Temperature-dependent development and oviposition models of *Riptortus clavatus* (Thunberg) (Hemiptera: Alydidae)

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Abstract

The temperature-dependent development, survival, longevity, and reproduction of *Riptortus clavatus* (Thunberg) (Hemiptera: Alydidae) were studied at constant temperatures in the laboratory. The mean developmental time from egg to adult emergence ranged from 18.8 d at 36.7°C to 67.0 d at 19.7°C and the lower temperature threshold for the total immature stage (egg to adult emergence) was 15.0°C. The nonlinear shape of temperature-dependent development was well described by the Lactin model. The standardized cumulative frequency distributions of developmental times for each life stage were fitted to the two-parameter Weibull function. Mean adult longevity ranged from 7.83 d at 34°C to 165.14 d at 17.5°C. Mean total fecundity ranged from 29.2 eggs at 34°C to 456.4 eggs at 25°C and was fitted to the extreme value function. Adult survival and the cumulative oviposition rate of *R. clavatus* were fitted to the sigmoid and two-parameter Weibull function, respectively. We anticipate that the fitted models and parameters will be useful in developing a population model for *R. clavatus*.

Key words: *Riptortus clavatus*; temperature-dependent development; longevity; fecundity; population model

INTRODUCTION

The bean bug, *Riptortus clavatus* (Thunberg) (Hemiptera: Alydidae), distributed in Korea, Japan, and Taiwan (Kobayashi, 1981), has a wide range of host plants (Kobayashi, 1981; Ito, 1982; Chung et al., 1995; Bae et al., 2004b) and causes serious damage to the beans of leguminous plants and the fruits of fruit trees (Kono, 1989; Chung et al., 1995; Kang et al., 2003). Several studies have investigated control methods for *R. clavatus* (Huh et al., 2005; Paik et al., 2007; Son et al., 2008; Youn and Jung, 2008); however, these previous studies did not incorporate a population dynamics model for *R. clavatus*, even though this could enhance the effectiveness of control methods and strategies.

To develop a population dynamics model for *R. clavatus*, models of temperature-dependent development and fecundity of *R. clavatus* are essential. Previous studies on the development or fecundity of *R. clavatus* (Kamano, 1978; Kidokoro, 1978;

Kikuchi and Kobayashi, 1986; Kono, 1989; Lee et al., 1997; Bae et al., 2005) were conducted within limited temperature ranges. Thus, it is not possible to derive comprehensive models for development and stage transfer, survival, and reproduction of *R. clavatus* from these previous studies. This study was initiated to quantify and model the effect of various temperatures on the development, survival, and reproduction of *R. clavatus*.

MATERIALS AND METHODS

Development of immature stages. The colonies of *R. clavatus* used in our study were obtained from the Apple Research Station (National Institute of Horticultural & Herbal Science, Gunwi, Korea) in November 2003, and have been maintained in a laboratory at Seoul National University at 26±2°C, 45–65% RH, with a photoperiod of 16:8 (L:D)h. Approximately 20 pairs of adults were placed in five plastic cages (50×30×30 cm).

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Dried soybeans and water-soaked cotton were provided as food and water sources, respectively, and a soybean plant (V3–V4 stage) in a plastic pot (10 cm height, 10 cm diameter) was placed in the cage for oviposition. Soybean plants were checked daily for eggs and newly oviposited eggs (<1-d-old) were transferred to a plastic container (1 egg/container, 4 cm height, 10 cm diameter) with the bottom covered by cotton and sterilized gauze. A hole (4 cm diameter) was made in the lid of the container and covered with mesh cloth (20×20 mesh per cm²) for ventilation. The containers were then placed in incubators at one of seven temperatures (19.7, 21.3, 25.3, 27.4, 30.4, 33.8, and 36.7°C), photoperiod of 16:8 (L:D)h, and 50–70% RH. Eggs were undisturbed until hatching, and the hatched nymphs were provided with dried soybeans and water-soaked cotton. Development of *R. clavatus* was monitored at 24 h intervals.

Developmental rates were expressed as the reciprocal of developmental times (in days) of each stage. Best-fit linear lines were obtained by regressing the linear portion of the developmental rate curves for each stage using PROC REG in SAS (SAS Institute, 2002). The lower temperature threshold for development was calculated as the x -intercept of the fitted equation for each stage (Arnold, 1959). Furthermore, developmental rate curves of each stage were fitted to the Lactin model (Lactin et al., 1995):

$$r(T) = e^{(\rho t)} - e^{(\rho T - (T-t)/\delta)} + \lambda \quad (1)$$

where $r(T)$ is the mean developmental rate at temperature T (°C), ρ estimates the rate increase to the optimal temperature, t is the upper lethal temperature, and λ is the age of the developmental decline phase at high temperature.

The variation of developmental times for each stage was described by the cumulative proportion distribution of developmental times for each stage modeled using a two-parameter Weibull function (Kim et al., 2001):

$$F(px) = 1 - e^{-(px/\alpha)^\beta} \quad (2)$$

where $F(px)$ is the cumulative proportion of stage emergence at physiological age px , and α and β are the parameters. Physiological age (px) was calculated by Eq. (3) using nonlinear developmental rates (Lactin model):

$$px = \sum_{i=1}^n r(T_i) \quad (3)$$

where $r(T_i)$ is the developmental rate at temperature T (°C) at day i . The parameter values of the two-parameter Weibull function and Lactin model were estimated using PROC NLIN in SAS (SAS Institute, 2002).

Longevity, fecundity, and survival of adults.

Six constant temperatures (17.5, 22, 25, 28, 31, and 34°C) were used to determine the effect of temperature on the longevity and fecundity of adult *R. clavatus*. A pair of newly-emerged (<1-d-old) adults were placed in a plastic container (4 cm height, 10 cm diameter) with cotton and sterilized gauze covering the bottom. The containers were then placed in an incubator at one of six temperature regimes, a photoperiod of 16:8 (L:D) h, and 50–70% RH. The adults were provided with dried soybeans and water-soaked cotton as food and water sources, respectively. Female adult survival (longevity) and the number of eggs laid were examined daily.

The reciprocals of longevity (in days) at the tested constant temperatures were used as the adult developmental rates. A function to describe the relationship between adult developmental rates and temperature was selected from the library of TableCurve (Jandel Scientific, 1996) based on the flexibility and simplicity of the function and its fit to the data. The function was

$$r(T) = a + be^T + cT^{0.5} \quad (4)$$

where $r(T)$ is the temperature-dependent developmental rate at temperature T (°C), and a , b , and c are fitted constants. Values of the parameters were estimated using TableCurve (Jandel Scientific, 1996).

Survival rates were calculated as the number of insects alive at any given physiological age divided by the total number tested. A sigmoid function was used to describe the survival distribution of female *R. clavatus*. The equation is as follows:

$$s(px) = \frac{1}{1 + e^{((\gamma - px)/\delta)}} \quad (5)$$

where $s(px)$ is the proportion of live females at the physiological age px , γ is the physiological age at

Table 1. Developmental time (day, mean $\pm$ S.E.) of immature *R. clavatus* at constant temperature

Temperature (°C)	Egg	1st instar	2nd instar	3rd instar	4th instar	5th instar	Egg–5th instar
19.7	17.4 $\pm$ 0.10 (60)	4.9 $\pm$ 0.08 (55)	8.3 $\pm$ 0.12 (27)	9.1 $\pm$ 0.23 (12)	10.5 $\pm$ 0.65 (4)	17.0 $\pm$ 1.00 (4)	67.0 $\pm$ 1.68
21.3	14.7 $\pm$ 0.13 (60)	4.2 $\pm$ 0.06 (55)	6.5 $\pm$ 0.30 (37)	8.1 $\pm$ 1.33 (16)	8.7 $\pm$ 1.33 (6)	11.6 $\pm$ 0.40 (5)	50.0 $\pm$ 1.82
25.3	9.9 $\pm$ 0.05 (120)	2.4 $\pm$ 0.05 (117)	3.9 $\pm$ 0.08 (112)	4.5 $\pm$ 0.11 (92)	5.7 $\pm$ 0.18 (54)	7.1 $\pm$ 0.19 (22)	31.9 $\pm$ 0.59
27.4	7.5 $\pm$ 0.07 (60)	2.0 $\pm$ 0.03 (55)	3.2 $\pm$ 0.11 (48)	3.7 $\pm$ 0.10 (44)	4.3 $\pm$ 0.11 (39)	5.9 $\pm$ 0.13 (30)	25.7 $\pm$ 0.33
30.4	6.0 $\pm$ 0.04 (60)	1.9 $\pm$ 0.04 (56)	2.8 $\pm$ 0.08 (54)	2.8 $\pm$ 0.11 (49)	3.4 $\pm$ 0.11 (41)	4.7 $\pm$ 0.13 (36)	20.3 $\pm$ 0.20
33.8	5.3 $\pm$ 0.07 (60)	2.0 $\pm$ 0.04 (57)	2.2 $\pm$ 0.06 (52)	2.8 $\pm$ 0.11 (40)	3.2 $\pm$ 0.14 (34)	4.3 $\pm$ 0.11 (27)	19.1 $\pm$ 0.24
36.7	5.0 $\pm$ 0.00 (90)	1.5 $\pm$ 0.10 (47)	2.8 $\pm$ 0.19 (43)	2.5 $\pm$ 0.14 (29)	3.0 $\pm$ 0.13 (13)	4.0 $\pm$ 0.26 (5)	18.8 $\pm$ 0.70

Numbers in parentheses indicate the numbers of individuals observed.

50% survival, and δ is the parameter defining the steepness of the equation. The parameters were estimated using PROC NLIN in SAS (SAS Institute, 2002).

Mean total fecundity was calculated by dividing the sum of total eggs laid by all adults by the number of adults examined. An extreme value function (Kim and Lee, 2003) was used to describe the relationship between total fecundity and temperature:

$$f(T) = a \cdot e^{[1 + ((b-T)/k) - e^{((b-T)/k)}]} \quad (6)$$

where $f(T)$ is the number of total eggs produced by a female at temperature T (°C), a is the maximum reproductive capacity, b is the temperature (°C) at which maximum reproduction occurs, and k is a fitted constant. Values of the parameters were estimated using PROC NLIN in SAS (SAS Institute, 2002).

The mean cumulative oviposition rate for each physiological age was calculated by averaging the cumulative oviposition rates at the same physiological age for the respective temperature regime. The physiological age (px) of adults was calculated using Eq. (3). The two-parameter Weibull function [Eq. (2)] was used as the cumulative oviposition rate model. Parameter values were estimated using PROC NLIN in SAS (SAS Institute, 2002).

RESULTS

Development of immature stages

R. clavatus was able to develop from the egg to adult stage at all temperatures tested. Cumulative immature mortality decreased as temperature increased to 30.4°C. Overall, the developmental time of *R. clavatus* decreased as temperature increased (Table 1). The mean total developmental time

Fig. 1. Developmental rates (1/day) of eggs and first through fifth nymphs of *R. clavatus* reared under constant temperatures in the laboratory. Dotted straight lines are linear regression lines. Open circle data points were excluded in the linear regression analysis. Solid lines are non-linear regression lines. Fitted curve: Lactin model. All data points were included in the non-linear regression analysis.

ranged from 18.8 days at 36.7°C to 67.0 days at 19.7°C. The relationship between the developmental rate of each stage and temperature is shown in Fig. 1. The estimated parameter values of the linear model and the lower temperature threshold for each stage of *R. clavatus* are presented in Table 2. The

estimated base temperature ranged between 14.2 and 15.8°C. The nonlinear shape of temperature development was well described by the Lactin model [Eq. (1); Fig. 1; Table 3]. Developmental variation of each stage was well described by the two-parameter Weibull function [Eq. (2); Fig. 2; Table 4].

Adult longevity and fecundity

Temperature had a significant effect on the longevity of female adult *R. clavatus* ($F=36.37$; $df=5, 143$; $p<0.0001$). The longevity of female adults decreased with increasing temperature (Table 5). Longevity was greatest at 17.5°C (165.14 days) while it was smallest at 34°C (7.83 days). A nonlinear function [Eq. (4)] described adult developmental rates over the tested temperature range well (Fig. 3, $r^2=0.99$). The estimated parameter values for a , b , and c were -0.026 (S.E.=0.0089), $1.89e-16$ (S.E.=4.554e-18), and 0.007 (S.E.=0.0018), respectively. The relationship between survival and adult physiological age was well described by a sigmoid function [Eq. (5);

Fig. 4a; Table 6].

The pre-oviposition period of female adult *R. clavatus* decreased significantly as temperature increased ($F=99.03$; $df=5, 130$; $p<0.0001$; Table 5). Oviposition occurred at all temperatures tested, but relatively lower fecundity was observed at the lowest and highest temperatures (17.5°C and 34°C, respectively, Table 5). Fecundity was significantly

Table 2. Linear developmental model and lower temperature threshold for each immature stage of *R. clavatus*

Stage	Model	r^2	Lower temperature threshold (°C)
Egg	$0.0099x-0.1405$	0.99	14.2
1st instar	$0.0398x-0.5931$	0.99	14.9
2nd instar	$0.0233x-0.3378$	0.99	14.5
3rd instar	$0.0239x-0.3767$	0.99	15.8
4th instar	$0.0189x-0.2856$	0.99	15.1
5th instar	$0.0143x-0.2216$	0.99	15.5
Egg–5th	$0.0032x-0.048$	0.99	15.0

Fig. 2. Cumulative proportions of development in each stage of *R. clavatus* versus physiological age. A two-parameter Weibull function was applied.

Table 3. Estimated values of the parameters of the Lactin model fitted to the developmental rate (1/day) for egg and nymphal stages of *R. clavatus*

Stage	Parameters (estimated value $\pm$ S.E.)			
	ρ	δ	t	λ
Egg	0.0084 ± 0.0008	2.2450 ± 2.5339	45.1484 ± 8.8025	-1.1250 ± 0.0233
1st instar	0.0340 ± 10.4276	14.6960 ± 3076.7	59.0832 ± 358.6	-1.2283 ± 206.5
2nd instar	0.1681 ± 0.0372	5.9387 ± 1.3001	39.7453 ± 1.2026	-0.0172 ± 0.0903
3rd instar	0.0868 ± 0.0737	11.1461 ± 8.1983	46.8809 ± 10.4760	-0.3271 ± 0.6159
4th instar	0.1091 ± 0.0501	9.0773 ± 3.9782	44.6663 ± 5.0170	-0.1355 ± 0.1987
5th instar	0.0533 ± 0.0327	16.8143 ± 6.8791	54.7556 ± 10.4033	-0.4948 ± 0.4711

affected by temperature ($F=22.9$; $df=5, 143$; $p<0.0001$); fecundity increased as temperature increased up to 25°C and thereafter decreased. The relationship between the mean total fecundity and temperature was well described by the extreme value model [Eq. (6); Fig. 4b; Table 6]. The cumulative oviposition rate curve against the adult physiological age was well described by the two-parameter Weibull function (Fig. 4b; Table 6).

Table 4. Estimated parameter values for the distribution model (two-parameter Weibull function) of developmental time for each stage of *R. clavatus*

Stage	Parameter (estimated value $\pm$ S.E.)		r^2
	α	β	
Egg	0.962 ± 0.0097	15.390 ± 3.3988	0.88
1st instar	0.898 ± 0.0413	5.497 ± 1.6567	0.85
2nd instar	1.022 ± 0.0263	4.350 ± 0.6812	0.90
3rd instar	0.898 ± 0.0183	5.415 ± 0.7858	0.93
4th instar	0.927 ± 0.0124	6.376 ± 0.7425	0.95
5th instar	0.973 ± 0.0093	12.397 ± 1.9556	0.93

Fig. 3. Developmental rate curve (1/mean longevity) of adult *R. clavatus*. A nonlinear model function selected from the library of TableCurve was applied.

Fig. 4. Three temperature-dependent components for reproduction and survival of female adult *R. clavatus*. (a) Age-specific survival rate curve. A sigmoid function was applied (● observed, — estimated). (b) Temperature-dependent total fecundity curve. An extreme value model was applied (● observed, — estimated). (c) Age-specific cumulative oviposition rate curve. A two-parameter Weibull function was applied (○ observed, — estimated).

Table 5. Mean longevity, fecundity, and pre-oviposition period (mean $\pm$ S.E.) of female adult *R. clavatus* at constant temperature

Temp. (°C)	<i>n</i>	Longevity (day)	Fecundity	<i>n</i>	Pre-oviposition period (day)
17.5	14	165.14 ± 24.944 a	110.8 ± 31.35 a	11	26.9 ± 2.81 a
22	18	134.94 ± 15.582 ab	353.2 ± 63.52 b	17	11.1 ± 1.36 b
25	18	109.22 ± 12.159 b	456.4 ± 54.40 b	18	7.4 ± 0.71 c
28	45	64.60 ± 5.069 c	383.8 ± 29.44 b	41	3.3 ± 0.10 d
31	18	48.33 ± 6.677 cd	369.2 ± 58.71 b	14	3.9 ± 0.21 cd
34	36	7.83 ± 0.482 d	29.2 ± 4.00 a	35	2.1 ± 0.22 d

Means followed by the same letter within a column are not significantly different at $\alpha=0.05$, Tukey's studentized range test.

Table 6. Estimated values of parameters for survival rate, temperature-dependent total fecundity, and cumulative oviposition rate models of female adult *R. clavatus*

Models	Parameters	Estimated values	S.E.	r^2
Survival rate model	γ	0.96	0.005	0.93
	δ	-0.33	0.005	
Temperature-dependent total fecundity model	a	453.80	51.610	0.83
	b	25.94	0.973	
	k	-6.05	1.148	
Cumulative oviposition rate model	α	0.62	0.002	0.98
	β	1.65	0.016	

DISCUSSION

Developmental times and low threshold temperatures for nymphal development of *R. clavatus* differ among studies (Table 7). Different food sources and rearing conditions could be responsible for these observed differences. Bae et al. (2004a) reported that different rearing conditions affect nymphal development and the emergence rate of adult *R. clavatus*; these authors speculated that different amounts of ventilation under different rearing conditions could be responsible. It has also been shown that different food sources can affect the development of *R. clavatus* (Kidokoro, 1978; Bae et al., 2004b; Choi et al., 2005). In our study, we used soybeans while Kidokoro (1978), Kono (1989), Lee et al. (1997), and Bae et al. (2005) used a mixture of soybeans and rice, dried soybeans, kidney beans, and a mixture of soybeans and peanuts, respectively (Table 7).

It appears that adult *R. clavatus* is sensitive to high ($>31^{\circ}\text{C}$) and low ($<22^{\circ}\text{C}$) temperatures. Even though the longevity of female adult *R. clavatus* at the lowest temperature (17.5°C) was greatest (165.14 d) amongst all temperatures tested, fecundity at this temperature was significantly lower than at higher temperatures (22, 25, 28, and 31°C), with the exception of 34°C (Table 5). The fecundity and longevity of adult *R. clavatus* at 34°C were significantly lower and shorter, respectively, than at all other tested temperatures in this study. This trend has also been shown in a previous study, albeit with some differences in longevity and fecundity estimates. Bae et al. (2005) showed that the longevity and fecundity of adult *R. clavatus* were greater at mid-temperatures (24 and 28°C)

compared to high (32°C) and low (20°C) temperatures. The highest mean total fecundity was 456.4 eggs at 25°C in our study, while Bae et al. (2005) reported a value of 67.0 eggs at 28°C . Thus, there is a large discrepancy between our study and that of Bae et al.'s in the mean total fecundity per female. Kikuchi and Kobayashi (1986) reported that the fecundity of *R. clavatus* ranged from 47 to 448 eggs, depending on the food source. Even though the variation in the fecundity of *R. clavatus* in Kikuchi and Kobayashi's (1986) study resulted from food source differences, the highest mean egg production was similar to our result, implying that the fecundity potential of *R. clavatus* could be higher than 400 eggs. The lower fecundity of *R. clavatus* observed in Bae et al.'s (2005) study might be due to dietary conditions, reduced sunlight, and/or limited ventilation, among other factors. Kaakeh and Dutcher (1993) demonstrated that insect fecundity could be modified by food. Kim and Lee (2008) reported that the fecundity of *Scotinophara lurida* (Burmeister) was much lower under laboratory conditions than greenhouse conditions, and speculated that reduced sunlight and limited ventilation might be responsible for the lower fecundity observed under laboratory conditions.

To select accurate models for the development and reproduction in *R. clavatus* in our study, we placed more emphasis on the shape-fitting ability and simplicity of the models than their biological meaning. Besides the Lactin model, we also investigated a biophysics model (Sharpe and DeMichele, 1977), Logan model (Logan et al., 1976), and Briere model (Briere et al., 1999) when fitting developmental rates for immature stages of *R. clavatus*; of all these models, however, the Lactin model (Lactin et al., 1995) fit best. For female adult development, none of the models mentioned above fit well; therefore, we selected a model from the library of TableCurve (Jandel Scientific, 1996). To describe the relationship between the total fecundity of insects and temperature, several models have been used, such as a square root exponential function (Brown et al., 1978), a quadratic function (Shaffer and Gold, 1985), a linear function (Dover et al., 1979), a Logan (Logan et al., 1976) function (Berry et al., 1991), and an extreme value function (Kim and Lee, 2003). We selected the extreme value function for total fecun-

Table 7. Developmental time and low-threshold temperature for each life stage of *R. clavatus* on different food sources

Temp. (°C)	Egg	1st	2nd	3rd	4th	5th	1st–5th	Egg–5th	Food source (variety)	Reference
15	43.4									Lee et al. (1997)
17	30.0									Kidokoro (1978)
19.7	17.4	4.9	8.3	9.1	10.5	17	50.0	67.0	Soybeans	Present data
20	16.0						54.0		Soybeans+rice	Kidokoro (1978)
20	19.0						76.1		Kidney beans	Lee et al. (1997)
20	16.7	3.5	7.3	8.3	9.2	10.1	37.8		Soybeans+peanuts	Bae et al. (2005)
21.3	14.7	4.2	6.5	8.1	8.7	11.6	35.8	50.0	Soybeans	Present data
24	10.0						26.5		Soybeans+rice	Kidokoro (1978)
24	10.1	2.9	5.4	6.1	7.6	8.1	30.4		Soybeans+peanuts	Bae et al. (2005)
25	9.9						29.3		Kidney beans	Lee et al. (1997)
25		2.5	3.5	4.1	5.2	6.7	21.9		Soybeans (Myongjunamulkong)	Choi et al. (2005)
25		2.0	4.1	4.1	5.5	6.3	21.9		Soybeans (Eunhakong)	Choi et al. (2005)
25		2.3	4.5	4.4	5.9	7.4	24.5		Soybeans (Punsannamulkong)	Choi et al. (2005)
25		2.7	4.1	4.0	4.9	7.3	22.9		Soybeans (IAC78-2318)	Choi et al. (2005)
25		2.7	5.5	5.5	5.0	13.5	31.5		Soybeans (Jangannogdu)	Choi et al. (2005)
25.3	9.9	2.4	3.9	4.5	5.7	7.1	22.2	31.9	Soybeans	Present data
26		2.4	4.1	4.3	4.7	5.7	20.7		Soybeans	Bae et al. (2004b)
26		2.5	5.1	6.0	6.9	7.3	27.7		Kidney beans	Bae et al. (2004b)
26		2.4	4.6	5.2	5.4	6.0	23.8		Peanuts	Bae et al. (2004b)
26		2.4	4.2	4.3	4.6	5.4	20.6		Soybeans+kidney beans	Bae et al. (2004b)
26		2.5	4.4	5.0	5.5	6.3	23.7		Kidney beans+peanuts	Bae et al. (2004b)
26		2.4	4.0	4.2	4.4	5.3	20.0		Soybeans+peanuts	Bae et al. (2004b)
27	7.0						19.6		Soybeans+rice	Kidokoro (1978)
27							19.0		Soybeans	Kidokoro (1978)
27							17.0		Adzuki beans	Kidokoro (1978)
27							25.6		Kidney beans	Kidokoro (1978)
27							29.3		Rice	Kidokoro (1978)
27.4	7.5	2.0	3.2	3.7	4.3	5.9	18.8	25.7	Soybeans	Present data
28	8.7	2.4	4.0	4.8	5.4	6.6	23.3		Soybeans+peanuts	Bae et al. (2005)
30	6.0						15.1		Soybeans+rice	Kidokoro (1978)
30	6.8						22.3		Kidney beans	Lee et al. (1997)
30.4	6.0	1.9	2.8	2.8	3.4	4.7	15.2	20.3	Soybeans	Present data
32	7.0	1.7	2.9	3.8	4.2	5.0	17.8		Soybeans+peanuts	Bae et al. (2005)
33.8	5.3	2.0	2.2	2.8	3.2	4.3	14.1	19.1	Soybeans	Present data
36.7	5.0	1.5	2.8	2.5	3.0	4.0	13.8	18.8	Soybeans	Present data
Low-threshold temp. (°C)	14.2	14.9	14.5	15.8	15.1	15.5	15.0	15.0	Soybeans	Present data
	10.3	9.3	12.7	10.0	11.0	8.7		10.0	Soybeans+peanuts	Bae et al. (2005)
	12.9						15.4	15.1	Kidney beans	Lee et al. (1997)
	12.2	11.4	13.7	12.2	13.5	14.1	13.1	13.3	Soybeans	Kono (1989)
	14.0						15.8	15.3	Soybeans+rice	Kidokoro (1978)

dity of *R. clavatus* based on its fit to the data.

Previously, several researchers (Kidokoro, 1978; Kono, 1989; Lee et al., 1997; Bae et al., 2005) have studied the effect of temperature on the development of *R. clavatus* and have used linear models to describe the relationship between temperature and the developmental rate. A linear model is usually very useful for estimating the lower temperature threshold and developing a simple degree-day

model. Nevertheless, in general, nonlinear models are better at describing the relationship between temperature and the developmental rate of insects (Logan et al., 1976; Lactin et al., 1995; Briere et al., 1999), and a linear model alone might not be sufficient to develop a comprehensive population model. In our study, both linear and nonlinear models were used to describe the relationship between temperature and the developmental rate. In

addition, developmental variation in *R. clavatus* populations, which was not investigated in previous studies, was also modeled using physiological age and the Weibull function. Furthermore, we present the first model of adult longevity and fecundity in our study, because to develop a comprehensive population dynamics model of *R. clavatus*, both development and oviposition models are essential.

We anticipate that the data and models presented in our study will form the basis for a more complete understanding of *R. clavatus* population dynamics. They will also be very useful to develop a phenology or population dynamics model of *R. clavatus* to predict the level of occurrence or stage present in the field, thereby contributing to the development of an effective management program for *R. clavatus*.

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