

Article

Impact of Temperature on Age–Stage, Two-Sex Life Table Analysis of a Chinese Population of Bean Bug, *Riptortus pedestris* (Hemiptera: Alydidae)

Xin-Yue Tian ^{1,2}, Yu Gao ¹ , Muhammad Yasir Ali ² , Xiao-Hua Li ¹, Ying-Lu Hu ¹, Wen-Bo Li ³, Zi-Jie Wang ⁴, Shu-Sen Shi ^{1,*} and Jin-Ping Zhang ^{2,*} 

- ¹ Key Laboratory of Soybean Disease and Pest Control (Ministry of Agriculture and Rural Affairs), College of Plant Protection, Jilin Agricultural University, Changchun 130118, China
- ² MARA-CABI Joint Laboratory for Biosafety, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, China
- ³ College of Biological Resource and Food Engineering, Qujing Normal University, Qujing 655011, China
- ⁴ Jiamusi Branch of Heilongjiang Academy of Agricultural Sciences, Jiamusi 154007, China
- * Correspondence: sss-63@263.net (S.-S.S.); j.zhang@cabi.org (J.-P.Z.); Tel.: +86-431-84533387 (S.-S.S.); +86-010-62898289 (J.-P.Z.)

Abstract: *Riptortus pedestris* Fabricius (Hemiptera: Alydidae) is an economically important pest of soybean that causes serious damage in the Huang-Huai-Hai region of China, which is the main soybean-producing area. However, the basic biological and ecological attributes of the Chinese populations of *R. pedestris* are still unknown. Temperature is a critical factor influencing insect population dynamics; therefore, understanding the effects of temperature on individual development and population growth of *R. pedestris* is helpful to forecast the pest's phenology as part of its control. In this study, we determined age–stage, two-sex life table parameters of *R. pedestris* at five constant temperatures (19, 22, 25, 28, and 31 °C) under laboratory conditions. The results demonstrated that the developmental period, preadult time, adult longevity, adult preoviposition period (APOP), and total preoviposition period (TPOP) were all significantly shortened when the temperature increased from 19 to 31 °C. The developmental time from egg to adult was 55.00 d at 19 °C but decreased to 24.43 d at 31 °C. The developmental threshold temperatures of the egg, nymph, female adult, male adult, and total generation (from egg to adult death) were 13.31, 10.91, 16.21, 17.13, and 13.44 °C, respectively, and the corresponding stage-specific day degree totals were 95.91, 260.51, 114.22, 147.35, and 582.04. The net reproductive rate ($R_0 = 2.36$ offspring), fecundity (58.00 ± 28.59 eggs), and population trend index (I) (7.89) were found to be optimal at 25 °C. These results could be useful for predicting the population dynamics of *R. pedestris* and improving the management of this pest in field crops.

Keywords: developmental threshold temperature; effective accumulative temperature; constant temperature; fecundity; life table; *Riptortus pedestris*



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1. Introduction

The bean bug, *Riptortus pedestris* Fabricius (Hemiptera: Alydidae), is a serious pest worldwide that is mainly distributed in East and Southeast Asia, including China [1], Korea [2], Japan [3], and India [4]. The nymphs and adults of *R. pedestris* use their piercing sucking mouth parts to suck sap from pods of host plants, resulting in stunted, weak, deflated, or deformed pods [5]. *Riptortus pedestris* has a wide host range, mainly feeding on Chinese milk vetch, *Astragalus sinicus* L. (Fabales: Fabaceae); cowpea, *Vigna unguiculata* L. (Fabales: Fabaceae); hairy vetch, *Vicia villosa* Roth (Fabales: Fabaceae); kidney bean, *Phaseolus vulgaris* L. (Fabales: Fabaceae); mung bean, *Vigna radiata* L. (Fabales: Fabaceae); red clover, *Trifolium pretense* L. (Fabales: Fabaceae); sesame, *Sesamum indicum* L. (Scrophulariales: Pedaliaceae); soybean, *Glycine max* L. (Fabales: Fabaceae); and certain other plants

of the Fabaceae, Pedaliaceae, Poaceae, and Cucurbitaceae [6]. In addition, it can damage fruit trees such as apples, *Malus pumila* Miller (Rosales: Rosaceae) and sweet persimmon, *Diospyros kaki* L.f. (Ebenales: Ebenaceae). The damage caused by *R. pedestris* in soybean is most severe from middle pod-elongation to early seed-thickening. When damage occurs as this stage, the proportion of empty pods or pods with undeveloped seeds increases. In addition, the feeding of this bug can transmit pathogens to soybean, causing severe losses [5].

In China, bean bug damages soybean in more than 20 provinces [7], including a recent outbreak in the Huang-Huai-Hai region, which is the main soybean-production area in [8], it is the alluvial plain of the Yellow River, Huai River, and Hai River. In 2010, in China, more than half of all soybean fields suffered some degree of damage from *R. pedestris*. Feeding of *R. pedestris* results in pod abortion and feeding in the soybean harvest period on leaves and stems causes the leaves of soybean to remain green (called the “stay green” syndrome) [9]. The “stay green” syndrome has been observed on many soybean cultivars [10], including Zhou dou 16, which was severely damaged in the Huang-Huai-Hai region (Leihe city, Henan Province) in 2010, with a yield reduction of 50–100%, while on other cultivars, the yield reduction was about 20% [10]. Similar damage levels have been reported by Hua et al. [11], with light infestations causing 20% to 40% reduction in yield, while in heavy infestations, losses may be up to 50% or even total crop loss. Besides such direct impacts on soybean production, summer soybean breeding fields in the Huang-Huai-Hai region were also destroyed by *R. pedestris* [9], harming the plant breeding program.

Many studies have demonstrated that examining the effects of abiotic factors, such as temperature, can improve our understanding of the population dynamics of pest insects [12,13]. Temperature is a critical factor influencing the rate of insect growth and development [14], and temperatures lower or higher than the optimum can have adverse effects [14,15]. High temperatures reduce the development, survival, longevity, and fecundity of insects [15]. Various genes are mobilized under high temperatures (38 °C) as a defense against heat stress [16]. Low temperatures hinder insect population growth because each life stage requires a minimal threshold temperature for development, and an entire generation requires sufficient effective accumulated heat, commonly measured as degree-days [17], to complete development. Ahn et al. reported that the Korean *R. pedestris* population can develop successfully (egg-to-adult female) over a range from 17.9 °C to 36.1 °C [18]. Chen et al. reported that the Chinese population failed to complete its development at 16 °C and could not lay eggs at 32 °C [19]. These studies suggest that temperatures above 16 °C and below 32 °C are potentially suitable for the development and fecundity of *R. pedestris* and should be assessed to determine the exact developmental lower threshold temperature and the number of degree-days required for complete development. This information will contribute to risk analyses, as well as forecasting and management strategies for managing pest levels [20].

Life tables are a useful tool for better understanding and analyzing insect population dynamics, making predictions and formulating integrated pest management plans [21]. Two-sex life tables incorporate differences between the sexes and account for variation in the developmental rates among individuals and life stages in a given population of an insect species [22]. Although a Korean population of *R. pedestris* has been studied and a life table constructed based on fluctuating temperatures [23], this has not been done for the Chinese populations. In this study, age-stage, two-sex life tables were constructed based on biological parameters of *R. pedestris* in China under five constant temperatures (19, 22, 25, 28, and 31 °C).

2. Materials and Methods

2.1. Host Plant Production and Insect Rearing

Adults of *R. pedestris* were collected from Cangzhou, Hebei province, China (43°48′47″ N, 125°25′4″ E) in 2019 and reared on soybean (var. Jinong 38) plants having six fully developed leaves. Plants were grown in flowerpots (diameter = 28 cm; depth = 20 cm) filled with

soil, which was collected at teaching station of Jilin Agricultural University (43°48′47″ N, 125°25′4″ E), and they were watered as needed. The *R. pedestris* cultures and soybean plants were held at 25 ± 1 °C, $80 \pm 5\%$ r.h. and 16 h:8 h L:D photoperiod. Approximately 5 generations of the bean bug had been reared before the beginning of this experiment on temperature. All experiments and rearing of the material was done at Jilin Agricultural University, Changchun, China.

2.2. Experimental Setup

Single, newly laid eggs of *R. pedestris* were placed individually in Petri dishes (dia = 5 cm) on moistened filter paper, and the dishes were held in artificial climate chambers at one of five constant temperatures (19, 22, 25, 28, and 31 °C). Eggs were checked daily until hatched. One hundred eggs were tested per temperature. After emerging from the egg, first instar nymphs were transferred individually to 50 mL centrifuge tubes where they were observed daily for molting, based on presence of exuviae. Bugs were reared on moistened soybean seeds, which soaked in water for 48 h before use, and then transferred into bottomless tubes (5 mL, one soybean seed per tube), along with a moistened plug of cotton to maintain humidity. These hydroponic seed holders were then placed inside the tubes and used to feed the nymphs during the experimental time period (Figure 1). The rearing tubes and their seed-holding apparatus were replaced every 24 h. We checked for molting events every day until the bug reached the adult stage. Same-day, newly emerged male and female adults were paired and transferred into the same test tubes as used in the above-mentioned nymphal development test. For each female, the number of eggs laid was recorded daily until the female died.

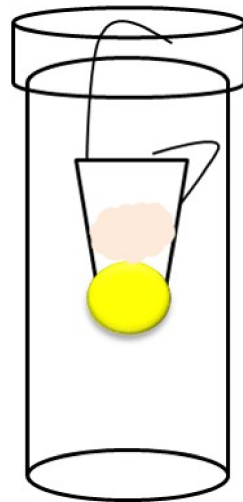


Figure 1. Insect rearing device used in the study, pink area is the moistened cotton to keep the soybean seed humidity, the yellow circle is the moistened soybean seed for *R. pedestris* feeding.

2.3. Estimation of Developmental Threshold Temperature and Effective Accumulated Temperature

The developmental threshold temperature (C) and the effective accumulated temperature (K) required for the total development of each developmental stage were calculated by the method adapted by Li and Wang [24] as follows:

$$C = \frac{\sum_{i=1}^n T_i D_i^2 - \bar{D} \sum_{i=1}^n T_i D_i}{\sum_{i=1}^n D_i^2 - n \bar{D}^2} \quad (1)$$

$$K = \frac{1}{n} \sum_{i=1}^n K_i \quad (2)$$

where T_i = exposure temperature; D_i = development rate at T_i ; \bar{D} = development rate at T_i ; K_i = effective accumulative temperature at the developmental threshold temperature.

2.4. Estimation of Population Trend Index

The population trend index (I) was determined based on the data derived from the life table using following equation [25].

$$\text{Population trend index } (I) = N_1/N_0 \quad (3)$$

where N_1 = the number of eggs after one generation; N_0 = the number of eggs at contemporary initiation.

When $I > 1$, the size of the next generation is higher than that of the previous one, while $I < 1$ means the next generation will be smaller than the previous one, and when $I = 1$, it means that the population density remains the same number between generations.

Number of eggs expected in the following generation = Adult \times Proportion female \times Number of eggs laid per female

2.5. Statistical Analysis

The developmental period, longevity, fecundity, developmental threshold, effective accumulated temperature, population parameters, and life table parameters of *R. pedestris* reared at different temperatures were analyzed by one-way ANOVA. All statistical analyses were carried out with the SPSS 21.0 software package.

All life table data for *R. pedestris* were analyzed using the TWOSEX—MSChart program [26]. Given that bootstrap analysis uses random resampling, it was necessary to reduce the error values. Therefore, a paired bootstrap test (100,000 runs) was employed to assess the variances and standard errors [27]. Sigmaplot v. 12.0 software was used to make the figures and graphs.

Only eggs that successfully hatched were used to calculate and analyze the life table parameters when calculating the developmental period of each stage, survival rate, and female fertility [28]. The age–stage-specific survival rate (s_{xj} , where x = age and j = stage), age-specific survival rate (l_x), age–stage-specific fecundity (f_{xj}), and age-specific fecundity (m_x), as well as the population parameters including net reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ), and mean generation time (T) were calculated according to Chi and Liu [29] and Chi [30] using the following equations:

$$l_x = \sum_{j=1}^{\beta} s_{xj} \quad (4)$$

$$m_x = \frac{\sum_{j=1}^{\beta} s_{xj} f_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \quad (5)$$

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (6)$$

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (7)$$

$$\Lambda = e^r \quad (8)$$

$$T = \frac{\ln(R_0)}{r} \quad (9)$$

where β is the number of life stages. The survival rate (s_{xj}) is defined as the probability that a newly laid egg will survive to age x and stage j , and fecundity (f_{xj}) is the number of hatched eggs produced by a female adult at age x . Age-specific fecundity (m_x) is calculated using data from individuals of different stages at age x . The net reproductive rate (R_0) is defined

as the total number of offspring that an individual can produce during its lifetime, whereas the intrinsic rate of increase (r) is calculated using the Euler–Lotka formula with age indexed from day “0” [31]. The mean generation time (T) represents the period that a population requires to undergo an R_0 -fold increase of its original size as time approaches infinity and the population growth rate stabilizes at the intrinsic rate of increase. Owing to the variable development rates in many insect populations, the overlapping of stages in their life history occurs in which individuals of the same age occur in different developmental stages [29]. The age–stage-specific life expectancy (e_{xj}), which is the length of time an individual of age x and stage j is expected to live, was calculated as follows:

$$e_{xj} = \sum_{i=x}^n \sum_{y=j}^m s'_{ij} \quad (10)$$

where e_{xj} is the probability that an individual of age x and stage y will survive to age i and stage j , which is calculated by assuming $s'_{ij} = 1$. The age–stage reproductive value (v_{xj}) is the contribution of an individual of age x and stage y to the future population, and is calculated as follows [32]:

$$v_{xj} = \frac{e^{r(x+1)}}{S_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^k S'_{iy} f_{iy} \quad (11)$$

3. Results

3.1. Developmental Period, Longevity and Fecundity of *R. pedestris* on Different Temperature

Egg, nymph, and adult developmental periods were significantly reduced as the temperature increased (all p value < 0.05). The development time (from egg to adult) was longest (55.00 ± 3.66 d) at 19°C and shortest (24.43 ± 0.98 d) at 31°C . As temperatures increased from 19°C to 31°C , longevity of both males and females decreased (females: from 95.50 ± 24.50 to $\sim 27.50 \pm 4.50$; males: from 114.50 ± 5.50 to $\sim 31.80 \pm 2.44$). Likewise, both the adult preoviposition period (APOP: the time period from adult emerged to first reproduction) and the total preoviposition period (TPOP: the time period from birth to first reproduction) decreased as temperature increased. The longest APOP and TPOP periods were at 19°C (32.00 ± 0.09 d and 80.00 ± 0.29 d), while the shortest values for these parameters were at 31°C (4.00 ± 0.34 d and 24.00 ± 0.82 d). Fecundity was highest at 25°C (58.00 ± 28.59 eggs), followed by 22°C (45.00 ± 15.36 eggs) (Table 1).

Table 1. Developmental periods of *Riptortus pedestris* reared at different temperatures.

Developmental Stage	Developmental Period (Days)				
	19 °C	22 °C	25 °C	28 °C	31 °C
Egg	17.25 ± 0.11 a	11.03 ± 0.02 b	8.63 ± 0.06 c	5.93 ± 0.04 d	5.10 ± 0.04 d
First instar	3.78 ± 0.08 a	3.04 ± 0.08 a	2.43 ± 0.08 b	1.93 ± 0.05 c	1.39 ± 0.06 c
Second instar	4.70 ± 0.36 a	4.43 ± 0.20 a	3.34 ± 0.20 a	2.26 ± 0.25 b	2.17 ± 0.18 b
Third instar	5.79 ± 0.54 a	5.33 ± 0.40 a	3.51 ± 0.24 a	3.23 ± 0.37 b	2.67 ± 0.31 b
Fourth instar	9.78 ± 0.74 a	6.93 ± 0.58 b	5.83 ± 0.27 b	4.17 ± 0.38 c	4.53 ± 0.23 c
Fifth instar	16.50 ± 2.05 a	11.67 ± 0.97 b	8.89 ± 0.56 b	6.90 ± 0.64 c	6.57 ± 0.41 c
Egg to adult	55.00 ± 3.66 a	42.44 ± 1.34 b	34.53 ± 0.67 c	25.40 ± 0.91 d	24.43 ± 0.98 d
Female longevity	95.50 ± 24.50 a	64.00 ± 8.33 b	51.73 ± 5.38 c	33.83 ± 3.25 d	27.50 ± 4.50 e
Male longevity	114.50 ± 5.50 a	64.83 ± 8.91 b	55.38 ± 6.43 c	50.50 ± 4.91 d	31.80 ± 2.44 e
APOP	32.00 ± 0.09 a	8.00 ± 0.71 b	7.50 ± 0.31 c	5.00 ± 0.05 d	4.00 ± 0.34 e
TPOP	80.00 ± 0.29 a	46.00 ± 0.70 b	43.30 ± 1.35 c	30.00 ± 0.07 d	24.00 ± 0.82 e
Fecundity	24.00 ± 11.83 d	45.00 ± 15.36 b	58.00 ± 28.59 a	30.00 ± 9.77 c	23.00 ± 11.09 d

Data are presented as mean ± SE. Different small letters in the same row indicate significant differences at $p < 0.05$. SEs were estimated by 100,000 bootstrap resampling.

3.2. Developmental Threshold and Effective Accumulated Temperature

The developmental threshold temperature (C) and effective accumulated temperature (K) of *R. pedestris* for one generation were 13.44 ± 0.05 °C and 582.04 ± 0.05 degree-days, respectively. The developmental threshold temperatures of the life stages were significantly different ($F = 626.53$, $df = 9$, $p < 0.05$), and were 13.31 ± 0.00 , 10.91 ± 0.35 , 16.21 ± 0.13 , and 17.13 ± 0.42 °C, for the egg, nymph, female adult, and male adult stages, respectively. The effective accumulated temperature was significantly different among life stages ($F = 546.33$, $df = 9$, $p < 0.05$). The effective accumulated temperatures (= number of day degrees required for complete development) of the egg, nymph, female, and male adult stages were 95.91 ± 0.07 , 260.51 ± 1.83 , 114.22 ± 2.35 , and 147.35 ± 5.79 degree-days, respectively. The effective accumulated temperature was lowest for the first instar (29.78 ± 0.44 degree-days), while it was highest for the adult male (147.35 ± 5.79 degree-days) (Table 2).

Table 2. Developmental threshold and effective accumulative temperature of *Riptortus pedestris*.

Developmental Stage	Developmental Threshold Temperature (°C)	Effective Accumulative Temperature (Degree-Days)	Coefficient of Variation (cv)
Egg	13.31 ± 0.00 b	95.91 ± 0.07 ef	0.06 ± 0.00 e
First instar	11.74 ± 0.21 bc	29.78 ± 0.44 h	0.08 ± 0.01 d
Second instar	11.61 ± 0.60 bc	40.93 ± 2.38 gh	0.12 ± 0.06 c
Third instar	10.43 ± 1.36 c	54.83 ± 6.82 g	0.09 ± 0.03 d
Fourth instar	10.57 ± 0.27 bc	82.20 ± 1.64 f	0.09 ± 0.00 d
Fifth instar	11.78 ± 0.23 bc	118.82 ± 1.69 d	0.04 ± 0.01 e
Nymph	10.91 ± 0.35 bc	260.51 ± 1.83 b	0.12 ± 0.05 c
Female adult	16.21 ± 0.13 a	114.22 ± 2.35 de	0.18 ± 0.02 b
Male adult	17.13 ± 0.42 a	147.35 ± 5.79 c	0.47 ± 0.05 a
Generation	13.44 ± 0.05 b	582.04 ± 0.05 a	0.04 ± 0.05 e

Data are presented as mean \pm SE. Different small letters in the same row indicate significant differences at $p < 0.05$. SEs were estimated by 100,000 bootstrap resampling.

3.3. Age–Stage-Specific Survival Rate

Riptortus pedestris successfully developed from the egg to the adult stage at all tested temperatures (19–31 °C). The developmental period of female bugs was shorter than for males at all tested temperatures (from 19 and 31 °C; female: 95.50 ± 24.50 and 27.50 ± 4.50 ; males: 114.50 ± 5.50 and 31.80 ± 2.44). Survival rates of each life stage first increased and then decreased as temperature increased from 19 to 31 °C. The survival rates were highest at 25 °C, being 98.33, 78.33, 55.00, 48.33, and 41.67% for development to first, second, third, fourth, and fifth instars, respectively (Figure 2). An obvious overlap in the age–stage survival curves was observed due to the individual differences in mortality under different temperatures.

3.4. Age-Specific Survival and Age–Stage-Specific Fecundity

Age-specific survival rates (l_x) decreased sharply as age of test insects increased within each temperature tested, from 19 to 31 °C (Figure 3). Fecundity (m_x) ended (no further oviposition) at ages (d) 95.00, 64.00, 95.00, 40.00, and 31.00 at 19, 22, 25, 28, and 31 °C, respectively. The total preoviposition period (TPOP) under the five different temperatures ranged from 24.00 d (31 °C) to 95.00 d (19 °C and 25 °C), whereas the highest age-specific fecundities were 3.00 (81.00 d, 19 °C), 6.00 (53.00 d, 22 °C), 2.50 (77.00 d, 25 °C), 3.00 (34.00 d, 28 °C), and 7.00 (29.00 d, 31 °C) eggs.

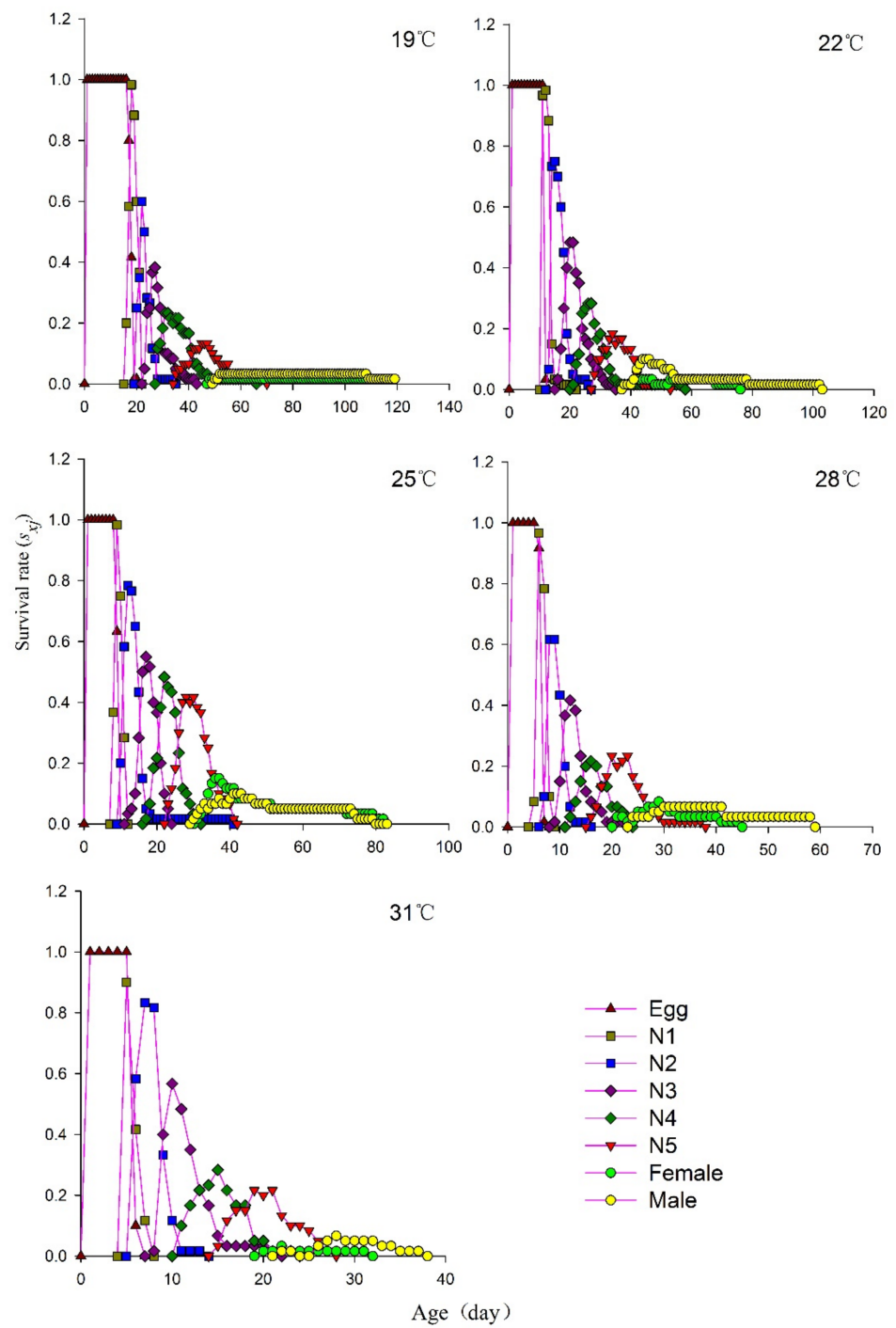


Figure 2. Age–stage-specific survival rates (s_{x_j}) of *R. pedestris* at different temperatures. Note: N1–N5 represent first, second, third, fourth, and fifth instars, respectively.

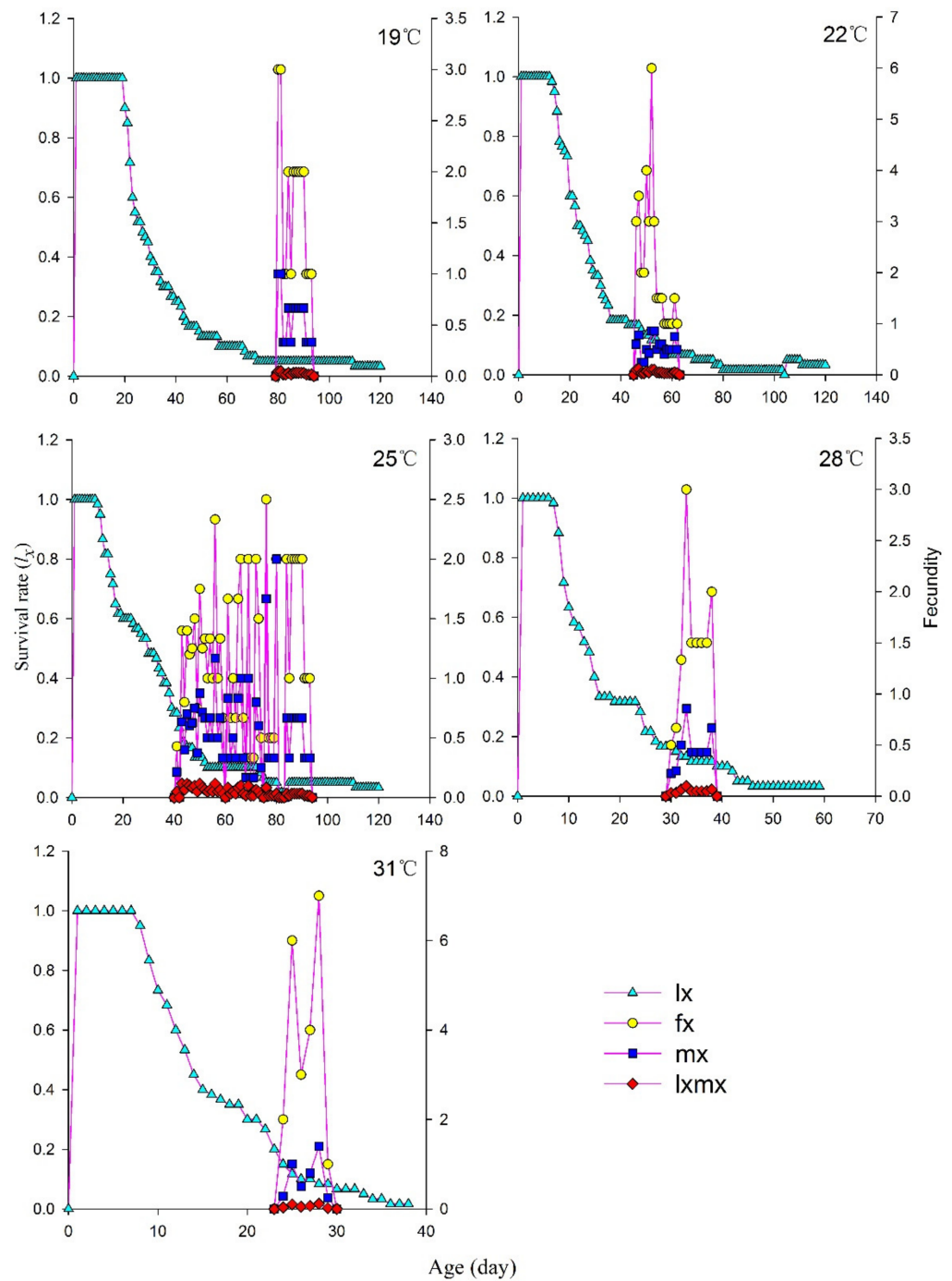


Figure 3. Age-specific survival (l_x), age-stage-specific fecundity (f_x), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *Riptortus pedestris* at different temperatures.

3.5. Age-Stage-Specific Life Expectancy

The e_{xj} value of a given stage decreased with increasing temperature and within the same temperature, decreased with increasing age. The highest adult female life expectancy was at 19 °C (49.00 d) and the lowest was at 31 °C (9.00 d) (Figure 4). Similarly, the highest adult male life expectancy was at 19 °C (64.50 d) and the lowest at 31 °C (7.80 d) (Figure 4).

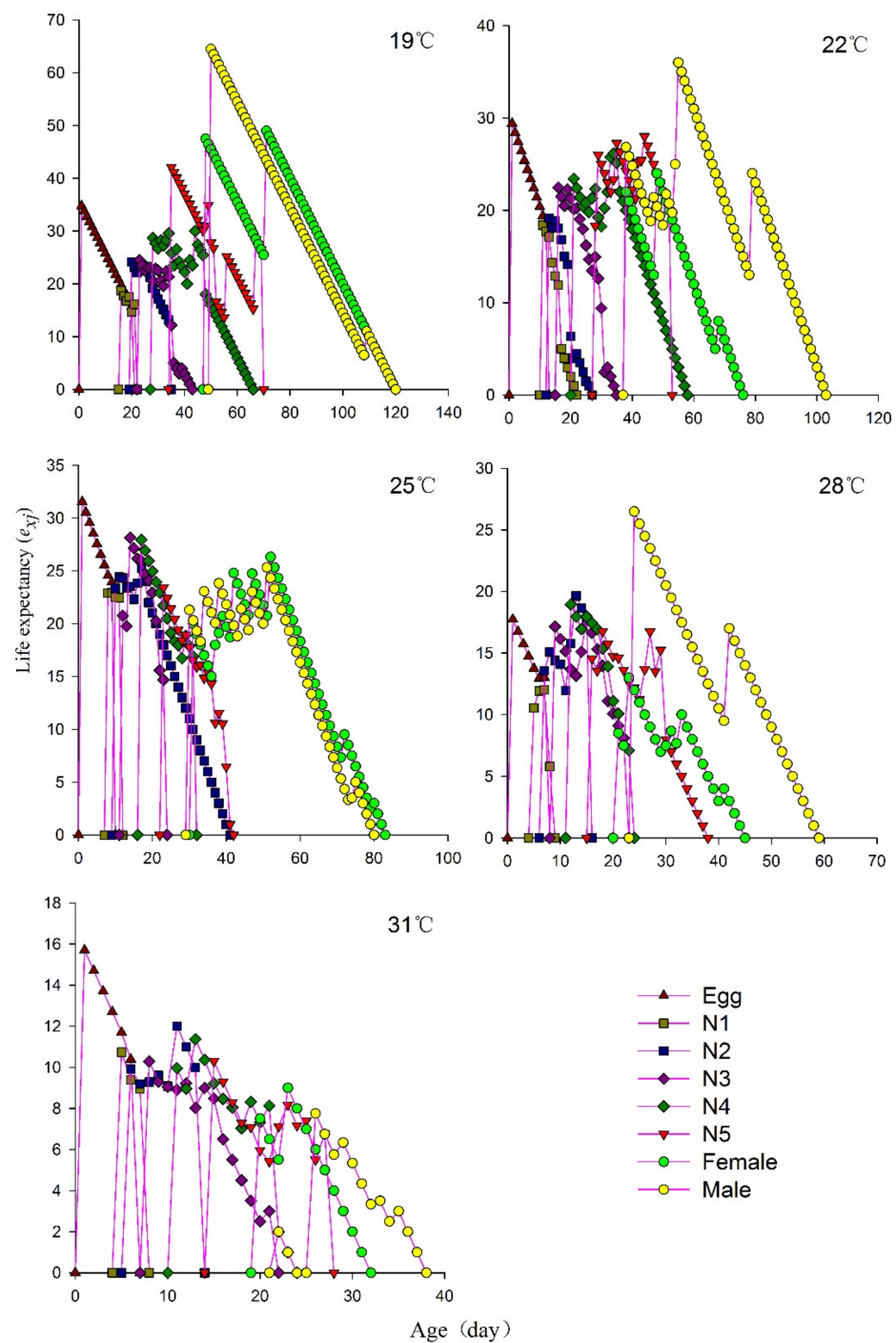


Figure 4. Life expectancy (e_{xj}) of each age–stage group of *Riptortus pedestris* at different temperatures. Note: N1–N5 represents first, second, third, fourth, and fifth instar, respectively.

3.6. Age–Stage-Specific Reproductive Values

Age–stage reproductive values (v_{xj}) gradually increased with increasing age (x) and stage (j) (Figure 5). The first v_{xj} values of adult females were found at 48.00 d, 38.00 d, 31.00 d, 21.00 d, and 20.00 d when tested at five temperatures between 19 and 31 °C, respectively. Additionally, the highest v_{xj} values of adult females occurred at 72.00 d (28.06 d^{-1}), 49.00 d (31.10 d^{-1}), 53.00 d (23.24 d^{-1}), 34.00 d (11.51 d^{-1}), and 24.00 d (26.00 d^{-1}) of age at the different temperatures (Figure 5).

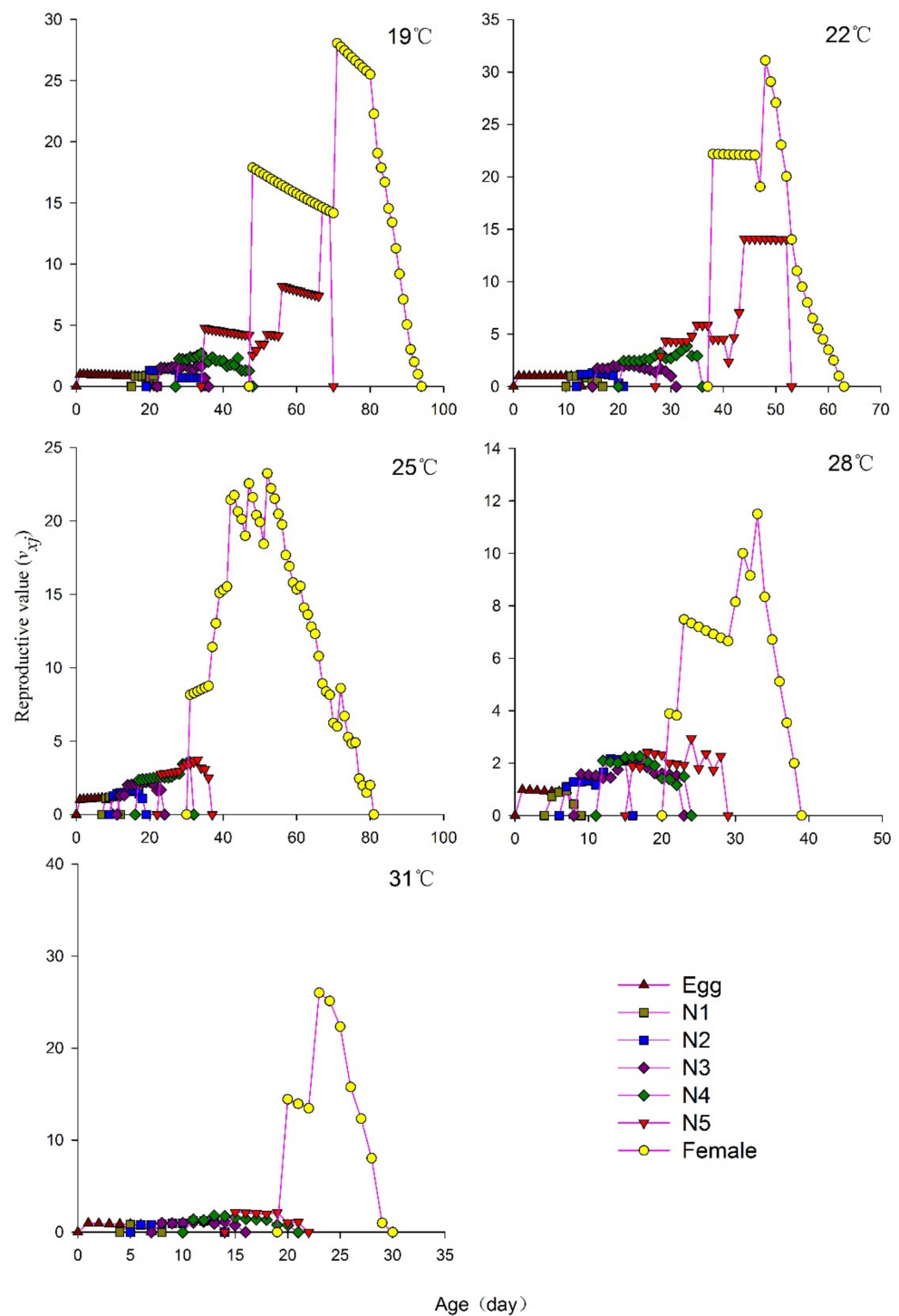


Figure 5. Reproductive value (v_{xj}) of each age–stage group of *Riptortus pedestris* at different temperatures. Note: N1–N5 represents first, second, third, fourth, and fifth instar, respectively.

3.7. Population Parameters at Different Temperatures

The mean generation time (T) was longest (86.76 ± 0.04 d) at 19 °C and shortest (27.50 ± 0.02 d) at 31 °C (Table 3). Only at 22 °C and 25 °C were the finite rate of increase (λ) values greater than 1 (indicating an increasing population). The intrinsic rate of increase ($r = 0.01 \pm 0.02$ d⁻¹) and finite rate of increase ($\lambda = 1.01 \pm 0.02$ d⁻¹) were significantly higher at 25 °C compared to other temperatures (r : $F = 9.73$, $df = 4$, $p < 0.05$; λ : $F = 14.99$, $df = 4$, $p < 0.05$). The lower r value (-0.02 ± 0.01 d⁻¹) and λ value (0.98 ± 0.02 d⁻¹) were

at 31 °C. The highest net reproductive rate ($R_0 = 2.36 \pm 1.69$ offspring) was at 25 °C, while the lowest R_0 value (0.60 ± 0.31) was at 31 °C (Table 3).

Table 3. Population parameters of *Riptortus pedestris* at different temperatures.

	Temperature °C				
	19	22	25	28	31
Net reproductive rate (R_0)	0.63 ± 0.32 b	1.52 ± 0.77 ab	2.36 ± 1.69 a	0.79 ± 0.40 b	0.60 ± 0.31 b
Mean generation time T (d)	86.76 ± 0.04 a	53.55 ± 0.09 b	56.44 ± 2.04 b	41.34 ± 9.86 c	27.50 ± 0.02 d
Intrinsic rate of increase r (per day)	−0.01 ± 0.01 b	0.01 ± 0.01 a	0.01 ± 0.02 a	−0.01 ± 0.01 b	−0.02 ± 0.01 b
Finite rate of increase λ (per day)	0.99 ± 0.01 b	1.01 ± 0.01 a	1.01 ± 0.02 a	0.99 ± 0.01 b	0.98 ± 0.02 b

Data are presented as mean ± SE. Different small letters in the same row indicate significant differences at $p < 0.05$. SEs were estimated by 100,000 bootstrap resampling.

3.8. Effect of Temperature on Population Parameters

The population trend index values (I) were >1 at 22, 25, and 25 °C but were <1 at 19 and 31 °C, which indicated that the population increased at temperatures in the 22, 25, and 25 °C range but decreased at higher or lower temperatures trend under the experimental temperature conditions. The population trend index (I) was significantly different among temperatures ($F = 66.65$, $df = 4$, $p < 0.05$). The highest (I) value was at 7.89 at 25 °C (Table 4).

Table 4. Effects of temperature on the life table parameters of *Riptortus pedestris*.

Developmental Stage	Number of Individuals Entering the Next Stage				
	19 °C	22 °C	25 °C	28 °C	31 °C
Egg	100.0 ± 0.00 a	100.0 ± 0.00 a	100.0 ± 0.00 a	100.0 ± 0.00 a	100.0 ± 0.00 a
First instar	82.35 ± 0.61 c	90.32 ± 0.64 b	95.45 ± 0.59 a	92.31 ± 1.12 b	83.33 ± 0.78 c
Second instar	49.41 ± 6.38 c	75.27 ± 6.59 a	81.13 ± 4.08 a	61.54 ± 1.21 b	79.16 ± 7.56 a
Third instar	41.18 ± 7.20 c	48.17 ± 1.91 bc	60.45 ± 3.83 a	47.69 ± 6.61 bc	58.33 ± 2.43 ab
Fourth instar	26.08 ± 3.09 c	34.62 ± 2.51 b	52.50 ± 3.44 a	32.31 ± 5.78 b	34.72 ± 2.16 b
Fifth instar	12.35 ± 0.51 d	21.07 ± 6.86 c	47.73 ± 8.65 a	27.69 ± 8.06 b	23.61 ± 9.19 bc
Adult	5.49 ± 1.87 d	13.55 ± 2.75 bc	30.23 ± 0.92 a	15.39 ± 3.57 b	9.72 ± 0.94 cd
Female ratio	0.50 ± 0.61 a	0.33 ± 0.73 b	0.58 ± 1.01 a	0.6 ± 0.54 a	0.29 ± 0.37 b
Number of eggs laid per female	24.00 ± 11.83 d	45.00 ± 15.36 b	58.00 ± 28.59 a	30.00 ± 9.77 c	23.00 ± 11.09 e
Number of eggs expected in the following generation	65.88 ± 3.65 c	259.35 ± 18.73 b	789.00 ± 23.78 a	277.02 ± 19.19 b	64.83 ± 6.38 c
Population trend index (I)	0.66 ± 0.72 c	2.59 ± 1.23 b	7.89 ± 2.34 a	2.77 ± 0.50 b	0.65 ± 0.23 c

Data are presented as mean ± SE. Different small letters in the same row indicate significant differences at $p < 0.05$. SEs were estimated by 100,000 bootstrap resampling.

4. Discussion

Temperature is the most important environmental factor determining the rate of development and reproduction of arthropods [33], affecting the immature time, longevity, fecundity, and survival rates of arthropods [34]. Information regarding the population stage structure and dynamics is useful in pest management. The objective of this study was to determine the effects of temperature on the growth and development of *R. pedestris* in the Huang-Huai-Hai region population. We studied the minimal temperature threshold and measured the effective accumulated temperature (number of required day degrees) of *R. pedestris*, as well as the effects of temperature on the development period and survival rate of each stage of *R. pedestris*. Under our test conditions, *R. pedestris* completed all of its developmental stages at temperatures from 19 to 31 °C. Previously, Ahn et al. [18] reported that *R. pedestris* females successfully developed from egg to adult at temperatures from 17.9 to 36.1 °C, but that populations failed to complete its development at 15.9 °C. Chen et al. [19] found that *R. pedestris* (populations were collected from the northeast of China, Jingyu county, Hunjiang City, Jilin Province, where the temperature is lower than Cangzhou) failed

to complete its growth and development at 16 °C and was unable to lay eggs at 32 °C in testing at 16, 20, 24, and 32 °C. The Chinese *R. pedestris* population therefore can be assumed to be able to complete its whole life cycle and lay eggs at temperatures from 16 to 32 °C. In our study, the developmental period, preadult (= total immature stage) period, adult longevity, adult preoviposition period (APOP), and total preoviposition period (TPOP) were all significantly shorter at 31 versus 19 °C. The longest APOP and TPOP periods occurred at 19 °C (32.00 d, 80.00 d), differing from the values reported by Ahn et al. [23], who found that the longest APOP and TPOP values in that study were at 24 ± 4 °C (9.9 d, 59.1 d). In our study, the shortest APOP and TPOP periods at 31 °C (4.00 d, 24.00 d), which were shorter than the 5.3 d and 39.5 d values observed at an average 24 ± 6 °C fluctuating temperature [23], indicating that females do not require long periods to develop sexual maturity, when low temperatures were not constant providing. This suggests that fluctuating temperatures can be beneficial to *R. pedestris* populations. Similarly, the parasitoid *Diaphorencyrtus aligarhensis* (Shafee, Alam, and Argarwal) (Hymenoptera: Encyrtidae) that required the number of degree-days for completion of development were 21% lower under fluctuating temperature regimens compared with constant temperatures [35]. Given that fluctuating temperatures are closer to field conditions, they are likely more reliable should be considered in future laboratory tests.

In our study, we used the linear regression method to calculate the developmental threshold temperature and effective accumulated temperature (number of required day degrees). We found that the lower developmental threshold was 13.44 °C for *R. pedestris*, which was lower than that found for the Korea population (14.1 °C) [18]. The developmental threshold temperature was lowest for the second instar and was highest in the fifth instar. Our findings are partially consistent with those of Chen et al. [19], who found that the lowest developmental threshold temperature occurred in the third instar and the highest in the fifth instar nymph. The effective accumulated temperature (total number of required day degrees) for preimaginal *R. pedestris* was 231.21 degree-days in our study. It was shorter than for the Korea population (336.7 degree-days for the immature stage) [23]. Our data predict there should be three generations of *R. pedestris* at Cangzhou based on the yearly effective accumulated temperature of 1757.5 °C [36], using the formula of Ma and Jiang [37]. Field records have confirmed that there are three generations per year of *R. pedestris* in the Huang-Huai-Hai region and that these generations overlap in soybean fields [38].

The life tables are helpful tools to study the effects of environmental factors on pest population dynamics and are useful for prediction and pest management [39]. Our study presents, for the first time, the fecundity and two-sex life table parameters of a Chinese population of *R. pedestris* at different temperatures. The population trend index (*I*) was >1 when the temperature was at 22–28 °C. The fecundity in our study highest (58.00 eggs per female) and the population trend index (*I*) reached 7.89 at 25 °C. However, the population trend index (*I*) < 1 at 19 and 31 °C, and the population of *R. pedestris* should decrease at these temperatures. The mean generation time (*T*) was shortest at 31 °C due to shorter development time for the immature stages. However, low oviposition rates at 31 °C lead to a low net reproductive rate at this temperature. The annual extreme daily mean temperature was increased in the past three years in Cangzhou [36], with the global mean surface air temperature that has risen substantially [40], and the mean temperature could be higher in the future, so it can be predicted that the *R. pedestris* population will be decrease and degenerate when mean temperature rises to 31 °C, as based on our research results. Outhwaite et al. (2022) report that historical climate warming and intensive agricultural land use is associated with reductions of almost 50% in the abundance and 27% in the number of species within insect assemblages relative to those in less-disturbed habitats with lower rates of historical climate warming [41]. In our study, R_0 was highest (2.36) at 25 °C but much lower than Hu et al. [42], who reported the R_0 was 50.53 at 24 ± 1 °C with soybean pods as the food. This difference shows that diet and other factors besides temperature can influence population growth.

Riptortus pedestris is a widely distributed serious pest of soybean, causing outbreaks in the Huang-Huai-Hai region of China, which is the main soybean-production area of China. Understanding the development and fecundity of the local bean bug population in Cangzhou, China allows for the better prediction of *R. pedestris* populations. Based on our developmental threshold temperature of 13.44 °C, and the effective accumulated temperature of 582.04 degree-days, the population growth and dynamics can be predicted using the population trend index. The results of the present study will help support IPM actions taken against *R. pedestris*, although other factors such as photoperiod, humidity, feeding, density, and their interactions may also influence population size.

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