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Temperature-dependent NYMPHAL Development of *Paromius Exiguus* (Distant) (Hemiptera: Lygaeidae) on *Imperata Cylinderica* and *Calamagrostis Epigeios*

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Abstract:
The developmental of nymphal stages of *P. exiguus* was studied at eight different constant temperatures (17.5, 20, 22.5, 25, 27.5, 30, 32.5, and 35 °C) with a photoperiod of 14:10 (L:D) h on two host plants, *Imperata cylinderica* and *Calamagrostis epigeios*. On both plants, the developmental time decreased with increasing temperature. The developmental time was significantly longer on *I. cylinderica* for each nymphal stage and for the total nymphal stage, as well. The relationship between developmental rate and temperature was fitted to a linear regression and the five nonlinear models (Lactin 1, Lactin 2, Briere 1, Briere 2, and Logan 6). The lower developmental thresholds for the first, second, third, fourth, fifth and total nymphal stages were 15.5, 15.7, 12.2, 10.1, 9.2, and 13.1°C, respectively on *I. cylindrica* and 5.7, 11.5, 9.5, 9.9, 11.2, and 10.0°C, respectively on *C. epigeios*. Thermal constants (DD, degree days) required for completion of the first, second, third, fourth, fifth and total nymphal stages, were 50.2, 43.1, 69, 103.6, 159.2, and 365.2DD, respectivelu on *I. cylindrica* and 60.9, 34.0, 44.3, 55.7, 90.9, and 277.5DD, respectively on*C. epigeios*. Lactin models and Logan 6 model were found to be better to describe the relationship between temperature and the developmental rate of *P. exiguus* nymphs on both host plants. The distribution of completion of each development stage was well described by the two-parameter Weibull function.

Keywords:
Paromius Exiguus, Developmental Time, Development Models, Imperata Cylinderica, Calamagrostis Epigeios

1. Introduction

Paromius exiguous (Distant) is a stink bug that sucks the rice panicles in rice fields. The bug has three generations per year, and five nymphal stages, and hibernates as an adult. After overwintering, in mid-May, the adults aggregate on the panicles of *Imperata cylindrica*, spending the first generation. Then, adults and few late occurring old nymphs of the first generation move to *Calamagrostis epigeios*, then spend the second generation. Then newly emerged adults disperse to the rice plants mostly and other gramineae weeds in early August. Afterwards, they complete the third generation and then move to the overwintering site [14].

Although the seasonal occurrence and age structure of *P. exiguus* on major host plants and temperature-dependent development model of egg and nymphal stages were studied on rice [14,15], additional information is still required to develop the phenology model of *P.exiguus* to predict its seasonal occurrence in the field. For example, nymphal development on two host plants, *I. cylindrica* and *C. epigeios* was not studied yet. Reliable prediction of insect phenology is essential for effective pest management [7]. Since insect development is temperature-dependent, a temperature-dependent insect population phenology or population dynamics models are often used for prediction of the seasonal occurrence of insects in the field [6,9,10,13]. Therefore, this research was carried out to investigate the nymphal development of *P. exiguus* on two other host plants, *I. cylindrica* and *C. epigeios* to develop a temperature-dependent development phenology model of *P. exiguous*

2. Materials and Methods

The adults were collected from the Shiwa reclaimed land, Ansan, Gyeonggi-do, Korea and reared on the rice panicles in the laboratory condition. Newly hatched nymphs were transferred individually by fine-hair paint brush to a plastic tube (2.5cm diameter, 15cm length). The plastic tubes were prepared by putting the absorbent cotton roll soaked with water at the base and provided the panicle of *I. cylindrica or C. epigeios*. The sponge was secured over the top of each tube for ventilation. The tubes were maintained in the growth chambers with eight different temperature regimes (17.5, 20, 22.5, 25, 27.5, 30, 32.5 and 35°C) at a photoperiod of 14:10 (L:D) h, and the replication of 60 times on each host and for each temperature.

Nymphal development was observed and recorded for individual nymphs daily. Each nymph was monitored through five nymphal instars to adult emergence. The cotton roll at the base of each tube was soaked with water daily to maintain the moisture. Panicles were replaced in all tubes at 2-3 days intervals, depending on freshness.

The relationship between developmental rates and temperatures was fitted to the linear regression and five nonlinear models [12,11,2] (Table 1). The x-intercepts, obtained from the linear regression model, were used to approximate the lower developmental threshold for each stage for each host [1]. The degree-day heat unit was calculated by taking the inverse of the slope of the linear regression line of temperature and development rate for each stage. The age scale in days of each stage was transformed to physiological age (*Px*) by the rate summation method [4]:

$$P_x = \sum_{i=1}^{n} r(T_i)$$

where r(Ti) is the development rate of each stage at temperature (°C) of ith day after emergence to the stage.

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Cumulative proportion for the completed development at a physiological age for each nymphal stage was fitted by a two-parameter Weibull function (Cockfield et al., 1994). The equation is:

$$F(P_x) = 1 - e^{-\left(\frac{P_x}{\alpha}\right)^{\beta}}$$

where *F(Px)* is the cumulative proportion of stage emergence at physiological age Px, α and β are parameters.

Development times at different temperatures on each host plant and at the same temperature between two hosts were compared by using the general linear model procedure (PROC GLM in SAS) [18] for each instar separately as well as the total nymphal stage. Means were separated using the Duncan Multiple Range Test ($p<0.05$, DMRT). The estimates of model parameters for the nonlinear regression models and Weibull function were obtained using TableCurve 2D [8].

3. Results

The nymphs of *P. exiguus* developed successfully to the adult stage at all temperatures tested. On both host plants, the developmental time decreased with increasing temperatures (17.5 to 35 °C) (Table 2 and Table 3). On both host plants, developmental times of each nymphal stage were significantly different among low and intermediate temperatures (17.5-27.5 °C) but were not significant different at high temperatures (30-35 °C), in general. Overall, nymphal developmental times were significantly longer on *I. cylindrical* than on *C. epigeios* except for the first instar nymph at 35 °C and the second instar nymph at 32.5 and 35 °C (Figure 1). The total nymphal development time was thus significantly longer on *I. cylindrical* than on *C. epigeios* at all temperatures. It was 69.6 days at 17.5 °C and 16.6 days at 35 °C on I. cylindrical, and was 38.6 days at 17.5 °C and 13.8 days at 35 °C on C. epigeios. The highest mortality occurred in the fifth nymphal stage at all temperatures on both host plants. Overall, the total nymphal mortality tended to be higher on *I. cylinderica* than on *C. epigeios* (Table 2 and Table 3).

Table 1. *The nonlinear developmental rate models that have been created to describe temperature-dependent development of insects and related arthropods.*

Model	Equation	Reference
Lactin 1	$r(T)=e^{(\rho T)} - e^{(\rho T_L - (T_L - T)/\Delta T)}$	Lactin et al. (1995)
Lactin 2	$r(T)=(e^{(\rho T)} - e^{(\rho T_L - (T_L - T)/\Delta T)})+\lambda$	Lactin et al. (1995)
Briere 1	$r(T)= \alpha T(T-T_0)(T_L-T)^{1/2}$	Briere et al. (1999)
Briere 2	$r(T)= \alpha T(T-T_0)(T_L-T)^{1/m}$	Briere et al. (1999)
Logan 6	$r(T)= \Psi(e^{(\rho T)} - e^{(\rho T_{max} - (T_{max} - T)/\Delta T)})$	Logan et al. (1976)

In both Lactin 1 and 2 models, r(T) is developmental rate, T is the rearing temperature (°C), ρ is a constant defining the rate of optimal temperature, T_L is the high temperature threshold, ΔT is the temperature range over which physiological breakdown becomes the overriding influence. In both Briere 1 and 2 models, T and T_L are as in the Lactin 1 model, and T_0 is the low temperature threshold. In Logan 6 model, T and ρ are as in the Lactin 1 model, T_{max} is the high temperature threshold, and Ψ is the maximum developmental rate.

Table 2. *Developmental time (day) (mean±SEM) for immature stages of P. exiguus at constant temperatures on I. cylindrica.*

Temp. (°C)	Nymphal stage					Total nymph
	1st nymph	2nd nymph	3rd nymph	4th nymph	5th nymph	
17.5	14.6±1.21 a (50.0)	12.5±0.60 a (86.7)	12.0±0.70 a (88.5)	15.3±1.05 a (78.3)	18.6±1.53 a (38.9)	69.6±3.26 a (11.7)
20	13.8±0.87 a (51.6)	11.9±0.47 a (87.5)	9.0±0.55 b (92.9)	10.3±1.03 b (92.3)	15.7±1.06 b (62.5)	56.3±1.66 b (24.2)
22.5	7.7±0.43 c (75.4)	6.5±0.24 ab (89.1)	6.5±0.29 c (92.7)	8.1±0.50 c (86.8)	11.6±0.62 c (75.8)	38.8±0.99 c (41.0)
25	5.7±0.24 d (75.8)	6.2±0.24 b (91.5)	6.3±0.30 c (88.4)	6.9±0.48 cd (89.5)	10.2±0.85 cd (52.9)	33.7±1.59 d (29.0)
27.5	4.2±0.21 e (75.8)	4.0±0.15 c (82.6)	4.6±0.17 d (100)	6.1±0.37 de (84.2)	8.6±0.65 de (59.4)	26.7±1.10 e (31.1)
30	3.3±0.07 ef (88.9)	2.6±0.10 d (92.9)	3.6±0.16 e (96.2)	4.9±0.28 ef (88.0)	7.4±0.55 e (54.5)	20.8±0.91 f (33.1)
32.5	2.9±0.09 f (75.0)	2.4±0.18 d (82.2)	3.2±0.18 e (97.3)	4.4±0.30 f (86.1)	6.9±0.46 e (48.4)	18.7±0.66 fg (25.0)
35	2.6±0.09 f (86.9)	2.3±0.09 d (88.7)	3.2±0.18 e (85.1)	4.4±0.22 f (80.0)	6.3±0.30 e (37.5)	16.6±0.66 g (19.7)
n	355	312	289	248	135	135
F ratio	109.51	225.29	88.78	40.34	24.99	154.68
df	7, 347	7, 304	7, 281	7, 240	7, 127	7, 127
P	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001

Values followed by the same letter within a column are not significantly different (p>0.05, DMRT)

The numbers in parenthesis are the survival rate (%)

Table 3. *Developmental time (day) (mean±SEM) for immature stages of P. exiguus at constant temperatures on C. epigeios.*

Temp. (°C)	Nymphal stage					Total nymph
	1st nymph	2nd nymph	3rd nymph	4th nymph	5th nymph	
17.5	5.2±0.19 a (96.7)	5.7±0.22 a (98.3)	6.1±0.17 a (96.5)	7.8±0.29 a (89.1)	14.6±0.68 a (28.6)	38.6±1.55 a (23.3)
20	4.4±0.17 b (95.0)	4.4±0.15 b (100)	4.3±0.14 b (98.2)	5.9±0.24 b (100)	12.2±1.02 b (35.7)	29.8±1.61 b (33.3)
22.5	3.4±0.1 c (95.0)	2.8±0.10 c (100)	3.2±0.16 c (98.2)	4.0±0.12 c (100)	7.5±0.21 c (64.3)	20.3±0.40 c (60.0)
25	3.3±0.1 c (96.7)	2.5±0.08 d (98.3)	2.7±0.10 d (100)	3.7±0.09 c (100)	6.3±0.19 d (82.5)	18.2±0.23 d (78.3)
27.5	2.8±0.07 d (100)	2.3±0.08 d (98.3)	2.6±0.08 d (100)	3.1±0.12 d (96.6)	5.7±0.17 d (86.0)	16.2±0.27 e (81.7)
30	2.8±0.09 d (95.0)	2.2±0.06 d (94.7)	2.2±0.07 e (100)	2.9±0.12 d (98.1)	4.4±0.13 e (81.1)	14.1±0.17 f (71.7)
32.5	2.4±0.07 e (95.0)	2.4±0.08 d (100)	2.1±0.09 e (96.5)	2.7±0.11 d (100)	4.6±0.14 e (92.7)	14.1±0.15 f (85.0)

35	2.4±0.09 e (88.3)	2.2±0.09 d (92.5)	2.4±0.11 ef (87.8)	2.7±0.09 d (81.4)	4.4±0.20 e (51.4)	13.8±0.27 f (30.0)
n	457	447	435	418	278	278
F ratio	71.97	120.98	126.98	117.21	102.72	203.96
df	7, 449	7, 439	7, 427	7, 410	7, 270	7, 270
P	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001

Values followed by the same letter within a column are not significantly different (p>0.05, DMRT)

The numbers in parenthesis are the survival rate (%)

The linear and nonlinear relationships between development rates (1/ days) of P. exiguus and temperature (°C) on *I. cylindrica* and *C. epigieos* were shown in Figure 2 and Figure 3, respectively. The estimated parameter values of the linear models, lower developmental thresholds, and thermal constants for each nymphal stage of P. exiguus on *I. cylindrica* and *C. epigieos*, are shown in Table 4 and Table 5, respectively. The estimated parameter values for nonlinear models on *I. cylindrica* and *C. epigieos* are presented Tables 6 and 7, respectively. Overall, the lower developmental thresholds for the nymph appeared to be higher on *I. cylindrical* and *C. epigieos*. Thermal constants (DD: degree days) required for completion of the total nymphal stage were 365.2DD, and 277.5DD on *I. cylindrica* and *C. epigieos*, respectively.

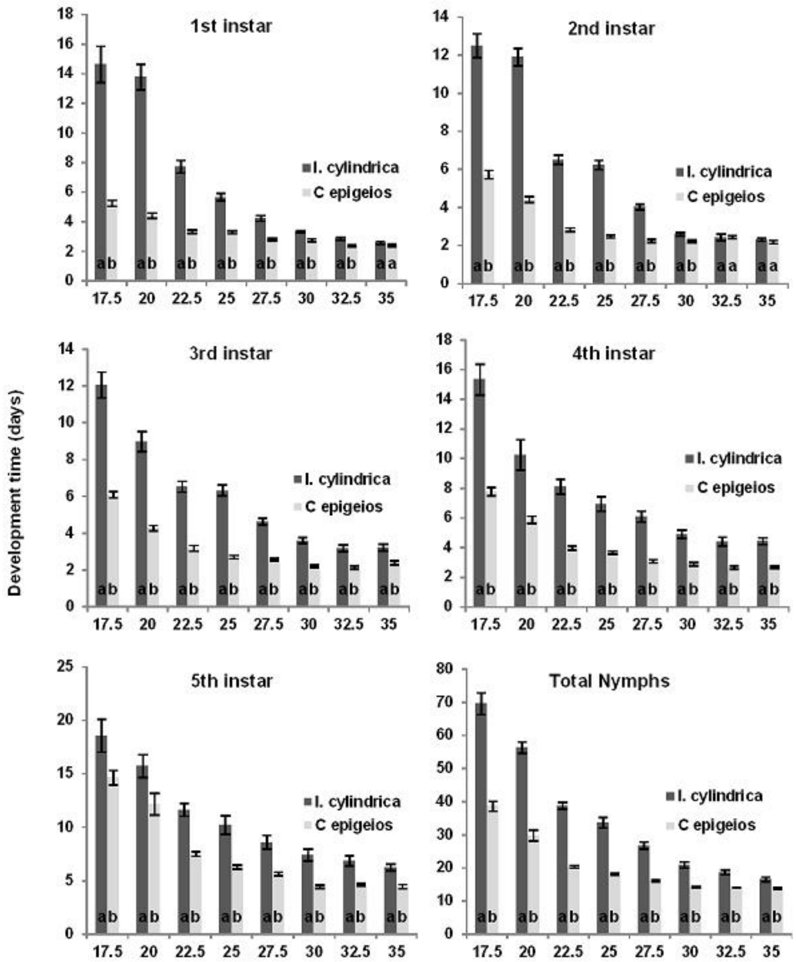

Figure 1. *Mean developmental time (days) (±SEM) for nymphal stages of P. exiguus at different temperatures, when reared on either I. cylindrical or C. epigeios. Means with the same letter at the same temperature are satistically equivalent.*

Table 4. *Lower threshold temperature and thermal constants estimated by linear regression for P. exiguus on I. cylindrica.*

Stage	Regression equation	r^2	Lower threshold temperature (°c)	Degree days (DD)
1st nymph	y=0.0199x - 0.3081	0.98	15.5	50.2
2nd nymph	y=0.0232x - 0.3651	0.94	15.7	43.1
3rd nymph	y= 0.0145x - 0.177	0.96	12.2	69.0
4th nymph	y= 0.0096x - 0.0971	0.98	10.1	103.6
5th nymph	y= 0.0063x - 0.0576	0.99	9.2	159.2
Total nymph	y= 0.0027x - 0.036	0.99	13.1	365.2

Table 5. *Lower threshold temperature and thermal constants estimated by linear regression for P. exiguus on C. epigieos.*

Stage	Regression equation	r^2	Lower threshold temperature (°c)	Degree days (DD)
1st nymph	y= 0.0164x - 0.0939	0.96	5.7	60.9
2nd nymph	y= 0.0294x - 0.3398	0.97	11.5	34.0
3rd nymph	y= 0.0226x - 0.2144	0.97	9.5	44.3
4th nymph	y= 0.018x - 0.1777	0.97	9.9	55.7
5th nymph	y= 0.011x - 0.1235	0.95	11.2	90.9
Total nymph	y= 0.0036x - 0.0362	0.98	10.0	277.8?

All nonlinear models fitted the observed data well, as provided the high values of adjusted coefficient of determination (r^2> 0.91). However, Briere models appeared to be not appropriate for describing nympah development of P. exiguus because they seemed to overestimate the upper threshold and optimal temperature on I. cylindrica or C. epigeios (Table 6 and Table 7). The Lactin 1, 2 and Logan 6 models estimated the similar values of optimal and upper threshold temperature on both host plants, in general.

Table 6. *Parameter estimates for non-linear models describing the relationship between temperature (°C) and development rate (1/day) of all immature stages of P. exiguus on I. cylindrica.*

Model	Parameter & r^2	Nymphal stages					Total nymph
		First	Second	Third	Fourth	Fifth	
Briere 1	A	0.00012	0.00014	0.00010	0.00008	0.00004	0.00001
	T_0	13.62946	14.11597	10.00316	8.41157	3.44338	8.01920
	T_L	54.69576	54.74145	47.55289	44.20173	50.57494	66.78283
	T_{opt}	45.00000	46.00000	40.00000	37.00000	42.00000	54.00000
	r^2	0.98453	0.91424	0.94634	0.98085	0.99397	0.98923
Briere 2	A	0.00052	0.00066	0.00035	0.00021	0.00007	0.00006
	T_0	12.25584	13.07037	4.89842	1.42844	1.69085	5.32050
	T_L	35.18529	35.00000	35.00000	35.26163	43.54095	35.20483
	M	26.83739	92.89904	83.20665	15.17688	3.47681	46.00075
	T_{opt}	36.00000	35.00000	35.00000	35.00000	39.00000	35.00000
	r^2	0.98674	0.92164	0.96932	0.98502	0.99211	0.98871
Lactin 1	P	0.15400	0.16289	0.15198	0.14163	0.13204	0.14015
	T_L	44.18610	42.81676	41.25146	41.18051	42.43619	44.44216
	ΔT	6.48518	6.13173	6.56906	7.04762	7.56165	7.13292
	T_{opt}	37.70092	36.68502	34.68240	34.13290	34.87454	37.30924
	r^2	0.97336	0.92212	0.97026	0.98444	0.98835	0.99149
Lactin 2	P	0.15675	0.15681	0.14860	0.13717	0.13562	0.14320

	T_L	41.86950	41.52046	41.28075	41.43804	42.65179	43.49145
	ΔT	6.36891	6.36413	6.71642	7.27426	7.36411	6.98095
	Λ	0.04115	0.06373	0.01101	0.00680	-0.00932	0.00116
	T_{opt}	35.50059	35.15633	34.56433	34.16378	35.28768	36.51050
	r^2	0.99037	0.92335	0.95996	0.97959	0.98714	0.99040
Logan 6	Ψ	0.00496	0.00494	0.01715	0.01217	0.01554	0.00238
	P	0.16380	0.14814	0.09279	0.11348	0.11082	0.13326
	T_{max}	39.96902	38.01549	37.52563	40.81687	43.90996	42.89746
	ΔT	4.50743	2.71211	1.74800	5.32999	7.27731	5.96204
	T_{opt}	35.46159	35.30338	35.77763	35.48687	36.63265	36.93542
	r^2	0.98918	0.94827	0.97697	0.97919	0.98934	0.99038

r^2 Adjusted coefficient of determination

T_{opt} Optimal temperature, in Lactin 1 and 2, Logan 6 models, the optimal temperature was T_L - ΔT (Lactin et al. 1995; Roy et al. 2002). In Briere models, the optimal temperature was x at dy/dx= 0 [2,17].

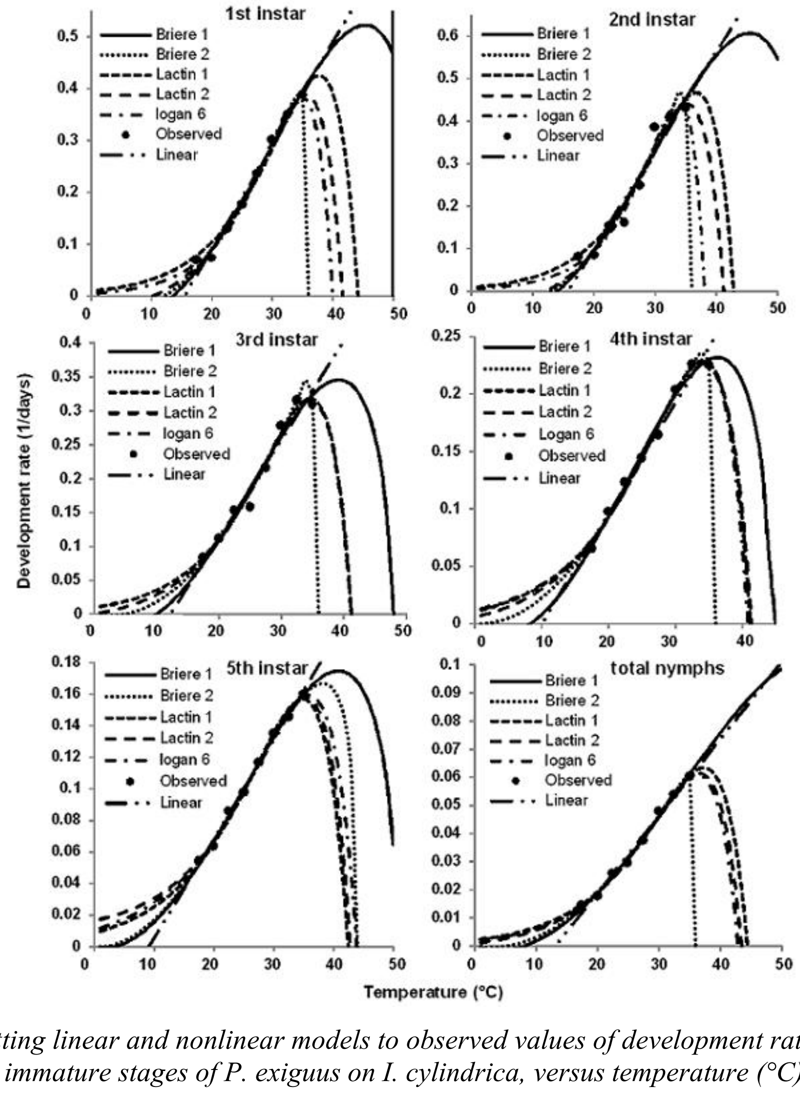

Figure 2. *Fitting linear and nonlinear models to observed values of development rates (1/ days) of immature stages of P. exiguus on I. cylindrica, versus temperature (°C).*

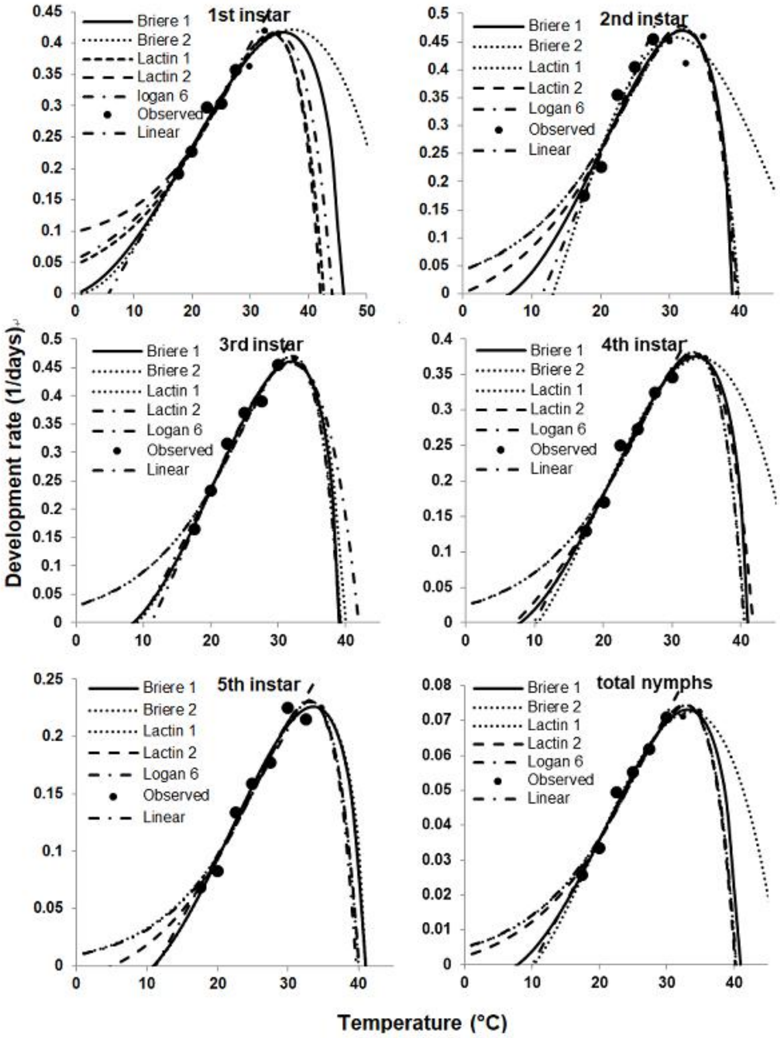

Figure 3. *Fitting linear and nonlinear models to observed values of development rates (1/ days) of immature stages of P. exiguus on C. epigieos, versus temperature (°C). Smaller markers are the deviation points from the linear regression line.*

Table 7. *Parameter estimates for non-linear models describing the relationship between temperature (°C) and development rate (1/day) of all immature stages of P. exiguus on C. epigieos.*

Model	Parameter & r^2	Nymphal stages					Total nymph
		First	Second	Third	Fourth	Fifth	
Briere 1	A	0.00009	0.00022	0.00024	0.00016	0.00011	0.00003
	T_0	-5.23000	6.82888	8.53645	7.91429	10.88744	7.80100
	T_L	45.25000	38.77900	38.72000	40.66000	40.38000	40.29000
	T_{opt}	37.00000	32.00000	32.00000	33.00000	34.00000	33.00000
	r^2	0.95151	0.82733	0.97984	0.97958	0.95966	0.97744
Briere 2	A	0.00002	0.00000	0.00021	0.00003	0.00011	0.00001
	T_0	0.13059	13.07763	9.06443	10.43165	11.01159	10.22213
	T_L	55.96000	55.67410	39.36221	49.08489	40.72790	46.77175
	M	0.98959	0.45517	1.78845	0.92991	1.90802	1.03190
	T_{opt}	38.00000	31.00000	32.00000	34.00000	34.00000	33.00000
	r^2	0.93637	0.87463	0.97331	0.97775	0.94623	0.97576
Lactin 1	P	0.11094	0.12542	0.13828	0.13375	0.14792	0.13398
	T_L	42.57000	39.92184	39.25460	40.54458	39.96789	40.33160

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	ΔT	8.92350	7.90512	7.19120	7.44215	6.74875	7.45724
	T_{opt}	33.60000	32.01672	32.06340	33.10243	33.21914	32.87436
	r^2	0.93831	0.75359	0.95904	0.95696	0.94415	0.95293
Lactin 2	P	0.13094	0.12243	0.06944	0.10315	0.13680	0.13209
	T_L	41.42000	39.85319	45.44647	42.71510	40.34147	40.31646
	ΔT	7.60611	8.07892	12.80272	9.53392	7.28939	7.56289
	Λ	-0.07711	0.05147	0.55786	0.12520	0.02696	0.00298
	T_{opt}	33.80000	31.77427	32.64375	33.18119	33.05208	32.75357
	r^2	0.91451	0.69085	0.97346	0.96375	0.93579	0.94038
Logan 6	Ψ	0.08821	0.11970	0.06500	0.05428	0.01957	0.01143
	P	0.09293	0.12073	0.13109	0.12698	0.14347	0.12677
	T_{max}	44.03000	39.91044	39.24240	40.52635	39.70044	40.36761
	ΔT	8.68300	7.59422	6.80042	7.04409	6.25585	7.09493
	T_{opt}	35.30000	32.31622	32.44199	33.48226	33.44458	33.27268
	r^2	0.92603	0.67116	0.94522	0.94246	0.92619	0.93712

r^2 Adjusted coefficient of determination

Topt Optimal temperature, in Lactin 1 and 2, Logan 6 models, the optimal temperature was T_L - ΔT [11,17]. In Briere models, the optimal temperature was x at dy/dx= 0 [2,17].

Developmental variation of each stage of P. exiguus on each host was well described by the two-parameter Weibull function (Figure 4 and Figure 5). The estimated parameters were presented in Table 8 and Table 9.

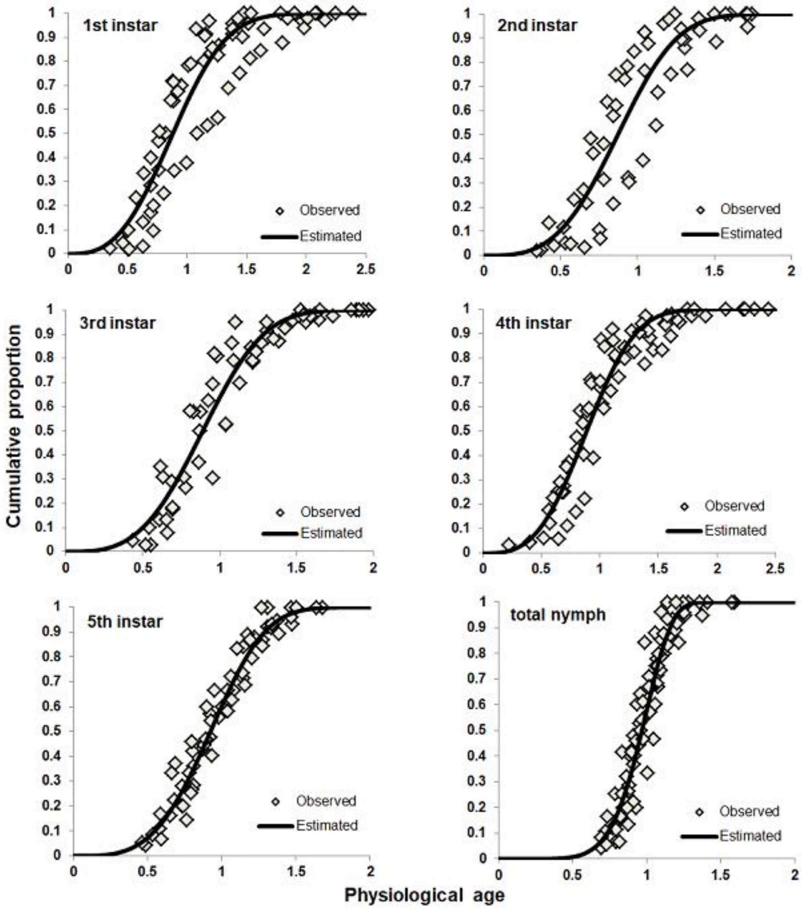

Figure 4. *Cumulative proportions of development for each stage of P. exiguus versus physiological age on I. cylindrica. A two-parameter Weibull function was applied.*

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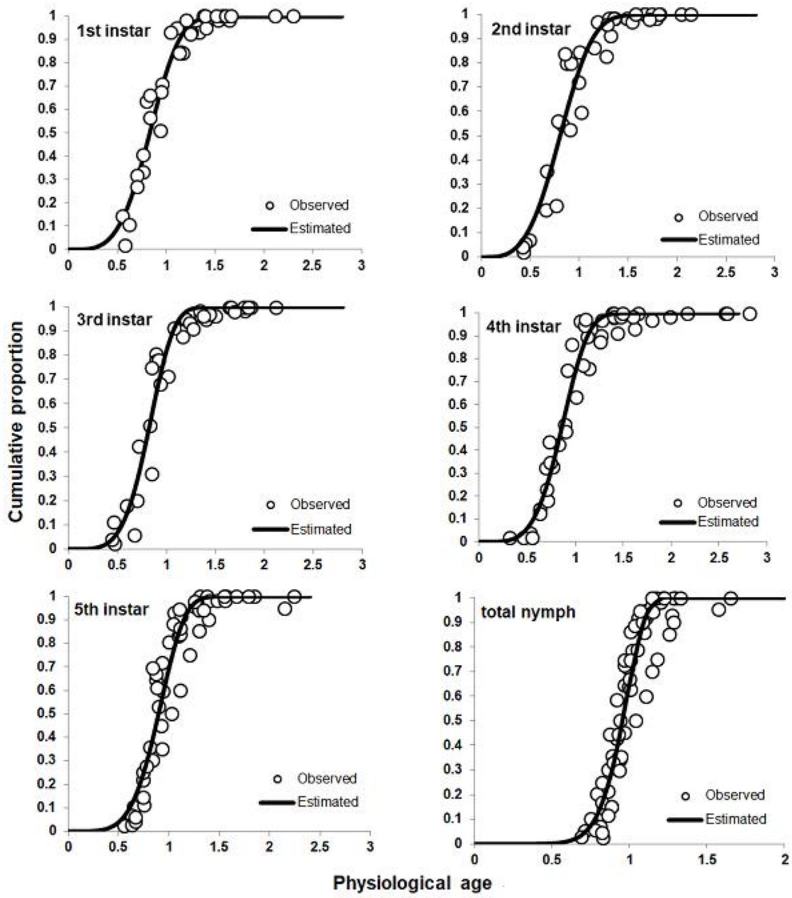

***Figure 5**. Cumulative proportions of development for each stage of P. exiguus versus physiological age on C. epigeios. A two-parameter Weibull function was applied.*

***Table 8.** Estimated parameters of the Weibull function for development completion of each immature stage of P. exiguus, on I. cylindrica.*

parameters	Nymphal Stages					Total nymphs
	1st	2nd	3rd	4th	5th	
α	0.9989	0.9737	0.9961	0.9965	1.0224	1.0235
β	2.8580	3.2920	3.2609	3.1173	3.6108	6.7832
r^2	0.86	0.82	0.91	0.91	0.96	0.91

***Table 9.** Estimated parameters of the Weibull function for development completion of each immature stage of P. exiguus, on C. epigieos.*

parameters	Nymphal Stages					Total nymphs
	1st	2nd	3rd	4th	5th	
α	0.9128	0.8942	0.8890	0.9345	0.9672	0.9947
β	3.8784	3.4955	4.6043	4.4580	4.9193	9.0921
r^2	0.94	0.92	0.93	0.96	0.90	0.89

4. Discussion

No previous study has presented quantitative information of *P. exiguus* development on non-rice host plants. Nymphal development times and lower threshold temperatures for *P. exiguus* were different among different food sources. On rice, total nymphal development time was 58.5, 44.8, 35.1, 28.2, 19.8, and 19.5 days at 20, 22.5, 25, 27.5, 30 and 32.5°C, respectively [14]. These are similar to those on *I. cylinderica* at 20 - 32.5°C. However, the lower developmental thresholds on rice were higher than those on both *I. cylindrica and C. epigeios*.

On *I. cylindrical*, the development rate of *P. exiguus* showed a linear increase with temperature in the range of all tested temperature (17.5-35°C) but it occurred only within the range of 17.5-27.5 or 30°C, on *C. epigeios*. The thermal constant for total nymphal development of *P. exiguus* was highest on *I. cylindrica* as 370.4DD and lowest on C. epigieos as 277.8DD in our study, and intermediate on the rice plant as 312.5DD [15]. It appears that *I. cylindrica* is the poorest host, and *C. epigieos* may be the most appropriate host plant.

There were marked differences in the estimated values of the optimal temperature (t_{opt}) and the higher threshold temperature or maximum temperature (t_{max}) from the fitted nonlinear models. The Lactin 1 and 2 and Logan 6 models estimated the upper threshold temperature in the range of 42.5-44.4°C and the optimal temperature in the range of 36.5-37.3°C, for the total nymphal stage of *P. exiguus* on *I. cylinderica.* On *C. epigeios*, Briere 1, Lactin 1 and 2 and Logan 6 models predicted the reliable estimation of optimal temperature in the range of 32.7-33.2°C and upper threshold temperature of around 40°C. Overall, it appears that Lactin 1 and 2, and Logan 6 models provided reliable optimal and upper threshold temperature of nymphal satges of *P. exiguus* on both I. *cylinderica* and *C. epigeios* (see Table 6 and Table 7). The optimal temperature and upper threshold temperature estimated for the development of total nymphs on rice was 32.7 and 37.8°C, respectively (Logan 6 model), and 34.6 and 41.6°C (Lactin 2 model), respectively [15]. It appears that optimal and upper threshold temperatures for the nymphal stage of *P. exiguus* are similar among these three host plants.

Insect development is a stochastic process with stage transitions occurring over time [19], therefore the variation in development times among individual is a key component to develop the insect population models. For many insect species, it has been observed that developmental time variation among individuals in a cohort is skewed toward longer times and that the underlying distributions against normalized times have identical shapes irrespective of temperatures [4, 19, 20]. Therefore, the Weibull function has described the distribution of development time variation [16,20,3]. In the current study, the two-parameter Weibull function was used to quantify the variation of *P. exiguus* nymphal development. The small value of the shape parameter (β) for the early nymphal stages (first and second instars) indicates that the development variation among individuals in those stages is greater than other stages. Overall, nymphal developmental variation was higher on *I. cylinderica* than on *C. epigeios*, and it is more distinctive at early instar nymphal stages

The survival rate of total nymphal stage on rice was 18.3, 43.7, 37.0, 53.3, 40.4, and 21.0% at 20, 22.5, 25, 27.5, 30, 32.5°C, respectively (Park et al., 2010), and was similar to that on *I. cylinderica* in our study. The nymphal survivorship was higher on *C. epigeios*. Our results, shorter development time and higher survivorship on *C. epigeios* indicate that *P. exiguus* performs better on *C. epigeios* than on rice and *I. cylinderica*. Therefore, *C. epigeios* can be regarded as a nutritionally more suitable host, in terms of the performance variables-development time, and survivorship in the laboratory, despite lack of knowledge about the nutritional constituents of *I. cylinderica* and *C. epigeios.*

Although the simple linear regression is easier for calculation of the lower developmental threshold temperature and thermal constant, nonlinear models (Lactin and Logan 6 models) were found to be better for calculation of nymphal developmental rates of *P. exiguus* on *I. cylinderica and C. epigeios*. The result of our study will be useful for a more complete understanding of *P. exiguus* population dynamics and can be used to forecast the occurence of different stages of *P. exiguus* in the fields, thereby contributing to the development of an effective management program for P. exiguous.

Conflicts of Interest

The authors declare that there is no conflict of interest regarding the publication of this article.

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