage, two-sex life table was constructed for this insect when reared on maize in the laboratory at five constant temperatures (18, 21, 24, 27, and 30 °C). Both the intrinsic rate of increase (r) and finite rate increase (λ) increased as temperature significantly increased and mean generation time (T) decreased significantly with increasing temperature. The highest values for net reproductive rate (R_0) and fecundity were observed at 24 °C. However, *M. loreyi* was able to develop, survive, and lay eggs at all temperatures tested (18–30 °C). Development rates at different temperatures for the egg, larval, pupal, as well as for a total preoviposition period, fit a linear equation. The lower threshold temperatures of egg, larval, pupal, preoviposition, and total preoviposition period were 8.83, 10.95, 11.67, 9.30, and 9.65 °C, respectively. And their effective accumulated temperatures were 87.64, 298.51, 208.33, 66.47, and 729.93 degree-days, respectively. This study provides insight into the temperature-based phenology and population ecology in *M. loreyi*. The results will benefit population dynamics monitoring, prediction, and management of this insect pest in the field.

Key words: *Mythimna loreyi*, life table, temperature, developmental threshold, effective accumulated temperature

The *Mythimna loreyi* (Duponchel) (often called the cosmopolitan) is a noctuid pest of grain crops found in Africa, Australia, the Near East, and the Middle East and undergoes multiple generations per year (Aloysius 2012). A variety of plants, including rice, wheat, barley, broom corn, maize, and sugarcane, are attacked by *M. loreyi*, but female moths express a definite oviposition preference for maize in Egypt (El-Sherif 1972). In Japan, *M. loreyi* has not been reported as a major pest of graminaceous crops, but it frequently occurs with a closely related species, *Mythimna separata* (Walker), which has profound negative effects on crop production (Hirai 1975). In China, *M. loreyi* has not been a major crop pest until recently. However, *M. loreyi* has begun to occur and damage plants together with *M. separata* (Guo et al. 2003), a notorious polyphagous pest of grain crops in China that annually inflicts huge crop production and

economic losses nationwide (Jiang et al. 2014a, b). The biology of *M. separata* is well documented in China (Li et al. 1964, Jiang et al. 2000). However, little is known about the ecology and biology of *M. loreyi*, for which the development of population monitoring strategies and management technologies has been extremely limited. Although the morphological characteristics of the larvae and pupae of these two armyworm species are highly similar, making it difficult to distinguish them in the field, preliminary studies and field observations have indicated that the development rate of *M. separata* is faster than that of *M. loreyi* at every stage and at every temperature between 15 and 20 °C (Hirai 1975). Therefore, population projections for the two armyworms are expected to differ in the field.

Insect population dynamics are influenced by many environmental factors, such as temperature, a major factor affecting

development, survival rate, and fecundity of insects (Broufas et al. 2009, Forster et al. 2011). Proper development of insects requires that the environment is within an optimum temperature range, because either high or low temperatures can have adverse effects on development, reproduction, and survival (Zhou et al. 2010). High temperatures suppress the development, survival, and fecundity of *Bemisia tabaci* type B (Guo et al. 2013), and similar results have been found for *Sitophilus granarius* (L.) (Mourier and Poulsen 2000). As is well known, insects at different stages require certain threshold temperatures to allow development. The completion of a certain developmental stage or an entire generation requires a particular effective accumulated temperature (Ma et al. 2008), which is hindered by temperatures that are too low. Insect developmental threshold temperatures and effective accumulated temperatures, commonly measured as degree-days, can be used to accurately predict an insect's period of occurrence and to determine the optimal timing of control (Wu et al. 2003).

Life table studies provide detailed information about the outside factors that influence insect survival, growth, development, and reproductive capacity. This information is critical to predicting population projection and appropriate timing for the prevention and control of pests (Chi and Su 2006). Life tables are also helpful in the context of insect mass-rearing (Chi and Getz 1988), and understanding the consequences of host preference on fitness (Yin et al. 2013). There are several theories and methods for constructing a life table, most notably the traditional female age-specific life table and the age-stage, two-sex life table. Unlike the former, the age-stage, two-sex life table approach accommodates variable development times among individuals, which results in overlapping stages. Furthermore, survival and fecundity can be properly manipulated, and sex ratio can be accounted for in the development of the population (Chi 1988). Projecting population growth based on an age-stage, two-sex life table can be accomplished using a computer program to simplify calculations, increase accuracy, and reduce the workload. This approach was used to study the influence of temperature on *Bradysia odoriphaga*, showing that different temperatures had different effects on population projections (Li et al. 2015). The age-stage, two-sex life table approach also has been applied to whiteflies (*Bemisia tabaci*, Jafarbeigi et al. 2014), lepidopterans (*Chrysodeixis chalcites*, Alami et al. 2014; *Spodoptera litura*, Tuan et al. 2014), thrips (*Frankliniella occidentalis*, Zhang et al. 2015), mosquitoes (*Aedes albopictus* and *Aedes aegypti*, Maimusa et al. 2016), and others.

Hirai (1975) focused on the effects of temperature and density on development of *M. loreyi* and *M. separata*, but no studies have addressed the effects of temperature on population projections for *M. loreyi*. Therefore, we built age-stage, two-sex life tables at 18, 21, 24, 27, and 30 °C under controlled conditions to obtain a comprehensive understanding of how temperature affects the population parameters of *M. loreyi*.

Materials and Methods

Insects

Larvae of *M. loreyi* were collected from Nanning City, Guangxi Province, in March 2014 and maintained under laboratory conditions at 24 ± 1 °C, $70\% \pm 5$ relative humidity (RH), and a photoperiod of 14:10 (L:D) h. Ten larvae were reared together in 700-ml glass bottles (14 cm high by 8 cm diameter) on fresh corn leaves. They pupated in sterilized soil with a moisture content of ~10–15%. When adults emerged, the moths were reared in pairs in an

insect cage (21 cm high by 9 cm diameter, 1,200 ml capacity) and provided a cotton ball soaked with 5% honey (vol/vol) solution. Folded waxed paper was placed on the bottom of the cage for egg-laying. Eggs laid on the second day of oviposition were selected for experiments. We began the experiments after five generations of laboratory rearing.

Experimental Setup

We collected waxed papers and cut them into pieces containing 30 eggs each. Three replications of 30 eggs (90 total) were placed in 700-ml glass bottles with fresh corn leaves and held in growth chambers (Jiangnan Instruments RXZ-430, Ningbo, China) at 18, 21, 24, 27, or 30 °C at 70% RH under a photoperiod of 14:10 (L:D) h. An extra set of insects were reared in parallel at each temperature to provide supplementary males for mating if needed. Egg survival rate and time to hatch in each temperature treatment were recorded. Larvae were reared in groups of 10 per bottle on fresh corn leaves from hatch to pupation. Food was replaced daily. Total developmental period from larva to pupa, and the number of surviving larvae were recorded. Pupal survival was calculated based on the number of emerging adults. Females and males that emerged on the same day from a given temperature treatment were paired and placed in the insect cages. If the number of males was less than that of females, males from the extra set run in parallel were used to ensure each female was paired. Cages were provided with wax paper for laying eggs, and 5% honey solution for adult feeding, both replaced daily. Number of eggs laid per female and adult mortality were recorded daily until all adults died.

The raw life history data of *M. loreyi* were analyzed using the age-stage, two-sex life table approach (Chi and Liu 1985, Chi 1988). For age-stage-specific survival rate (s_{xj} ; x = age, j = stage), the first stage corresponds to the egg, the second to larva, the third to pupa, the fourth to adult, and the fifth and sixth stages to female and male, respectively (Huang and Chi 2012). Female age-stage-specific fecundity (f_{xj} ; daily number of eggs produced by a female at age x and stage j), age-specific fecundity of the total population (m_x ; daily number of eggs produced by all females at age x), and age-specific survival (l_x ; probability that the newly oviposited egg will survive to age x), were calculated for each cohort from the daily record of the survival and fecundity of all individuals in the cohort. Population parameters were calculated based on s_{xj} , f_{xj} , l_x , and m_x (Huang and Chi 2012). The intrinsic rate of increase (r) was calculated using the bisection method from the Euler-Lotka equation: $\sum_{x=1}^{\infty} (e^{-rx} \sum_{j=1}^m f_{xj} s_{xj}) = 1$, with age indexed from 0 (Goodman 1982). The finite rate of increase (λ) was calculated as $\lambda = e^r$. Net reproductive rate (R_0) (total offspring produced by an individual during its lifetime) was calculated as $R_0 = \sum_{x=0}^{\infty} \sum_{j=1}^m s_{xj} f_{xj}$. Mean generation time, $T = (\ln R_0)/r$, was defined as the length of time necessary for a population to increase to R_0 -fold its population size at the stable stage distribution (Chi and Liu 1985, Yang et al. 2015). *Mythimna loreyi* population projection in the next generation can be predicted from the life table parameters using the TIMING-MSChart program (Chi 2016a).

Lower Threshold Temperature and Effective Accumulated Temperature

Data from the life table included time for all eggs to hatch, time for all larvae to develop into pupae, duration of the pupal stage, and female preoviposition period under each constant temperature. The effective accumulated temperature (K) and the lower threshold temperature (T_0) were calculated according to the method of thermal

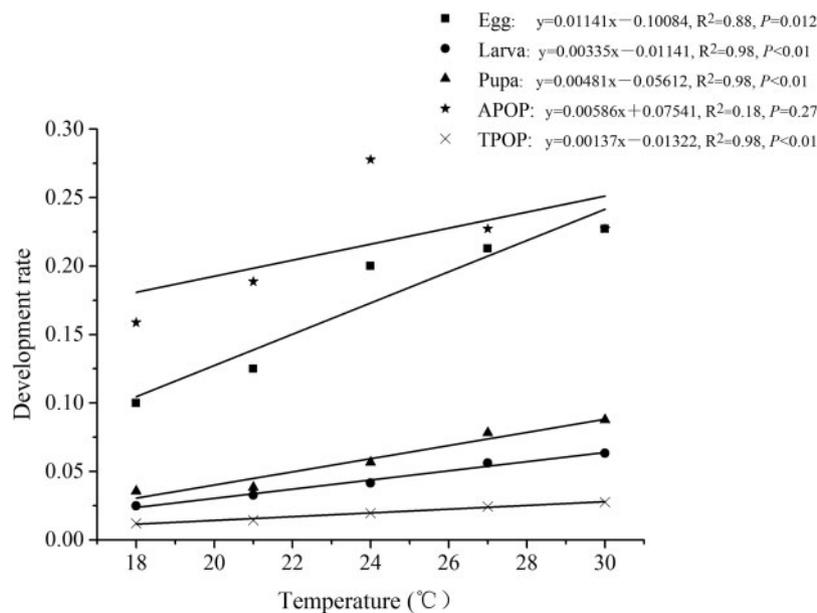
Table 1. *Mythimna loreyi* developmental durations and fecundity (mean \pm SE) at different constant rearing temperatures

Parameter	Stage; Sex	The no. of survival (<i>n</i>); Temp(°C)									
		<i>n</i>	18	<i>n</i>	21	<i>n</i>	24	<i>n</i>	27	<i>n</i>	30
Development time(d)	Egg	90	10.0 \pm 0.0a	90	8.0 \pm 0.0b	90	5.0 \pm 0.7c	90	4.7 \pm 0.8c	90	4.4 \pm 0.7c
	Larva	57	40.4 \pm 0.3a	58	30.5 \pm 0.9b	66	24.1 \pm 0.7c	60	17.8 \pm 0.9d	57	15.8 \pm 1.0e
	Pupa	44	28.1 \pm 0.9a	53	26.1 \pm 0.8b	60	17.7 \pm 1.0c	56	12.8 \pm 0.8d	45	11.4 \pm 0.5e
	APOP	23	6.3 \pm 0.8a	26	5.3 \pm 1.0b	28	3.6 \pm 0.7d	23	4.7 \pm 0.1c	20	4.4 \pm 0.4c
	TPOP	23	82.3 \pm 0.9a	26	69.3 \pm 1.0b	28	51.3 \pm 0.9c	23	41.0 \pm 0.8d	20	36.1 \pm 0.9e
Adult longevity (d)	Male	21	14.4 \pm 0.6ab	27	14.8 \pm 0.6a	29	13.8 \pm 0.2b	30	10.8 \pm 0.1c	18	10.3 \pm 0.3c
	Female	23	13.5 \pm 0.1a	26	12.9 \pm 0.2a	28	10.4 \pm 0.5b	23	9.7 \pm 0.4c	20	9.6 \pm 0.3c
Fecundity (eggs/female)	Female	23	359 \pm 44c	26	476 \pm 19b	28	633 \pm 25a	23	509 \pm 44b	20	434 \pm 25b

APOP, adult preoviposition period.

TPOP, total preoviposition period (from egg to first oviposition).

Means in the same row followed by the same lowercase letter are not significantly different (paired bootstrap test, $P < 0.05$).

**Fig. 1.** Regressions of developmental rate of *M. loreyi* at each stage on rearing temperature.

summation, which is based on the linear portion of the temperature–developmental rate relationship in Range II (Higly et al. 1986). The relationship between development rate ($1/D$, where D is development time) and temperature (t) during rearing can be represented appropriately by a straight line: $1/D = a + bt$, where a and b are regression parameters fitted to the observed data for each temperature. From this, T_0 can be calculated by setting $1/D = 0$; thus, $T_0 = -a/b$. K can be calculated by setting $1/D = 1$ and $a = 0$; thus, $K = 1/b$ (Campbell et al. 1974).

Statistical Analysis

Raw data for developmental duration, survival rate, longevity, and female daily fecundity were analyzed according to the age-stage, two-sex life table theory (Chi 1988) using the computer program, TWOSWX-MSCHART (Chi 2016b). The following parameters were calculated using the bootstrap method (Efron and Tibshirani 1993) included in the computer program TWOSWX-MSCHART: the age-stage-specific survival rate (s_{xj}), age-specific survival rate (l_x), age-stage-specific fecundity (f_{xj}), age-specific fecundity (m_x), intrinsic rate of increase (r), finite rate of increase (λ), mean generation

time (T), and net reproductive rate (R_0). Because bootstrap analysis uses random resampling, a small number of replications will generate variable means and standard errors. So we used 100,000 bootstrap iterations to reduce the variability of the results. The differences among five temperature treatments were analyzed by the paired bootstrap test (Efron and Tibshirani 1993). Linear regression was calculated using the Originpro 2015.

Results

Developmental Duration, Adult Longevity, and Fecundity

Mean duration of each stage, adult longevity, preoviposition period, generation time, and female fecundity of *M. loreyi* are shown in Table 1. According to the paired bootstrap test, developmental duration of each stage, including egg, larva, and pupa, was significantly affected by temperature. The differences were significant among the temperature treatments (Table 1). Developmental durations for the egg, larval, and pupal stages, were each shortest at

Table 2. Lower threshold temperature and effective accumulated temperatures for indicated life stages of *M. loreyi*

Stage	N	Lower threshold temperature (°C)	Effective accumulated temperature (degree-days)
Egg	450	8.83	87.64
Larva	296	10.95	298.51
Pupa	256	11.67	208.33
APOP	129	9.30	66.47
TPOP	245	9.65	729.93

30 °C. The developmental duration of each stage and adult longevity were negatively related to temperature, significantly decreasing as rearing temperature increased from 18 °C to 30 °C. In contrast, the preoviposition period was prolonged by high or low temperatures, and was shortest at 24 °C. Likewise, adults reared at 24 °C had the greatest fecundity.

Lower Threshold Temperature and Effective Accumulated Temperature

Linear regressions of developmental rates of each stage on experimental temperature were significant, except for the preoviposition

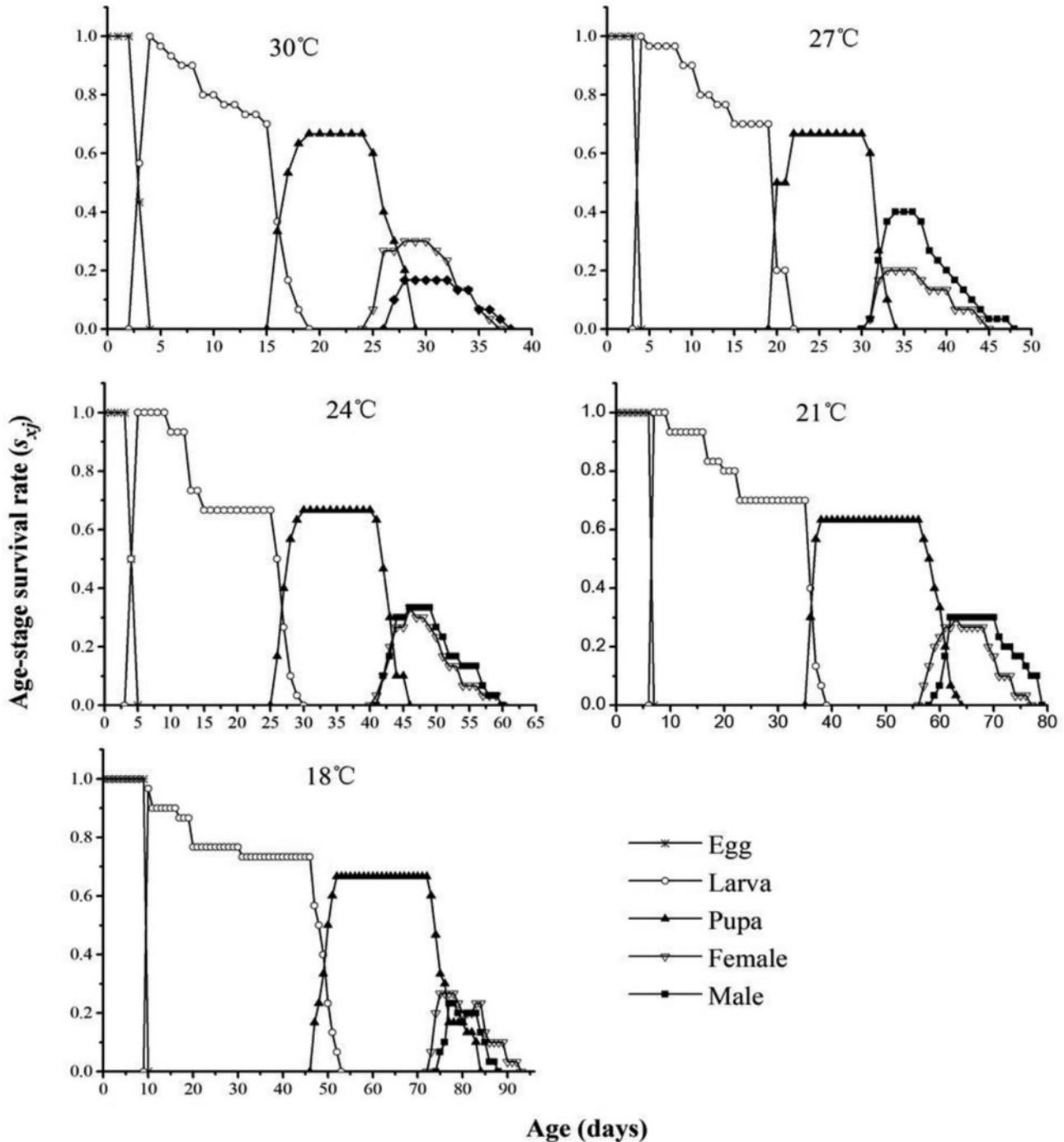


Fig. 2. Age-stage-specific survival rate (S_{xj}) of *M. loreyi* as affected by temperature.

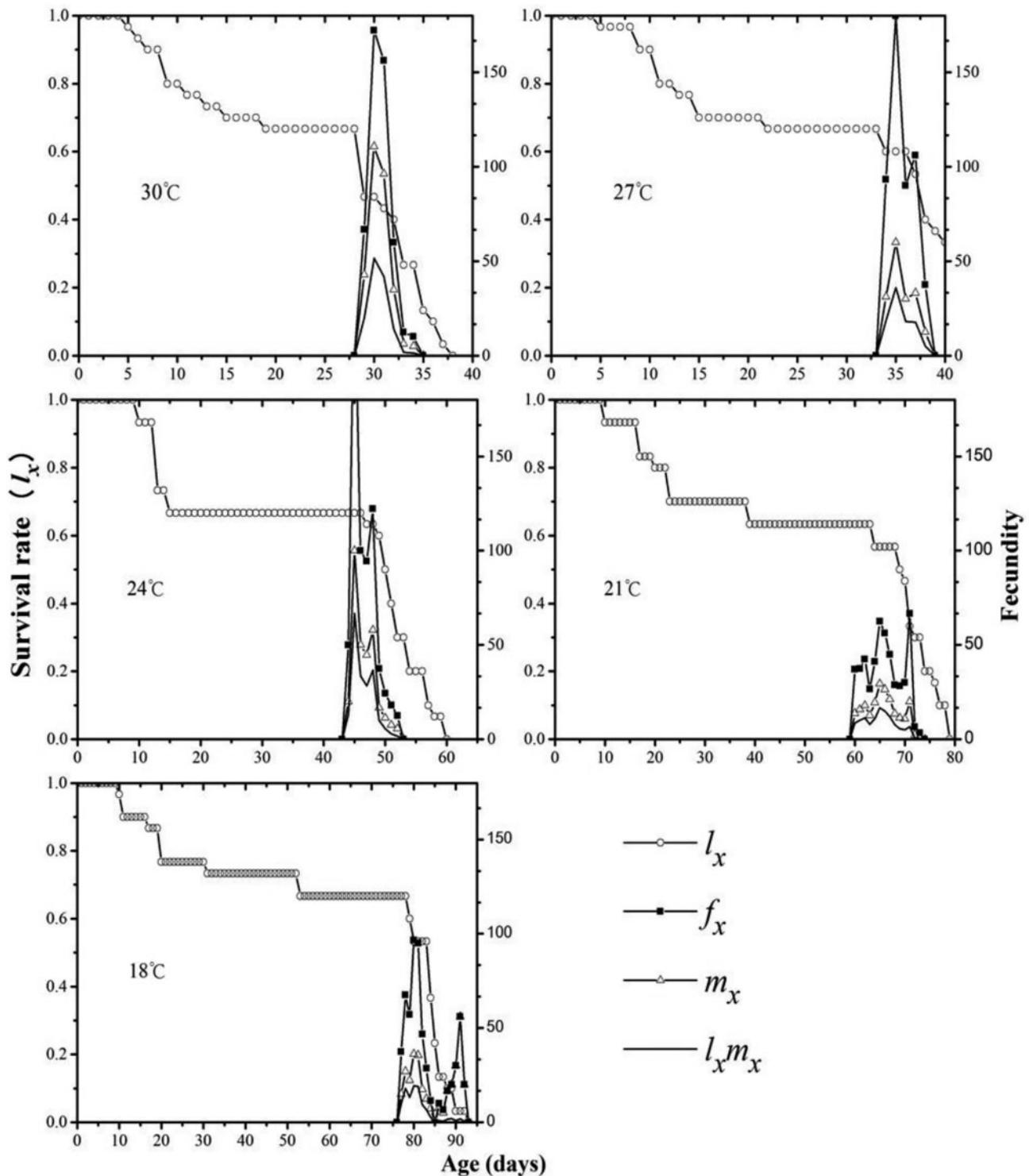


Fig. 3. Age-specific survival rate (l_x), female age-specific fecundity (f_x), age-specific fecundity of total population (m_x), and age-specific maternity ($l_x m_x$) of *M. loreyi* as affected by temperature.

period (Fig. 1), indicating good correlation between them. The developmental threshold temperature and effective accumulated temperature values of each stage were calculated (Table 2). The results demonstrated that the developmental threshold temperature of the pupa was the highest among different developmental stages, while the effective accumulated temperature of the larva was the highest, accounting for 41.3% of the generation total.

Age-Specific Survival Rate and Fecundity

The age-stage-specific survival rates (s_{xj}) of *M. loreyi* at different temperatures are shown in Fig. 2. This parameter indicates the probability that an egg will survive to age x and develop to stage j . Because the age-stage, two-sex life table takes into account variable developmental rates among individuals, there were overlaps in the survival curves between the stages. *Mythimna loreyi* was able to

Table 3. Mean generation time (T), net reproductive rate (R_0), intrinsic rate of natural increase (r), and finite rate of increase (λ) for *M. loreyi* as affected by temperature

Temp °C	Mean generation time T (d)	Net reproductive rate R_0 (offspring)	Intrinsic rate of increase r (d^{-1})	Finite rate of increase λ (d^{-1})
18	81.8 ± 0.6a	108.2 ± 20.5a	0.058 ± 0.0047c	1.06 ± 0.0049c
21	65.1 ± 0.4b	118.9 ± 32.7a	0.071 ± 0.0049c	1.08 ± 0.0053c
24	49.8 ± 0.2c	198.7 ± 34.4a	0.104 ± 0.0062b	1.11 ± 0.0068b
27	36.4 ± 0.5d	130.2 ± 27.4a	0.122 ± 0.0015b	1.13 ± 0.0013b
30	31.4 ± 0.6e	95.8 ± 18.4a	0.155 ± 0.0098a	1.17 ± 0.0011a

Means in the same row followed by the same letter are not significantly different (paired bootstrap test, $P < 0.05$).

complete its growth and development under all five temperatures tested. There was no egg mortality at any of the five temperatures tested (i.e., survival rate = 1.0). For larvae, the lowest survival rate (63.0%) was observed at 18 and 30 °C; for pupae the lowest survival rate (50.0%) was observed at 30 °C. The highest larvae and pupae survival rates (66.7% and 66.7%, respectively) occurred at 24 °C.

The age-specific survival rate (l_x), age-specific fecundity (f_x), age-specific fecundity of the total population (m_x), and age-specific maternity ($l_x m_x$) at different temperatures indicate *M. loreyi* can survive and reproduce at temperatures between 18 °C and 30 °C (Fig. 3). The l_x curve is a simplified version of S_{x_i} , as it ignores differences among individuals. At the five different temperatures, the l_x curve smoothly declined during the earlier life stages, indicating that the early mortality rate was low. The curve for the number of eggs laid per female each day (f_x) peaked at 24 °C. The highest m_x was observed at 30 °C.

Population Parameters

Table 3 shows the age-stage, two-sex life table parameters of *M. loreyi* at different temperatures. As the temperature increased from 18 °C to 30 °C, the intrinsic rate of increase (r) and the finite rate of increase (λ) also increased, while the mean generation time (T) significantly decreased. The highest value for net reproductive rate ($R_0 = 198.7$ offspring per individual) was recorded at 24 °C; this value was significantly greater than those at higher and lower temperatures, which did not differ significantly among themselves. The highest intrinsic rate of increase ($r = 0.155 d^{-1}$), the highest finite rate of increase (though not significantly greater than those for the 24 and 27 °C treatments; $\lambda = 1.17 d^{-1}$), and the shortest mean generation time ($T = 31.4 d$) were all recorded at 30 °C. These results indicate that if the population reaches the stable age-stage distribution and if there are no mortality factors other than physiological factors, the *M. loreyi* population could increase at 30 °C by ~ 1.17 times per day for an average T of $\sim 31.4 d$, with an exponential rate of increase of $0.155 d^{-1}$.

Population Projection

Based on the population life table parameters and TIMING-MSChart, Fig. 4 shows the expected population projection and population size of different stages of *M. loreyi* through the next generations. A significant difference occurred in the population growth trend of *M. loreyi* reared on different temperatures. The populations can complete two generations at 30 °C, more than one but less than two generations at 27 °C, and only one generation at 24 °C. They may not complete a single generation at 21 °C and 18 °C during a 60-d period. The population size will be greatest at 24 °C.

Discussion

Effective chemical and biological control of an insect pest requires information on its population dynamics to determine appropriate timing for pesticide application and liberation of natural enemies. The age-stage, two-sex life table approach can provide better information relevant to the timing of control measures than conventional life table studies (Chi 1990). As heterothermic poikilotherms, temperature has an important influence on the population distribution, life history, behavior, and species abundance of insects (Hoffmann et al. 2003, Cui et al. 2009). Our results using the age-stage, two-sex life table approach clarify the role of temperature in the growth, development, reproduction, and population parameters of *M. loreyi*.

Development of the immature stages of *M. loreyi* was inversely tied to temperature, presumably through direct effects of temperature on metabolism, a common phenomenon in most insects (Li and Wang 1986). Based on the developmental time to adulthood and female fecundity, the optimal range of temperatures for the growth and development of *M. loreyi* is between 24 and 30 °C. The suitable temperature range for other species is generally more narrow. For example, that for the mirid *Apolygus lucorum* is only between 24 and 27 °C (Zhao et al. 2012). The most favorable temperature range for the coccinellid *Harmonia dimidiata* (F.) is 20 to 25 °C (Kuznetsov and Pang 2002), and the adult of this species cannot reproduce at 30 °C (Yu et al. 2005). In contrast *M. loreyi* can successfully complete its growth and reproduction between a wide range of temperatures (18–30 °C), which is probably a major factor contributing to its pest status.

The intrinsic rate of increase (r) is a useful parameter describing population dynamics, which encompasses survival, development, and reproduction (Farhadia et al. 2011). In our research, the r and λ values for *M. loreyi* increased with increasing temperatures. The value of the net reproductive rate (R_0) was highest at 24 °C (Table 3). These results suggest that *M. loreyi* populations increase most rapidly at 24 °C, which may account for the peak in *M. loreyi* populations in North China that always occurs in June, July, and August when the average monthly temperature is ~ 24 °C.

A study addressing the development of *M. loreyi* in Japan found that the development of *M. loreyi* is slowest and the lower threshold temperature is lowest in the larval stage, while the effective accumulated temperature is highest (Hirai 1975). This contrasts with our results where the lowest developmental threshold temperature is in egg stage, with that of the larval stage being lower than in the pupal stage. The effective accumulated temperature from egg to adult in China (729.93 degree-days) is higher than Japan (628.2 degree-days). This indicates that the response to temperature of *M. loreyi* may differ depending on the population source. The lower threshold temperature and effective accumulated temperature are necessary to forecast development time and the emergence period under ambient temperatures, guiding decisions on appropriate measures to control *M. loreyi*. Combine with the age-stage, two-sex life table population

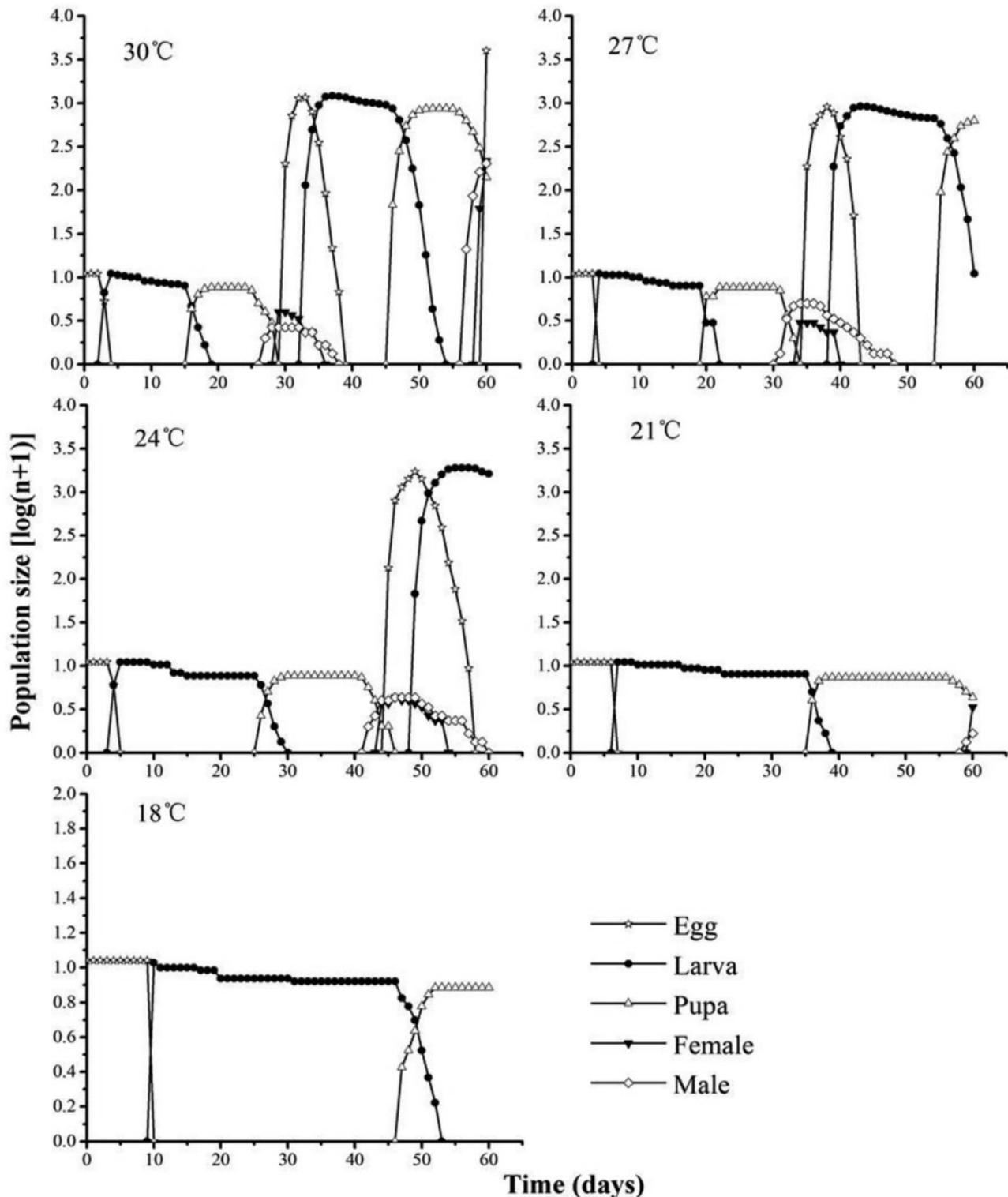


Fig. 4. Population projections over a 60-d period of *M. loreyi* reared at different temperatures, based on population parameters from an age-specific, two-sex life table analysis.

projection results, we can well know the emergence period and emergence size and give a proper prediction and controlling measure.

The effects of ecological, phenological, and environmental factors on population dynamics must be considered when managing a pest, and temperature is a key environmental factor affecting insect

population dynamics. Our experiment examined the effects of constant temperatures, but insect growth also has important relationships with food (Zhang et al. 2015), light (Tu et al. 2014), humidity (Yang et al. 2015), and fluctuating temperature (Fischer et al. 2011). For example, humidity is especially important for rain-driven dynamics of pests such as *Apolygus lucorum* (Lu and Wu 2011) and

Lygus lineolaris (Day 2009). It will be important to fully examine other key environmental variables as we attempt to build a framework for predicting population dynamics of *M. loreyi* for practical applications.

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