



Effects of temperature on the development, fecundity, and life table parameters of *Riptortus pedestris* (Hemiptera: Alydidae)

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Abstract

Riptortus pedestris (Fabricius) (Hemiptera: Alydidae) is an economically important insect pest of soybean. We investigated the developmental periods of each life stage as well as adult longevity and female fecundity. The study was conducted at eleven constant temperatures (12.0, 14.0, 15.9, 17.3, 19.3, 23.6, 28.3, 31.2, 34.2, 35.1, and 36.1 °C) for temperature-dependent development, and six constant temperatures (15.8, 19.7, 24.0, 27.8, 32.6, and 35.5 °C) for adult longevity and oviposition. *Riptortus pedestris* females showed successful egg-to-adult development from 17.9 to 36.1 °C, but failed to complete development under 15.9 °C. Using linear regression, lower developmental threshold (LDT) and thermal constant (K) for the total immature stage were estimated as 14.1 °C and 336.7°-day (DD), respectively. Higher and lower temperature threshold (TH and TL, respectively) were calculated using Lobry–Rosso–Flandrois (LRF) and Sharpe–Schoolfield–Ikemoto (SSI) models; a wider TL-to-TH temperature range (31.4 °C) was observed for LRF than for SSI (18.6 °C). The adult emergence frequency over the full range of constant temperatures was simulated using nonlinear developmental rate functions and the Weibull function. The daily egg production was predicted with respect to temperature and adult age. Biological characteristics of *R. pedestris* from different local populations are discussed.

Keywords *Riptortus pedestris* · Life table analysis · Nonlinear function · Oviposition · Temperature

Introduction

Riptortus pedestris (Fabricius) (Hemiptera: Alydidae) is one of the important pests in Asian countries including Korea, Japan, and India (Kono 1989; Leal et al. 1995; Lim 2013; Son et al. 2000; Visalakshi et al. 1976; Wada et al. 2006). Both adults and nymphs of *R. pedestris* feed on leguminous plants such as Chinese milk vetch (*Astragalus sinicus* L.), cowpea [*Vigna unguiculata* (L.)], hairy vetch (*Vicia villosa* Roth), kidney bean (*Phaseolus vulgaris* L.), mung bean (*Vigna radiata* L.), red clover (*Trifolium pretense* L.), sesame (*Sesamum indicum* L.), and soybean (*Glycine max* L.), as well as fruit trees such as apples (*Malus pumila* Miller) and sweet persimmon (*Diospyros kaki* L.f.) (Bae et al. 2009; Chung et al. 1995; Kimura et al. 2008; Kono 1989; Mainali and Lim 2012; Seo et al. 2011; Son et al. 2000). They

directly damage the soybean pod and seed by piercing and sucking, in addition to transmitting microorganisms to soybean, resulting in serious economic losses (Jung et al. 2005, 2010; Kimura et al. 2008; Kono 1989). The damage caused by *R. pedestris* was severe from middle pod-elongation to earlier seed-thickening of soybean. Specially, when the pod stage of soybean was injured by *R. pedestris*, the empty pods and undeveloped seeds were increased. The economic loss of soybean yield depended on the life stage and density of *R. pedestris* and the timing of their feeding (Jung et al. 2005; Kono 1989; Suzuki et al. 1991).

Life table analysis is an important tool for understanding and analyzing the biological process of insects, for studying population growth, and for establishing management programs. Life table studies describe the survival, reproduction, and rate of increase of a population (Birch 1948; Goodman 1982; Maia et al. 2000; Sánchez-Ramos et al. 2017). Although Rahman and Lim (2017) created a fertility life table for *R. pedestris* on a limited food resource, they did not assess the effects of temperature on the life table parameters for *R. pedestris*. Temperature is one of the main abiotic factors affecting development, growth, reproduction,

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and survival of insects and mites (Park et al. 2017; Ramalho et al. 2015; Sugawara et al. 2017). The previous studies have often overlooked the effect of the lower and higher temperature range on the development of *R. pedestris* (Bae et al. 2005; Kidokoro 1978; Kim et al. 2009; Kono 1989; Lee et al. 1997). Although Kim et al. (2009) developed temperature-dependent development and oviposition models for *R. pedestris*, they emphasized more on the goodness-of-fit and simplicity of models rather than the biological interpretation of models. The main objective of this study was to investigate the effects of temperature on the development and reproduction of *R. pedestris*, to construct temperature-dependent development and oviposition models for the species and to analyze a fertility life table for *R. pedestris*.

Materials and methods

Insect colony

Riptortus pedestris (about 200) were obtained from the National Institute of Agricultural Sciences (NIAS), Wanju-gun, Republic of Korea, in 2016. Colonies of *R. pedestris* were maintained in acrylic cages (30 cm × 30 cm × 35 cm) with one door and two meshed screens in the lateral sides for ventilation at 25 ± 1 °C, $60 \pm 10\%$ relative humidity and 16:8 h light:dark photoperiod. Dry soybean seeds and water were supplied as food sources. Three pieces of gauze (10 cm × 4.5 cm) were placed at the bottom of each cage as oviposition sites. *Riptortus pedestris*, which were captured seasonally in the field of Jeju, were added about 100 adults (we did not identify the sex) in the cage for mass rearing three times (spring, summer, and fall seasons) per year, to avoid inbreeding depression.

Experimental procedure for egg-to-adult development

New eggs (< 24 h old) on the gauze were randomly selected from the insect-rearing system and placed in Petri dishes (10.0 cm diameter and 4.0 cm height, with a 4.0 cm-diameter air hole on the lid covered with 0.05 mm mesh, SPL, Pocheon, Korea) with cotton soaked with water for maintaining humidity. When the eggs hatched, the first instar nymphs were randomly selected with a brush and placed individually in Petri dishes (5.0 cm diameter and 1.5 cm height with a 1.3 cm-diameter air hole on the lid covered with 0.05 mm mesh). Each dish was first filled with cotton soaked with water and three dried soybean seeds. The dried soybean seeds were placed in a small plastic band, so that seeds do not roll over in the Petri dishes. Soybean seeds and water were supplied as a food source for the nymphs.

The developmental periods of *R. pedestris* stages from egg-to-adult emergence were studied at temperatures of 12.0, 14.0, 15.9, 17.3, 19.3, 23.6, 28.3, 31.2, 34.2, 35.1, and 36.1 °C. The temperature inside the cages was very similar to that of the chamber (WTH-305, Daihan Scientific, Co. Ltd, Seoul, Korea). Sample sizes were greater than 200 eggs per treatment. Observations were made visually at 24 h intervals to distinguish between the nymph instars, which were identified using the exuviae. The eggs were allowed to complete development until adults within the Petri dishes, and the developmental time for each life stage was recorded. Dried soybean seeds were replaced with new ones whenever needed.

Experimental procedure for adult longevity and fecundity

To obtain newly emerged female and male adults (< 24 h old), fifth instar nymphs were chosen from the mass rearing system and transferred into acrylic cages (30 cm × 30 cm × 35 cm). The new female adults were paired with new males and placed in Petri dishes (10.0 cm diameter and 4.0 cm height, with a 4.0 cm-diameter air hole on the lid covered with 0.05 mm mesh). A given pair of *R. pedestris* adults was maintained in the same Petri dish. We replaced the female or male if they died within 1 week. The fecundity and longevity of *R. pedestris* individuals were studied at temperatures of 15.8, 19.7, 24.0, 27.8, 32.6, and 35.5 °C. We followed the same procedure as the developmental time experiment. Rolled pieces of gauze (10 cm × 4.5 cm) were placed in the bottom of each Petri dish as oviposition substrate. The longevity and fecundity of *R. pedestris* were examined and recorded at 24 h intervals using visual observation. To assess the daily fecundity and hatchability, eggs laid by the female were removed from the containers daily, and it was observed whether they hatch or not.

Data analysis

Developmental time, longevity, and fecundity data for *R. pedestris* were analyzed using the PROC GLM in SAS (SAS Institute 2002). Statistical differences in development periods, longevity, and fecundity across the tested temperatures were determined using the Tukey's studentized range test ($p < 0.05$). The data for hatchability were normalized by arcsine-square-root transformation and were then analyzed using Tukey's test. The parameters for the linear and non-linear functions were estimated using least-square method in TableCurve 2D (Jandel Scientific 1996) or R-statistics (version 3.2.2; R Core Team 2015).

Analysis of developmental data

The relationship between temperature and developmental rates (1/developmental periods) was analyzed using linear and nonlinear functions. The lower developmental threshold ($LDT, -\frac{b}{a}$) and thermal constant ($K, \frac{1}{a}$) were estimated by linear function ($y = aT + b$: where y = developmental rate and T = temperature tested) (Campbell et al. 1974).

Many researchers have suggested and evaluated nonlinear equations that explain the relationship between developmental rates and temperature (Kim et al. 2017; Kontodimas et al. 2004; Mirhosseini et al. 2017; Ratkowsky and Reddy 2017; Roy et al. 2002; Shi et al. 2016, 2017). We selected two nonlinear equations, the Lobry–Rosso–Flandrois (LRF) model and the Sharpe–Schoolfield–Ikemoto (SSI) model, based on the evaluation by Ratkowsky and Reddy (2017) and Shi et al. (2017):

$$r(T) = \mu_{opt} \frac{(T - T_{max})(T - T_{min})^2}{(T_{opt} - T_{min})[(T_{opt} - T_{min})(T - T_{opt}) - (T_{opt} - T_{max})(T_{opt} + T_{min} - 2T)]} \tag{1}$$

Equation (1) is the LRF model (Lobry et al. 1991; Ratkowsky and Reddy 2017; Rosso et al. 1993). The LRF model has been generally considered in food microbiology and not previously well applied in population entomology before introducing by Ratkowsky and Reddy (2017). The model was developed by Lobry and colleagues and which has the important features that all parameters of the model have biological meaning. In this model, $r(T)$ is the developmental rate (1/developmental time) at different temperatures ($^{\circ}K$), T is the absolute temperature (K), μ_{opt} is the development rate at the optimum temperature, T_{max} is the temperature above which no development occurs, T_{min} is the temperature below which development is no longer observed, and T_{opt} the optimal temperature for development:

$$r(T) = \frac{\rho_{\phi} \frac{T}{T_{\phi}} \exp \left[\frac{\Delta HA}{R} \left(\frac{1}{T_{\phi}} - \frac{1}{T} \right) \right]}{1 + \exp \left[\frac{\Delta HL}{R} \left(\frac{1}{TL} - \frac{1}{T} \right) \right] + \exp \left[\frac{\Delta HH}{R} \left(\frac{1}{TH} - \frac{1}{T} \right) \right]} \tag{2}$$

Equation (2) is the SSI model (Ikemoto 2005; Schoolfield et al. 1981; Sharpe and DeMichele 1977). The SSI model based on thermodynamics was proposed by Sharpe and DeMichele (1977) and modified by Schoolfield et al. (1981) and Ikemoto (2008). The model has been developed to describe temperature-dependent reaction rates of a theoretical rate-controlling enzyme that is in its active temperature ranges. Parameters of the SSI model were estimated using an R script, which improved the fitting method of parameter estimates, developed by Shi et al. (2017). In this model, $r(T)$

represents the developmental rate at absolute temperature T ($^{\circ}K$), ΔHA , ΔHL , and ΔHH are enthalpy changes ($Jmol^{-1}$), R is the universal gas constant, ρ_{ϕ} is the developmental rate at T_{ϕ} , TL and TH are temperatures at which the rate-controlling enzyme has equal probability to be active or inactive by low- or high-temperature inactivation, respectively, and T_{ϕ} is the intrinsic optimum temperature. T_{ϕ} is the optimal temperature at which the species can optimize its fitness to the environment (Sharpe and DeMichele 1977):

$$P_2(T) = \frac{1}{1 + \exp \left[\frac{\Delta HL}{R} \left(\frac{1}{TL} - \frac{1}{T} \right) \right] + \exp \left[\frac{\Delta HH}{R} \left(\frac{1}{TH} - \frac{1}{T} \right) \right]} \tag{3}$$

Equation (3) is the probability that the rate-controlling enzyme is in the active state. The maximum probability of $P_2(T)$ is observed at T_{ϕ} .

The relationship between the cumulative proportion

of adult emergence and normalized developmental times (developmental time/mean developmental period) was estimated using the three-parameter Weibull function (Wagner et al. 1984; Weibull 1951). The parameters for the Weibull function were estimated using least-square method:

$$F(t) = 1 - \exp \left(- \left(\frac{t - \gamma}{\eta} \right)^{\beta} \right), \tag{4}$$

where $F(t)$ is the cumulative frequency at normalized time t , and γ , η , and β are the parameters of the Weibull function.

The emergence proportion of *R. pedestris* adults was simulated with respect to constant temperature ($^{\circ}C$) and time (day) by combining the two nonlinear functions and Weibull function:

$$F(x, T) = 1 - \exp \left(- \left(\frac{xr(T) - \gamma}{\eta} \right)^{\beta} \right), \tag{5}$$

where $F(x, T)$ is the emergence frequency of *R. pedestris* adults at time x and constant temperature $T(^{\circ}C)$, x is time (day), $r(T)$ is the developmental rate from selected model, and γ , η , and β are parameters from the Weibull equation. The results of $F(x, T)$ were estimated by subtracting the simulation result at time x_i from the result at time x_{i+1} .

Oviposition model structure and life table parameters

The oviposition model of *R. pedestris* was constructed using temperature-dependent adult aging rate, the

age-specific survival rate, age-specific cumulative oviposition rate, and temperature-dependent total fecundity. The relationship between the temperatures and adult aging rates ($1/\text{longevity}$) was described by the Lactin model (Eq. 6) (Lactin et al. 1995):

$$r(T) = e^{\rho T} - e^{\left(\rho T_M - \frac{T_M - T}{\Delta T}\right)}, \quad (6)$$

where $r(T)$ represents the aging rate at temperature T ($^{\circ}\text{C}$), ρ is a constant that defines the rate of optimal temperature, T_M is the higher threshold, and ΔT is the temperature window for inducing physiological action of insect adult aging.

The age-specific survival rate of *R. pedestris* was fitted with a Weibull frequency distribution (Pinder et al. 1978):

$$S(t) = \frac{1}{\exp\left[\left(\frac{t}{a}\right)^b\right]}, \quad (7)$$

where $S(t)$ is the proportion of living females at a normalized time t , t is the normalized time (age of each adult female/average longevity of tested female), and a and b are parameters. Age-specific cumulative oviposition rate was analyzed using the three-parameter Weibull function (Eq. 4). The relationship between the mean total fecundity per female and temperatures was estimated by the equation proposed by Briere et al. (1999):

$$f(T) = cT(T - T_L)(T_M - T)^{1/m}, \quad (8)$$

where $f(T)$ is the number of total eggs laid by one female at each temperature ($^{\circ}\text{C}$), T and T_M are terms from the Lactin model. T_L is the lower developmental threshold, and c and m are empirical constants of the equation.

The number of eggs produced by a cohort of females was estimated between t_i (i.e., normalized age at i th day) and t_{i+1} using the equation (Kim and Lee 2003):

$$f(T) * F(t_{i+1} - t_i) * \left(\frac{S_{t_{i+1}} + S_{t_i}}{2}\right), \quad (9)$$

where $f(T)$ and $S(t)$ are already defined above and $F(t)$ is the cumulative oviposition proportion of living females at a normalized time t .

The parameters of fertility life table for *R. pedestris*, including net reproductive rate (R_0), mean generation time (T), doubling time (DT), finite rate of increase (λ), and intrinsic rate of natural increase (r_m), were estimated using methods proposed by Maia et al. (2000). The statistical differences in life table parameters across the tested temperatures were determined using the two-tailed t test.

Results

Riptortus pedestris developed successfully from the egg to the adult stage in the range of 17.9–36.1 $^{\circ}\text{C}$ (Table 1). The eggs could not hatch at 12.0 and 14.0 $^{\circ}\text{C}$, and nymphs could not develop into adult stage under 15.9 $^{\circ}\text{C}$. The developmental periods of each life stage and total immature period were significantly influenced by temperatures (i.e., combined: Egg $F_{8, 2204} = 24655.40$, $p < 0.0001$, first nymph stage $F_{8, 1877} = 1688.40$, $p < 0.0001$, second nymph stage $F_{8, 1631} = 1962.74$, $p < 0.0001$, third nymph stage $F_{8, 1532} = 1877.59$, $p < 0.0001$, fourth nymph stage $F_{7, 1461} = 2705.14$, $p < 0.0001$, fifth nymph stage $F_{7, 1428} = 1960.42$, $p < 0.0001$, total nymph stage $F_{7, 1336} = 16804.70$, $p < 0.0001$, and total immature stage $F_{8, 1336} = 26840.50$, $p < 0.0001$). The time required to complete development decreased when the temperature increased from 17.9 to 34.2 $^{\circ}\text{C}$. The mean developmental time for egg-to-adult emergence ranged from 81.7 days at 17.9 $^{\circ}\text{C}$ to 16.9 days at 34.2 $^{\circ}\text{C}$. The lower developmental threshold (LDT) and thermal constant (K) for each life stage of *R. pedestris* were obtained by the linear regression analysis. LDT values of egg, first, second, third, fourth, and fifth nymph stages were 13.2, 13.5, 13.2, 14.4, 14.8, and 14.6 $^{\circ}\text{C}$, respectively. K values of egg, first, second, third, fourth, and fifth nymph stage were 104.7, 31.6, 51.2, 41.5, 45.0, and 70.6 DD, respectively. LDT and K of total immature period were 14.2 $^{\circ}\text{C}$ and 336.7 DD.

The estimated parameters of two nonlinear functions are presented in Table 2. The temperature-dependent development for total immature period was described by two functions, and the curve performance of two models was right-skewed bell-shape (Fig. 1a). The maximum developmental rate was observed at 37.1 and 36.8 $^{\circ}\text{C}$ from the LRF and SSI models, respectively. The three critical temperature thresholds of rate-controlling enzyme for *R. pedestris* total immature stage were estimated using the SSI model (Fig. 1b). The intrinsic optimum temperatures of the control enzyme for egg, first, second, third, fourth, fifth, and total immature period were 24.1, 33.5, 32.5, 26.0, 33.3, 33.4, and 32.6 $^{\circ}\text{C}$, respectively. The temperature window for the development of *R. pedestris* could be approximated from TL to TH. The temperature range for the nymph stages was 29.8–33.1 and 17.0–20.6 $^{\circ}\text{C}$ based on the LRF and SSI models, respectively.

The cumulative proportion of development completion for *R. pedestris* total immature stage was analyzed using a three-parameter Weibull distribution function (Fig. 1c) ($\gamma = 0.7071$, $\eta = 0.2893$, $\beta = 6.7314$, $F_{2, 62} = 1393.73$, $p < 0.0001$, $r^2 = 0.98$). Adult emergence proportion for *R. pedestris* over the full range of constant temperature was obtained using the two nonlinear models and the

Table 1 Developmental time (days) (mean ± SEM) and survivorship for each life stage of *Riptortius pedestris* at different temperatures

Sex	Stage	Temperature (°C)									
		15.9	17.9	19.3	23.6	28.3	31.2	34.2	35.1	36.1	
Combined	Initial <i>N</i>	274	209	301	276	286	242	555	453	516	
	Egg	34.9 ± 0.14a	22.5 ± 0.09b	16.6 ± 0.06c	9.7 ± 0.04d	6.6 ± 0.03e	5.3 ± 0.04f	5.2 ± 0.02f	5.3 ± 0.03f	5.1 ± 0.10f	
	<i>n</i>	233 (85.0)	205 (98.1)	275 (91.3)	239 (86.6)	252 (88.1)	224 (92.6)	463 (83.4)	264 (58.3)	51 (9.9)	
	1st <i>N</i>	13.3 ± 0.27a	6.8 ± 0.06b	4.9 ± 0.08c	2.9 ± 0.03d	1.9 ± 0.01e	2.1 ± 0.08e	1.3 ± 0.02f	1.4 ± 0.04f	2.0 ± 0.15e	
	<i>n</i>	123 (44.9)	193 (92.3)	269 (89.4)	232 (84.1)	247 (86.4)	151 (62.4)	443 (79.8)	240 (52.9)	51 (9.9)	
	2nd <i>N</i>	20.6 ± 1.42a	10.8 ± 0.12b	7.9 ± 0.07c	4.5 ± 0.05d	3.1 ± 0.03e	2.9 ± 0.06ef	2.4 ± 0.03f	2.6 ± 0.04ef	2.9 ± 0.45ef	
	<i>n</i>	11 (4.0)	171 (81.8)	252 (83.7)	222 (80.4)	241 (84.3)	142 (58.7)	399 (71.9)	209 (46.1)	22 (4.3)	
	3rd <i>N</i>	22.5 ± 2.42a	10.7 ± 0.12b	7.7 ± 0.07c	4.5 ± 0.04d	2.9 ± 0.03e	2.2 ± 0.05e	2.1 ± 0.03e	2.1 ± 0.05e	2.4 ± 0.50e	
	<i>n</i>	4 (1.5)	162 (77.5)	248 (82.4)	214 (77.5)	234 (81.8)	140 (57.9)	362 (65.2)	193 (42.6)	10 (1.9)	
	4th <i>N</i>	–	12.5 ± 0.12a	9.5 ± 0.08b	5.0 ± 0.05c	3.2 ± 0.03d	2.5 ± 0.07def	2.3 ± 0.04ef	2.3 ± 0.05f	3.0 ± 0.48de	
	<i>n</i>	–	149 (71.3)	240 (79.7)	210 (76.1)	232 (81.1)	137 (56.6)	330 (59.5)	180 (39.7)	6 (1.2)	
5th <i>N</i>	–	18.1 ± 0.20a	14.8 ± 0.14b	7.6 ± 0.09c	5.1 ± 0.06de	4.1 ± 0.09def	3.5 ± 0.08f	3.6 ± 0.05ef	5.3 ± 1.63d		
<i>n</i>	–	144 (68.9)	239 (79.4)	210 (76.1)	227 (79.4)	136 (56.2)	312 (56.2)	175 (38.6)	3 (0.6)		
Total <i>N</i>	–	59.2 ± 0.22a	44.9 ± 0.14b	24.7 ± 0.09c	16.5 ± 0.06d	13.8 ± 0.10e	11.6 ± 0.07f	11.9 ± 0.09f	15.0 ± 2.82de		
<i>n</i>	–	124 (59.3)	226 (75.1)	204 (73.9)	219 (76.6)	129 (53.3)	282 (50.8)	154 (33.9)	2 (0.4)		
Total <i>I</i>	–	81.7 ± 0.24a	61.5 ± 0.16b	34.5 ± 0.09c	23.2 ± 0.07d	19.2 ± 0.11ef	16.9 ± 0.07g	17.2 ± 0.09fg	20.5 ± 3.53e		
Initial <i>N</i>	92	93	83	83	90	66	126	70	2		
Female	Egg	22.5 ± 0.17a	16.7 ± 0.10b	9.7 ± 0.06c	6.5 ± 0.05d	5.3 ± 0.07e	5.3 ± 0.07e	5.1 ± 0.03e	5.2 ± 0.06e	5.5 ± 0.70e	
	1st <i>N</i>	6.9 ± 0.08a	4.8 ± 0.14b	2.9 ± 0.06c	1.9 ± 0.02d	1.8 ± 0.09d	1.8 ± 0.09d	1.4 ± 0.04d	1.3 ± 0.07d	2.0 ± 0.00d	
	2nd <i>N</i>	10.8 ± 0.18a	7.8 ± 0.09b	4.5 ± 0.06c	3.0 ± 0.06d	2.8 ± 0.07d	2.8 ± 0.07d	2.3 ± 0.04d	2.6 ± 0.07d	2.5 ± 0.70d	
	3rd <i>N</i>	10.5 ± 0.19a	7.6 ± 0.10b	4.5 ± 0.07c	2.9 ± 0.05d	2.9 ± 0.07d	2.2 ± 0.07d	2.0 ± 0.04d	2.1 ± 0.08d	2.0 ± 0.00d	
	4th <i>N</i>	12.6 ± 0.16a	9.4 ± 0.12b	5.1 ± 0.09c	3.2 ± 0.06d	3.2 ± 0.06d	2.4 ± 0.10d	2.3 ± 0.05d	2.1 ± 0.06d	2.5 ± 0.70d	
	5th <i>N</i>	18.4 ± 0.23a	14.5 ± 0.22b	7.6 ± 0.14c	5.3 ± 0.12de	4.3 ± 0.16de	4.3 ± 0.16de	3.6 ± 0.11e	3.6 ± 0.08e	6.0 ± 2.82cd	
	Total <i>N</i>	59.4 ± 0.34a	44.3 ± 0.19b	24.8 ± 0.17c	16.5 ± 0.09d	13.7 ± 0.15ef	11.6 ± 0.10f	11.6 ± 0.10f	12.0 ± 0.13f	15.0 ± 2.82de	
	Total <i>I</i>	82.0 ± 0.36a	61.1 ± 0.16b	34.6 ± 0.16c	23.1 ± 0.10d	19.0 ± 0.16ef	16.8 ± 0.10f	16.8 ± 0.10f	17.3 ± 0.13f	20.5 ± 3.53e	
	Initial <i>N</i>	32	133	121	121	129	63	156	84	2	
	Male	Egg	22.4 ± 0.20a	16.6 ± 0.09b	9.7 ± 0.06c	6.7 ± 0.04d	5.3 ± 0.08e	5.3 ± 0.08e	5.3 ± 0.04e	5.3 ± 0.06e	5.3 ± 0.70e
		1st <i>N</i>	6.9 ± 0.14a	4.9 ± 0.11b	2.9 ± 0.03c	1.9 ± 0.02d	2.0 ± 0.11d	2.0 ± 0.11d	1.2 ± 0.04e	1.1 ± 0.04e	2.0 ± 0.00d
2nd <i>N</i>		10.5 ± 0.23a	7.9 ± 0.11b	4.4 ± 0.08c	3.2 ± 0.04d	2.9 ± 0.10de	2.9 ± 0.10de	2.4 ± 0.04f	2.6 ± 0.07ef	2.5 ± 0.70d	
3rd <i>N</i>		11.1 ± 0.35a	7.7 ± 0.10b	4.5 ± 0.06c	3.0 ± 0.05d	2.2 ± 0.08e	2.2 ± 0.08e	2.1 ± 0.04e	2.1 ± 0.05e	2.0 ± 0.00d	
4th <i>N</i>		12.9 ± 0.26a	9.6 ± 0.10b	5.0 ± 0.06c	3.2 ± 0.04d	2.7 ± 0.11e	2.7 ± 0.11e	2.3 ± 0.04f	2.3 ± 0.05f	2.0 ± 0.00d	
5th <i>N</i>		18.1 ± 0.51a	14.8 ± 0.18b	7.6 ± 0.11c	5.1 ± 0.05d	4.0 ± 0.12e	4.0 ± 0.12e	3.4 ± 0.11e	3.6 ± 0.06e	2.0 ± 0.00d	
Total <i>N</i>		59.7 ± 0.49a	45.1 ± 0.20b	24.6 ± 0.11c	16.5 ± 0.09d	14.0 ± 0.15de	14.0 ± 0.15de	11.6 ± 0.09e	11.8 ± 0.10e	15.0 ± 2.82de	
Total <i>I</i>		82.2 ± 0.58a	61.8 ± 0.23b	34.4 ± 0.11c	23.2 ± 0.09d	19.3 ± 0.14e	16.9 ± 0.09e	16.9 ± 0.09e	17.2 ± 0.11e	20.5 ± 3.53e	

Means followed by the same letter within a row are not significantly different ($p < 0.05$, Tukey's studentized range test). 'Initial *N*' means the number of initial sample size at each temperature. '*n*' means the number of surviving individual at each life stage. In parentheses, survivorship of each temperature. '*N*' means nymph stage of *R. pedestris*. '*I*' means immature stage from egg to fifth instar nymph. '–' means *R. pedestris* could not develop next life stage. The statistical results of combined sexes are in the text

Female: Egg $F_{7, 613} = 5163.76$, $p < 0.0001$, first nymph stage $F_{7, 613} = 578.89$, $p < 0.0001$, second nymph stage $F_{7, 613} = 974.67$, $p < 0.0001$, third nymph stage $F_{7, 613} = 933.35$, $p < 0.0001$, fourth nymph stage $F_{7, 613} = 1438.65$, $p < 0.0001$, fifth nymph stage $F_{7, 613} = 1125.41$, $p < 0.0001$, total nymph stage $F_{7, 613} = 8227.99$, $p < 0.0001$, and total immature $F_{7, 613} = 13287.80$, $p < 0.0001$

Male: Egg $F_{6, 704} = 5527.09$, $p < 0.0001$, first nymph stage $F_{6, 704} = 623.56$, $p < 0.0001$, second nymph stage $F_{6, 704} = 862.59$, $p < 0.0001$, third nymph stage $F_{6, 704} = 1071.80$, $p < 0.0001$, fourth nymph stage $F_{6, 704} = 1772.35$, $p < 0.0001$, fifth nymph stage $F_{6, 704} = 1276.28$, $p < 0.0001$, total nymph stage $F_{6, 704} = 876.75$, $p < 0.0001$, and total immature $F_{6, 704} = 1516.62$, $p < 0.0001$

Table 2 Parameter estimates of two nonlinear developmental rate models for *Riptortus pedestris*

Function	<i>P</i>	Life stage						
		Egg	First	Second	Third	Fourth	Fifth	Total <i>I</i>
LRF	μ_{opt}	0.1928	0.7303	0.3947	0.4684	0.4346	0.2791	0.0592
	T_{max}	318.6361	309.2751	311.3804	311.3690	309.9779	309.6391	310.2412
	T_{min}	282.0142	276.1498	279.4238	281.2476	280.0817	279.1228	278.8385
	T_{opt}	308.3072	308.7888	306.8911	307.2142	307.3987	307.5019	307.3859
	r^2	0.99	0.96	0.99	0.98	0.99	0.99	0.99
SSI	ρ_{ϕ}	0.1088	0.6449	0.3815	0.2739	0.4311	0.2794	0.0578
	T_{ϕ}	297.2567	306.6539	305.6604	299.1790	306.5007	306.6023	305.8003
	ΔHA	16698.1	10927.32	6880.663	15974.6	8271.32	8602.327	8640.81
	ΔHL	-77172.03	-91198.08	-60646.74	-108900.6	-46589.42	-43779.48	-46143.72
	ΔHH	52702.96	728533.5	263016.4	102252.3	327512.5	377951.4	239232.4
	TL	288.2614	290.0920	291.7942	289.4847	292.6543	292.2029	291.6853
	TH	310.1009	309.4029	310.1090	310.1261	309.7083	309.4469	309.9894
	χ^2	0.00058	0.00943	0.00076	0.00027	0.00052	0.00034	0.000002
	r^2	0.99	0.98	0.99	0.99	0.99	0.99	0.99

'*P*' means parameters of nonlinear functions. 'Total *I*' means immature stage from egg to fifth instar nymph. LRF model: Egg $F_{3,5}=505.67$, $p<0.0001$, first nymph stage $F_{3,5}=35.48$, $p<0.0008$, second nymph stage $F_{3,5}=144.78$, $p<0.0001$, third nymph stage $F_{3,5}=619.28$, $p<0.0001$, fourth nymph stage $F_{3,4}=376.47$, $p<0.0001$, fifth nymph stage $F_{3,5}=694.48$, $p<0.0001$, and total immature $F_{3,4}=1077.84$, $p<0.0001$

development completion process. The results of the simulation were assessed by two nonlinear models (Fig. 2).

Riptortus pedestris adults survived at all the tested temperatures. The longevity of *R. pedestris* females decreased with increasing temperature (Table 3). The longevity of *R. pedestris* males was longer than that of females at different temperatures (sex $F_{1,304}=42.88$, $p<0.0001$, temperature $F_{5,304}=32.45$, $p<0.0001$, and interaction effect of sex and temperature $F_{1,304}=8.93$, $p<0.0001$). The fecundity (total egg production/female) increased with increasing temperature until 24.0 °C. Fecundity and hatchability were significantly affected by the temperature (total egg per female: $F_{4,125}=10.91$, $p<0.0001$; hatchability: $F_{4,125}=32.83$, $p<0.0001$). *Riptortus pedestris* female did not oviposit at 15.8 °C.

The relationship between adult aging rate and temperature was analyzed using the Lactin model (Fig. 3a and Table 4). Three important components of the oviposition model of *R. pedestris* are shown in Fig. 3 and Table 4. Each component was described well by the selected models. The estimated maximum number of eggs produced per female was 186.0 eggs at 25.2 °C. The estimated egg production per day in relation to adult age and temperature is presented in Fig. 4. Age-specific female survival and daily fecundity are presented in Fig. 5. The survival curve presents a sharp decline after 28 days at 19.7 °C, after 49 days at 24.0 °C, after 13 days at 27.8 °C, and after 10 days at 32.6 and 35.5 °C. The daily fecundity declined gradually after peaking.

The estimated values of life table parameters for *R. pedestris* are presented in Table 5. The net reproductive rate was similar at 24.0 and 27.8 °C. The mean generation time decreased with increasing temperature up to 32.6 °C. The finite rate of increase ($\lambda=1.12$) and intrinsic rate of increase ($r_m=0.11$) were the highest at 32.6 °C.

Discussion

We investigated a wide range of temperatures for *R. pedestris* development and reproduction, determined the developmental times and fecundity, estimated important parameters for understanding biological processes using linear and nonlinear functions, and calculated the life table parameters of *R. pedestris*. Temperature affects the developmental time of *R. pedestris* as in other insect pests, such as *Acrosternum hilare* (Say), *Aphis glycines* (Matsumura), *Halyomorpha halys* (Stål), and *Megacopta cribraria* (Fabricius) in soybean fields (Baek et al. 2017; Hirano et al. 1996; Nielsen et al. 2008; Shi et al. 2014; Simmons and Yeorgan 1988). The developmental periods of *R. pedestris* for each life stage decreased as the temperature increased up to 34.2 °C (Table 1). These results disagree with those reported by Kim et al. (2009) for *R. pedestris*, who found that the developmental times for each life stage except the second instar nymph stage decreased continuously from 19.7 to 36.7 °C. *Riptortus pedestris* nymphs could not develop into adult stage under 15.9 °C in this study. This result was similar to

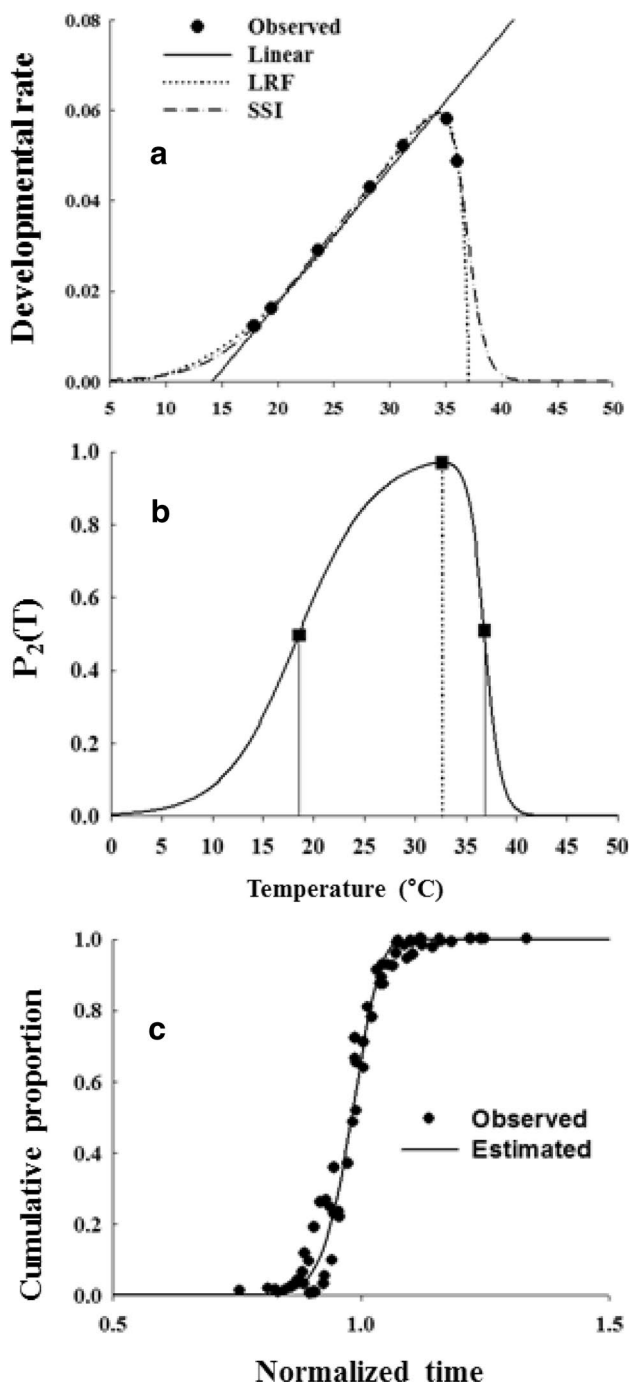


Fig. 1 **a** Linear and two nonlinear functions fitted to the data of developmental rates (day^{-1}) for total immature (egg-to-adult emergence) period of *Riptortus pedestris*. **b** $P_2(T)$ is the probability that rate-controlling enzyme is in the active stage. The closed three squares from left to right represent the development rates at T_L, T_ϕ and T_H . T_L and T_H which are temperatures at which the control enzyme has equal probability to be active or inactive by low- or high-temperature inactivation, and T_ϕ is the intrinsic optimum temperature. **c** Cumulative proportions of development completion for total immature period of *R. pedestris*

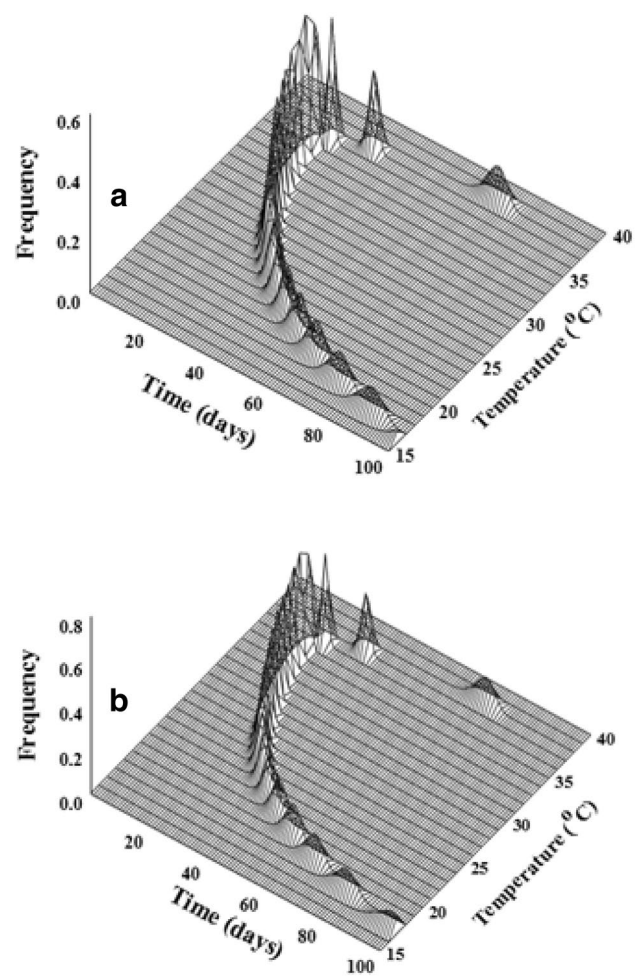


Fig. 2 Simulated temperature-dependent adult emergence of *Riptortus pedestris* using two nonlinear functions: **a** LRF model and **b** SSI model

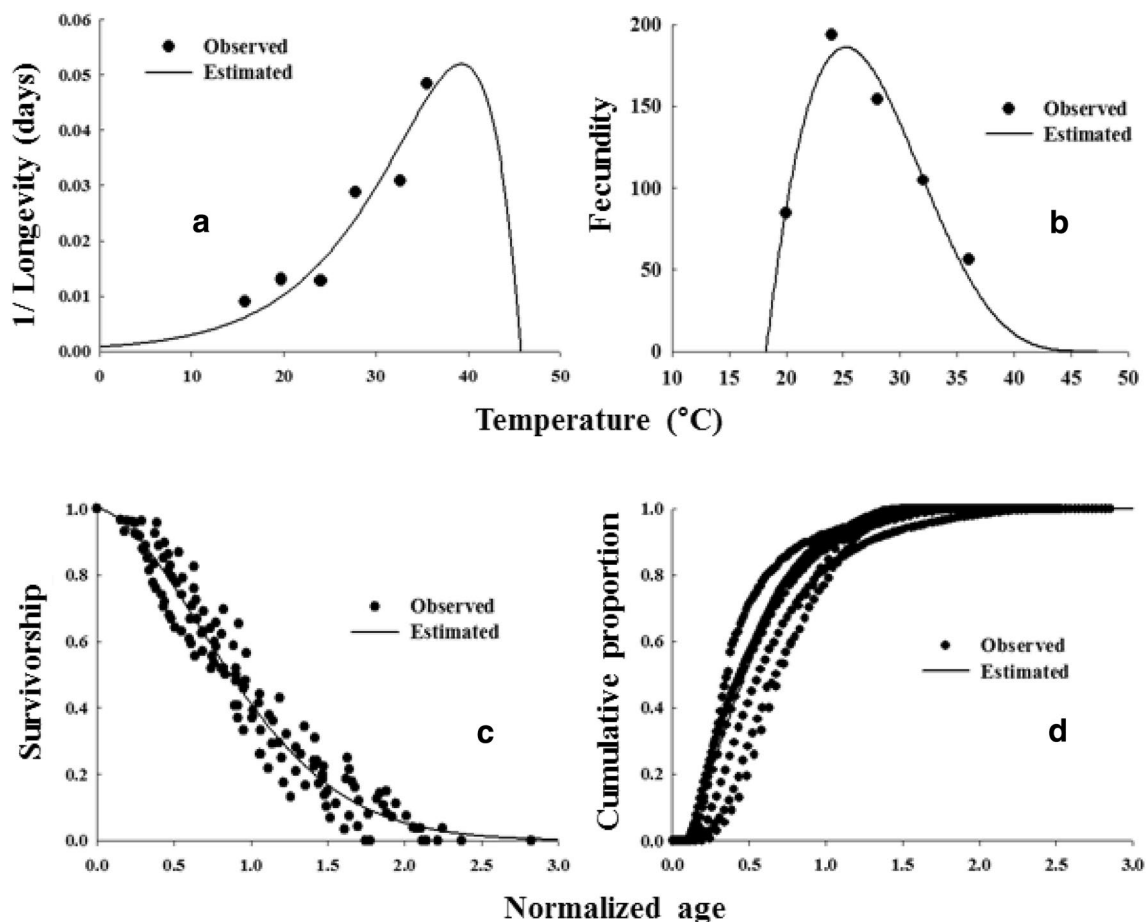
those reported by Kidokoro (1978) (17 °C) and Lee et al. (1997) (15 °C). The developmental periods for each life stage from this study were shorter than those reported by Kidokoro (1978), Lee et al. (1997), Bae et al. (2005), and Kim et al. (2009). It is inferred that the difference among developmental times is attributable to the food source or variety consumed, source of the insect population, and environmental conditions before the experiment.

In contrast to our study, Bae et al. (2005) reported lower LDTs for different nymph stages (8.7–12.7 °C) and total immature stage (10.0 °C) than our results (13.2–14.8 °C, 14.2 °C, respectively). However, Kim et al. (2009) reported higher values (14.5–15.8 °C) than the results of this study. The thermal constant of the total immature period in our study (336.7 DD) was lower than those reported by Kidokoro (1978) (385.0 DD) and Lee et al. (1997) (429.2 DD), and higher than those reported by Kono (1989) (326.8 DD) and Kim et al. (2009) (312.5 DD). These differences may be

Table 3 Preoviposition period, oviposition days, longevity (female and male) fecundity (eggs/female), and hatchability (%) (mean \pm SE) of *Riptortus pedestris* at different temperatures

Temperature (°C)	N	Pre-oviposition	Oviposition	Longevity		Fecundity	Hatchability (%)
				Female	Male		
15.8	28			110.4 \pm 15.61a	122.2 \pm 15.19b	–	
19.7	27	10.8 \pm 0.32a	52.4 \pm 7.65a	76.6 \pm 9.86a	206.9 \pm 22.11a	84.4 \pm 9.30c	62.3 \pm 12.21b
24.0	29	7.5 \pm 0.18b	64.7 \pm 6.32a	77.8 \pm 6.56a	122.9 \pm 11.15b	196.6 \pm 17.30a	79.2 \pm 14.97ab
27.8	27	5.2 \pm 0.45c	23.7 \pm 3.40b	34.7 \pm 3.99b	95.6 \pm 8.37b	154.3 \pm 25.79ab	84.0 \pm 16.48a
32.6	24	4.7 \pm 0.61c	26.1 \pm 2.36b	32.5 \pm 3.44b	34.6 \pm 4.47c	104.7 \pm 13.79bc	20.6 \pm 4.31c
35.5	23	5.6 \pm 0.72c	13.0 \pm 1.36b	20.6 \pm 1.25b	31.2 \pm 2.96c	56.1 \pm 8.55c	32.8 \pm 7.00c

Means followed by the same letter within a column are not significantly different ($p < 0.05$, Tukey's studentized range test). 'N' means the number of sample size at each temperature for statistical process. '–' means *R. pedestris* female did not oviposit. Pre-oviposition period: $F_{4, 123} = 30.02$, $p < 0.0001$, oviposition days: $F_{4, 123} = 19.20$, $p < 0.0001$, female longevity: $F_{5, 152} = 15.14$, $p < 0.0001$, male longevity: $F_{5, 152} = 23.16$, $p < 0.0001$, fecundity: $F_{4, 125} = 10.91$, $p < 0.0001$, and hatchability: $F_{4, 125} = 32.83$, $p < 0.0001$

**Fig. 3** Important components of oviposition model on *Riptortus pedestris*. **a** adult aging rate curve ($1/\text{mean longevity}$), **b** temperature-dependent total fecundity curve, **c** age-specific cumulative survival rate curve, and **d** age-specific cumulative oviposition rate curve

related to the differences in experimental conditions such as the nutrient of food resources, the origin of populations, and measurement of temperature.

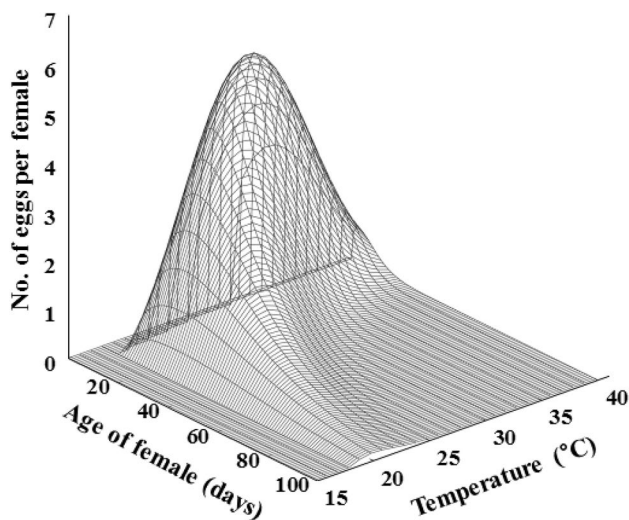
The developmental rate of *R. pedestris* was well fitted by two nonlinear models, which were then used to calculate

the developmental thresholds. In our study, the least-squares estimators are 0.96–0.99 and the estimated parameters presented the minimum variance. The models explained well the pooled development rates throughout the biokinetic temperature ranges tested. In contrast to the LRF model, SSI

Table 4 Parameter estimates for oviposition models of *Riptortus pedestris*

Models	Parameters	Estimated values	SE	R ²
Adult aging rate model	ρ	0.1562	0.0758	0.91
	T_M	45.7120	16.5921	
	ΔT	6.3974	3.1024	
Age-specific survival rate model	a	1.0756	0.0130	0.96
	b	1.7256	0.0532	
Age-specific cumulative oviposition rate model	γ	0.0587	0.0213	0.94
	η	0.5389	0.0252	
	β	1.3959	0.0753	
Temperature-dependent fecundity model	c	0.000003	0.00006	0.96
	T_L	18.2364	1.1041	
	T_M	47.3789	1.8248	
	m	0.2469	0.2678	

Adult aging rate model: $F_{2,3}=15.29$, $p<0.0267$, age-specific survival rate model: $F_{1,146}=3207.66$, $p<0.0001$, age-specific cumulative oviposition rate model: $F_{2,484}=3844.36$, $p<0.0001$, temperature-dependent fecundity model: $F_{3,2}=17.15$, $p<0.0556$

**Fig. 4** Simulated oviposition density curves of *Riptortus pedestris* related to temperatures (°C) and cohort age

model has clear biophysical meanings and gives thermodynamic information among model parameters. The intrinsic optimum temperature values in our study (32.6 °C) and that by Kidokoro (32.1 °C) using the SSI model were similar, and differed from those of Kim et al. (2009) (27.3 °C) and Bae et al. (2005) (26.9 °C). The temperature ranges for insect development were estimated from TL to TH using the SSI model (van der Have 2002; Dixon et al. 2009). The ranges were 18.3, 18.6, 19.9, and 20.9 for the present study, Kidokoro (1978), Bae et al. (2005), and Kim et al. (2009), respectively. The activation states of the rate-controlling enzyme from our study and Kidokoro (1978) were similar compared with other results. It can be inferred that the thermal tolerance for immature development of *R. pedestris*

from our study and Kidokoro is similar compared with the other results.

This study presents substantial evidence that temperature has a significant effect on the longevity and fecundity of *R. pedestris* adults and that the provided models constitute a crucial step towards establishment of population dynamic model. The longest pre-oviposition, oviposition periods, and total longevity for *R. pedestris* were at 19.7 °C and no significant differences were found in the range from 27.8 to 35.5 °C. The female longevity values in our study were shorter than those of male longevity. The difference in longevity between females and males has also been reported in *Corythucha cydoniae* (Fitch) (Neal and Douglass 1990) and *Monosteira unicastata* (Mulsant & Rey) (Sánchez-Ramos et al. 2017). It could be attributed to the oviposition behaviors of females, who invest substantial resources and energy to produce eggs and search for oviposition sites (Gibbs et al. 2010; Jervis et al. 2008).

The reproductive capacity of *R. pedestris* increased up to 24.0 °C and gradually decreased at higher temperatures. High fecundity was observed at 24.0 and 27.8 °C, with 196.6 and 154.3 eggs/female produced, respectively. Therefore, the optimum temperature for reproduction is likely between 24.0 and 27.8 °C. Kim et al. (2009) found relatively higher values of fecundity from 22.0 to 31.0 °C (353.2–369.2 eggs/female), whereas Bae et al. (2005) reported lower values from 20.0 to 32.0 °C (21.1–67.0 eggs/female). The number of eggs produced in our study was lower than that reported by Kim et al. (2009), and higher than that presented by Bae et al. (2005). In our study, the egg production was the lowest at the highest temperature (35.5 °C). Bae et al. (2005) and Kim et al. (2009) found a low reproductive capacity for *R. pedestris* when the females were reared at 20.0 and 34.0 °C, respectively. The estimated temperature for maximum

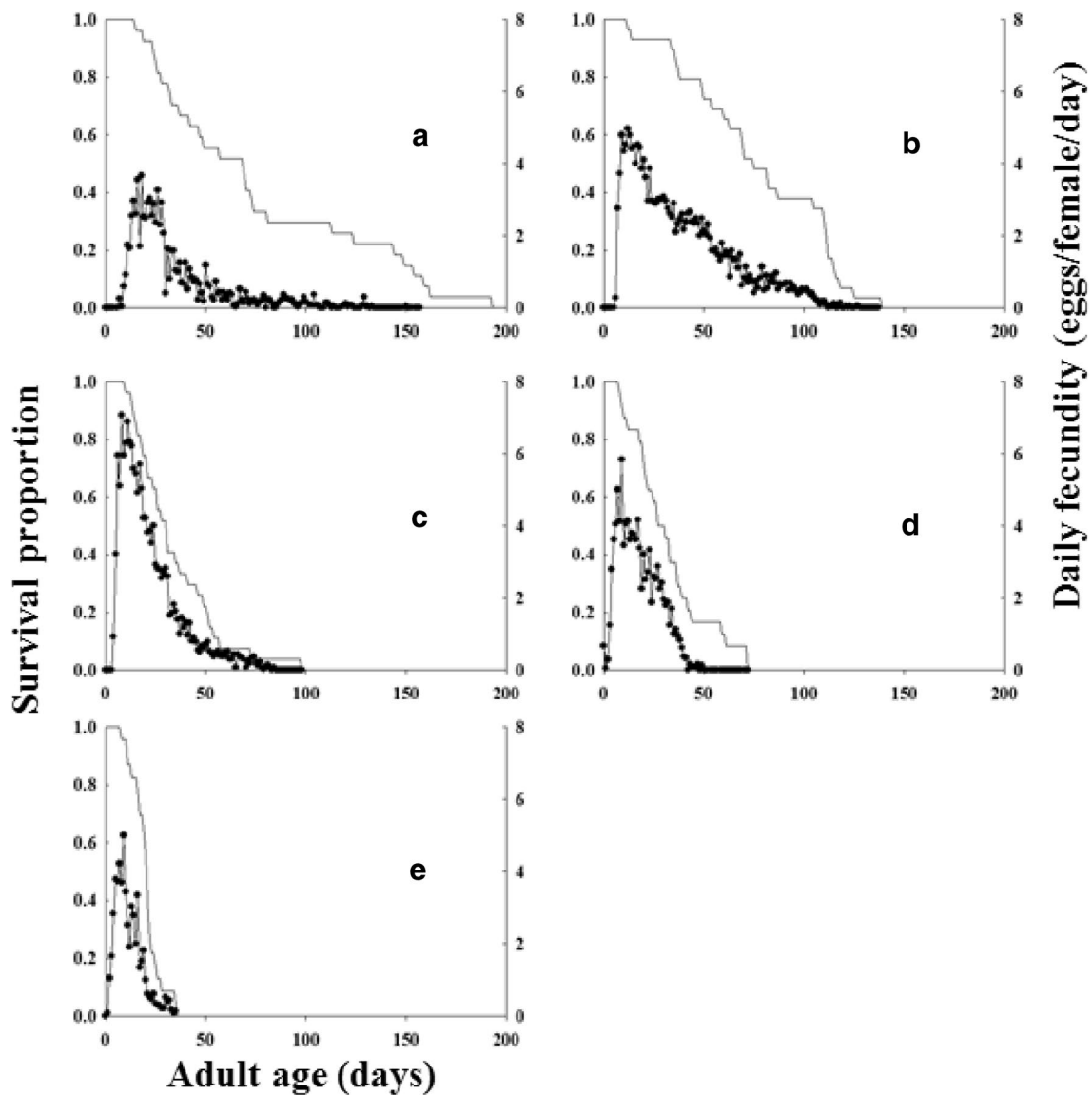


Fig. 5 The survival proportion and daily fecundity (mean eggs/female/day) of *Riptortus pedestris* at different constant temperatures. **a** 19.7 °C, **b** 24.0 °C, **c** 27.8 °C, **d** 32.6 °C, and **e** 35.5 °C

Table 5 Life table parameters of *Riptortus pedestris* at different temperatures

Temperature (°C)	Parameters (mean ± SD)				
	R_0	T (days)	DT (days)	λ	r_m
19.7	26.06 ± 5.80b	80.29 ± 4.76a	17.03 ± 0.97a	1.04 ± 0.002c	0.04 ± 0.002c
24.0	58.13 ± 10.51a	61.46 ± 3.74b	10.47 ± 0.52b	1.06 ± 0.003b	0.06 ± 0.003b
27.8	46.92 ± 15.82a	37.96 ± 5.18c	6.81 ± 0.82c	1.11 ± 0.013a	0.10 ± 0.012a
32.6	28.56 ± 8.55b	30.76 ± 1.46d	6.33 ± 0.51c	1.12 ± 0.009a	0.11 ± 0.008a
35.5	0.21 ± 0.07c	41.70 ± 3.90c	-18.85 ± 5.37d	0.96 ± 0.011d	-0.03 ± 0.01d

Means followed by the same letter in a column are not significantly different using Student's *t* test for pairwise group comparison at $p < 0.05$

reproductive capacity from our study and Kim et al. (2009) was similar at around 25 °C, but the estimated number of eggs reported by Kim et al. (2009) (453.8) was higher in comparison with our study (186.0). Nitrogen quality and the quantity of soybeans consumed may be responsible for the observed variation in fecundity across studies (Barnes et al. 2008).

We found that the intrinsic rate of increase (r_m) was three-fold higher when the temperature was increased from 19.7 to 32.6 °C. At 35.5 °C, the r_m value was negative. It means that the population growth of *R. pedestris* would decrease when they are exposed to this temperature. The results (0.22 and 0.23) of Rahman and Lim (2017) were higher than those from our study. The highest net reproductive rates (R_0) were observed at 24.0 and 27.8 °C in this study. The mean generation time (T) decreased with increasing temperature up to 32.6 °C.

In conclusion, our results provide valuable information about the biological traits of *R. pedestris* at various temperatures compared to the previous study—development time of male and female nymphs, longevity of female and male, and life table analysis, in addition to the estimated parameters of temperature-dependent development and oviposition models. We present the simulated temperature-dependent adult emergence frequency and oviposition density curves of *R. pedestris*. They could serve as a basis to improve management programs directed at controlling *R. pedestris* in crop plant systems.

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