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Modeling of the effect of temperature on developmental rate of common green lacewing, *Chrysoperla carnea* (Steph.) (Neuroptera: Chrysopidae)

Hossein Ranjbar Aghdam^{1*}  and Zahra Nemati²

Abstract

Background: The common green lacewing *Chrysoperla carnea* (Steph.) (Neuroptera: Chrysopidae) is a polyphagous and efficient predatory species commonly found in a wide range of agricultural habitats. It plays an important role in biological control of pests.

Main body: The effect of temperature on developmental rate of the predator *C. carnea* was studied at 7 constant temperatures, 15, 20, 25, 27, 30, 32, and 35 °C, 50 ± 10% RH, and a photoperiod of 16:8 h (L:D). Six nonlinear models were evaluated to determine the trend of developmental rate of the predator in examined temperatures and to estimate thermal thresholds of development. Nonlinear models were evaluated based on coefficient of determination (R^2), adjusted coefficient of determination (R^2_{adj}), residual sum of squares (RSS), and Akaike information criterion (AIC), beside biological significance of the estimated values for the model parameters. Among evaluated nonlinear models, Lactin-2 for all immature stages was the best-fitted model on observations, considering statistical criteria and biological significance of the estimations. The values of the lower temperature threshold by using Lactin-2 were 9.90, 10.90, 11.90, 11.40, 11.11, 11.61, and 11.30 °C for incubation period, 1st, 2nd, and 3rd larval instars, overall larval period, and pupal and total immature stages, respectively. The values of the upper temperature threshold for the mentioned developmental stages were 33.82, 37.66, 33.14, 34.04, 33.58, 32.14, and 32.18 °C, respectively. Estimated values for the optimal temperature for incubation period, 1st, 2nd, and 3rd larval instars, overall larval period, and pupal and total immature stages were 30.69, 30.22, 30.90, 30.34, 30.90, 31.75, and 31.72 °C, respectively.

Short conclusion: The results, in addition to determine thermal tolerance for the development of *C. carnea*, provided advantage information for better use of *C. carnea* in biological control programs.

Keywords: *Chrysoperla carnea*, Thermal index, Developmental periods, Model

Background

Increasing resistance of different insect species to commonly used insecticides, the tendency to use unauthorized food without residues of chemical pesticides, and the increasing concern about human health and the gradual reduction of conventional insecticide

usage have allowed researchers to evaluate the possibility of using other forms of low-risk pest control methods (Athanasidou et al. 2004). Meanwhile, the roles of predators have been approved practically as effective and efficient agents in biological control programs.

The common green lacewing *Chrysoperla carnea* Stephen (Neuroptera: Chrysopidae) widely preys on small arthropods with a soft body such as aphids, whiteflies, thrips, butterfly eggs and larvae, and mites (Rimoldi et al. 2008). It is a cosmopolitan

* Correspondence: hrap1388@gmail.com

¹Iranian Research Institute of Plant Protection, Agricultural, Research, Education and Extension Organization (ARREO), Tehran, Iran
Full list of author information is available at the end of the article

polyphagous and efficient predator commonly found in a wide range of agricultural habitats (Varma and Shenhmar 1983). Many studies have been carried out on *C. carnea* regarding its geographical distribution, prey range, and adaptation potential. In addition, its relatively easy mass-rearing in the laboratory and the possibility of short-term storage of eggs and long-term storage of adults (Ashfagh et al. 2002), large appetite, and high searching ability of the lacewing larvae justifies its release against pests such as aphids, mites, and bollworms (Ashfagh et al. 2007). Besides, some of the researchers have focused on improving its rearing on different laboratory and natural hosts (Khanzada et al. 2018).

Temperature is the most important abiotic factor in biological changes of arthropods. Its effect on survival, reproduction, and population growth can be demonstrated by special functions of the temperature and can be used to predict interaction effect of natural enemies and pests (Roy et al. 2002). Developmental rate, expressed as the reciprocal of time taken to develop from one stage to another (Cossins and Bowler 1987), is nil at the lower temperature threshold, increases with temperature before leveling off at the optimal temperature, and then decreases rapidly as the upper temperature threshold is approached (Roy et al. 2002). This relationship is curvilinear near the extremes but approximately linear at moderate temperatures (Wagner et al. 1984). To describe the developmental rate more realistically and over a wider temperature range, several non-linear models have been applied (e.g., Logan et al. 1976, Lactin et al. 1995, Briere et al. 1999, Roy et al. 2002, Arbab et al. 2006, and Ranjbar Aghdam et al. 2009). These models provide value estimates of lower and upper temperature thresholds and optimal temperature for development of a given stage.

Previously conducted studies confirmed the effect of different preys on biological characters of *C. carnea* (Balakrishnan et al. 2005, Zeraati et al. 2009, Hesami et al. 2011, and Jokar and Zarabi 2012). Sharifi Fard and Mossadegh (2006) studied the effects of different aphid prey on developmental time of *C. carnea*. Despite studying developmental time of *C. carnea* at different temperatures by Mirabzadeh et al. (2000), Yadav and Pathak (2010), Nadeem et al. (2012), and Saljoqi et al. (2015), there was no enough information concerning thermal tolerance range and thermal indices of *C. carnea* developmental stages.

The aim of the present study was focused on determination of the best descriptive model for temperature-dependent developmental rate of *C. carnea* and precise estimation of its thermal indices, lower temperature threshold, optimum temperature, and upper temperature threshold.

Materials and methods

Insect culture

Adults of *C. carnea* were collected from alfalfa fields of Firoozkooh region located in Tehran province, Iran. Rearing of the predator was carried out in an insectary located in Iranian Research Institute of Plant Protection (IRIPP) at 27 ± 1 °C, $60 \pm 10\%$ RH, and a photoperiod of 16L: 8D h. The second laboratory generation (F_2) was used in the present study.

Laboratory rearing

Eggs of the flour moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) were used for feeding *C. carnea*. The eggs were obtained from insectary culture of flour moth established in Biological Control Research Department (BCRD) of IRIPP. In order to prevent cannibalism, rearing of *C. carnea* larvae was carried out individually, using small rearing containers. These containers were transparent cubic with $1.5 \times 1.5 \times 1.5$ -cm dimensions. After pupation and emergence of adults, lacewings were transferred daily to plastic cylindrical containers with 30-cm height and 25-cm diameter for mating and oviposition. Upper side of the adult containers was closed using a fine mesh. Moreover, paper sheets (2×10 cm) were placed inside the containers as ovipositional substrate. In order to supply water for the adults, a small moist sponge was provided during mating and oviposition inside each Petri dish. Complementary, adults were fed on a 4:7:10 diet of yeast: honey: water (Malkeshi et al. 2004). Adult lacewings from these colonies served as the parent stock for the experiments.

Developmental time

Developmental time of incubation period, larval instars, total larval period, pupal period, and total immature stages were recorded at the 7 constant temperatures: 15, 20, 25, 27, 30, 32 and 35 ($\pm < 1$)°C, $50 \pm 10\%$ RH, and a photoperiod of 16L:8D h. Inside the growth chamber, 100–400 newly laid eggs (< 24 h) were located under each abovementioned temperatures to determine the incubation period by checking hatched eggs every 24 h. Newly emerged larvae were placed individually in plastic containers (50-mm diameter and 30-mm height). To provide enough ventilation, upper side of the containers had a 20×20 -mm hole in the middle part of the opening side, covered with a piece of fine net (2-mm mesh). Larvae fed on fresh eggs of *E. kuehniella*. Larval-rearing containers were examined once daily, and fresh eggs were added on them. Larval development to next instar was recorded by visiting larval head capsule until pupation. Pupae were checked daily until adult's exclusion for recording pupal period of individuals. In order to determine the effect of temperature on developmental time of each immature stage of *C. carnea*, data was analyzed

according to completely randomized design, and mean comparison was carried out using Tukey range test.

Mathematical models

In order to find the best descriptive model for temperature-dependent development of the *C. carnea*, 6 nonlinear models, namely, Briere-1, Briere-2, Lactin-2, Logan-6, Logan-10, and polynomial 3rd order, were evaluated (Table 1). Evaluation of the models for better describing temperature-dependent development of *C. carnea* was done according to the values of coefficient of determination (R^2), adjusted coefficient of determination (R^2_{adj}), Akaike information criterion (AIC), and residual sum of squares (RSS). Higher values of coefficient of determination and adjusted coefficient of determination and lower values of Akaike information criterion and residual sum of squares confirmed better fit.

Thermal indices

Lower temperature threshold (t_{min})

At the lower temperature threshold, or the zero development temperature, no measurable development was detected, or the rate of development was zero. The intersection point of regression line with temperature axis showed the lower temperature threshold of development (t_{min}). After calculation of this index, the standard error of t_{min} was calculated, using the following equation:

$$SE_{t_{min}} = \frac{\bar{r}}{b} \sqrt{\frac{s^2}{N \times \bar{r}^2} + \left(\frac{SEb}{b}\right)^2}$$

where S^2 is the mean square residual, r^2 is the developmental mean, and N is the number of samples (Kontodimas et al. 2004).

Optimal temperature (t_{opt})

At the optimal temperature (t_{opt}), the rate of development was the highest. It may be estimated directly from the equations of some non-linear models or as the

parameter value for which their first derivatives equal zero. The SE of t_{opt} was estimated from the non-linear models (Kontodimas et al. 2004).

Upper temperature threshold (t_{max})

Upper temperature threshold is the highest temperature, at which the rate of development was zero, or life cannot be maintained for a long time. Most non-linear models can estimate this temperature. The SE of t_{max} was estimated from non-linear models (Kontodimas et al. 2004).

Model selection criteria

Model selection was carried out according to statistical criteria and biological indices (with biological significance).

Statistical criteria

Four statistical criteria were used to evaluate the fitness of models with the data derived from laboratory observations:

- 1- The coefficient of determination: coefficient of determination or R^2 index was shown for the models. The higher the value of determination coefficient, the higher accuracy will increase. The highest value of determination coefficient was 1, so the closer the obtained value of coefficient to 1 was, the better fit of the data to the models.
- 2 The residual sum of squares: this index was shown by RSS. It showed the standard deviation of the data from the model, so the lower the value of RSS was, the better the fit of the data to the models.
- 3 The Akaike information criterion: this index was shown by AIC. The model with the lowest AIC was a model with the lowest amount of lost data (Akaike 1974; Burnham and Anderson 2002; Vucetich et al. 2002; Angilletta 2006). AIC was calculated by the following formula:

Table 1 Mathematical models used to describe the effect of temperature on the developmental rate of the common green lacewing, *Chrysoperla carnea*, and their capacity to estimate three important biological parameters

Model	T_{min}	T_{opt}	T_{max}	Equation	Reference
Briere-1	•	•	•	$\frac{1}{D} = aT(T - t_{min})\sqrt{(t_{max} - T)}$	Briere et al. (1999)
Briere-2	•	•	•	$\frac{1}{D} = aT(T - t_{min})(T_{max} - T)^{\frac{1}{2}}$	Briere et al. (1999)
Lactin-2	-	•	•	$\frac{1}{D} = e^{\rho T} - e^{(\rho T_L - (\frac{T - T_L}{\Delta T}))} + \lambda$	Lactin et al. (1995)
Logan-6	•	•	•	$\frac{1}{D} = \psi[e^{\rho T} - e^{(\rho T_{max} - \frac{T_{max} - T}{\Delta T})}]$	Logan et al. (1976)
Logan-10	•	•	•	$\frac{1}{D} = a[\frac{1}{1 + ke^{-\rho T}} - e^{(-\frac{T_{max} - T}{\Delta T})}]$	Logan et al. (1976)
Polynomial 3rd order	-	•	•	$\frac{1}{D} = aT^3 + bT^2 + cT + d$	Harcourt and Yee (1982)

*shows the model has ability to estimate this biological parameter

Table 2 Means development time (\pm SE) of the common green lacewing, *Chrysoperla carnea* immature stages at examined temperatures

Temperature (°C)	Incubation period	Larval instars			L3	Total larva period	Pupal period	Total immature stages
		L1	L2	L3				
15	12.494 \pm 0.027 ^f (n = 354)	10.936 \pm 0.034 ^e (n = 233)	9.801 \pm 0.034 ^f (n = 231)	10.414 \pm 0.037 ^e (n = 215)	31.129 \pm 0.045 ^f (n = 140)	36.129 \pm 0.047 ^f (n = 140)	79.714 \pm 0.052 ^f (n = 140)	
20	6.208 \pm 0.390 ^e (n = 197)	5.117 \pm 0.028 ^d (n = 145)	4.062 \pm 0.034 ^e (n = 144)	4.446 \pm 0.045 ^d (n = 139)	13.556 \pm 0.050 ^e (n = 123)	14.691 \pm 0.052 ^e (n = 123)	34.431 \pm 0.060 ^e (n = 123)	
25	4.050 \pm 0.020 ^d (n = 120)	3.239 \pm 0.046 ^c (n = 88)	2.771 \pm 0.046 ^d (n = 83)	2.671 \pm 0.065 ^c (n = 82)	8.629 \pm 0.058 ^d (n = 70)	9.800 \pm 0.048 ^d (n = 70)	22.443 \pm 0.069 ^d (n = 70)	
27	3.448 \pm 0.046 ^c (n = 116)	2.907 \pm 0.031 ^b (n = 86)	2.167 \pm 0.041 ^c (n = 84)	2.200 \pm 0.045 ^b (n = 80)	7.303 \pm 0.065 ^c (n = 76)	8.079 \pm 0.052 ^c (n = 76)	18.618 \pm 0.070 ^c (n = 76)	
30	3.000 \pm 0.000 ^b (n = 152)	2.785 \pm 0.036 ^a (n = 131)	1.597 \pm 0.043 ^a (n = 131)	1.961 \pm 0.052 ^a (n = 131)	6.297 \pm 0.045 ^a (n = 111)	6.432 \pm 0.049 ^a (n = 111)	15.730 \pm 0.057 ^a (n = 111)	
32	3.224 \pm 0.032 ^b (n = 174)	2.819 \pm 0.038 ^{ab} (n = 105)	1.905 \pm 0.029 ^b (n = 105)	2.171 \pm 0.037 ^b (n = 105)	6.835 \pm 0.041 ^b (n = 84)	6.821 \pm 0.049 ^b (n = 84)	16.845 \pm 0.040 ^b (n = 84)	

Means with different letters in each column (development stage) are significantly different (Tukey, $P < 0.05$)
n number of individuals

Table 3 Comparison of six non-linear models of developmental rate for describing the effect of temperature on developmental rate of the common green lacewing, *Crysoperla carnea*

Stage	Model	Parameters	R^2 ($\times 10^{-2}$)	RSS ($\times 10^{-4}$)	AIC	R^2_{adj} ($\times 10^{-2}$)
Incubation period	Briere-1	3	97.79	5.04	- 50.30	96.32
	Briere-2	4	99.94	0.27	- 65.84	99.86
	Lactin-2	4	99.95	0.23	- 66.70	98.88
	Logan-6	4	99.74	1.27	- 56.57	99.34
	Logan-10	5	99.90	3.38	- 60.52	99.51
	Polynomial	4	99.17	0.26	- 49.76	97.94
1st larval instar	Briere-1	3	99.88	0.74	- 61.83	99.79
	Briere-2	4	99.88	0.73	- 59.86	99.69
	Lactin-2	4	99.82	0.08	- 57.67	99.56
	Logan-6	4	98.89	4.01	- 46.32	97.22
	Logan-10	5	99.86	5.85	- 49.82	99.33
	Polynomial	4	99.96	0.01	- 66.33	99.89
2nd larval instar	Briere-1	3	93.45	5.61	- 31.57	89.09
	Briere-2	4	98.57	3.33	- 38.60	96.41
	Lactin-2	4	97.76	4.43	- 35.27	94.39
	Logan-6	4	98.98	5.67	- 41.46	97.45
	Logan-10	5	99.05	6.95	- 39.83	95.26
	Polynomial	4	94.25	5.86	- 29.99	85.62
3 rd larval instar	Briere-1	3	99.24	1.89	- 42.36	98.74
	Briere-2	4	99.83	1.73	- 54.71	99.56
	Lactin-2	4	99.75	6.37	- 53.22	99.37
	Logan-6	4	99.86	2.92	- 51.58	99.66
	Logan-10	5	99.87	6.35	- 51.96	99.35
	Polynomial	4	99.18	5.23	- 43.96	97.96
Larval period	Briere-1	3	98.98	1.21	- 58.87	98.29
	Briere-2	4	99.91	0.11	- 71.49	99.78
	Lactin-2	4	99.95	0.05	- 75.67	99.89
	Logan-6	4	99.59	0.49	- 62.26	98.98
	Logan-10	5	99.83	2.58	- 65.64	99.17
	Polynomial	4	99.07	0.42	- 57.43	97.68
Pupal period	Briere-1	3	98.27	2.15	- 55.41	97.12
	Briere-2	4	98.90	0.47	- 56.13	97.24
	Lactin-2	4	99.53	4.12	- 60.90	98.84
	Logan-6	4	98.89	1.14	- 57.21	97.22
	Logan-10	5	99.27	4.51	- 57.79	96.33
	Polynomial	4	98.20	2.16	- 53.38	95.51
Total immature stages	Briere-1	3	98.78	0.24	- 68.47	97.96
	Briere-2	4	99.77	0.04	- 77.93	99.43
	Lactin-2	4	99.86	4.49	- 79.42	99.65
	Logan-6	4	99.37	0.11	- 71.35	98.43
	Logan-10	5	99.64	3.74	- 72.98	98.21
	Polynomial	4	98.79	4.22	- 66.84	96.99

Table 4 Values of fitted coefficients and measurable parameters of 6 developmental rate models to describe immature stage development of the common green lacewing, *Chrysoperla carnea*

Model	Parameters	Egg	1st larval instar	2nd larval instar	3rd larval instar	Total larval period	Pupal period	Total immature stages	
Briere-1	A	2.34×10^{-4}	2.35×10^{-4}	3.81×10^{-4}	3.38×10^{-4}	9.69×10^{-5}	7.59×10^{-5}	3.58×10^{-5}	
	t_{min} (°C)	10.967	9.507	12.224	11.222	10.662	10.335	10.462	
	t_{max} (°C)	35.660	36.338	37.113	36.479	37.177	40.379	38.172	
	t_{opt} (°C)	29.90	30.20	31.21	30.56	31.03	33.52	31.79	
Briere-2	a	4.11×10^{-3}	2.25×10^{-4}	9.09×10^{-4}	7.25×10^{-4}	2.13×10^{-4}	1.92×10^{-4}	8.59×10^{-5}	
	t_{min} (°C)	5.235	9.584	8.286	9.293	7.602	9.350	6.821	
	t_{max} (°C)	32.303	36.536	32.000	32.404	32.346	33.453	32.147	
	t_{opt} (°C)	30.82	30.21	31.71	30.91	30.76	31.22	31.06	
Lactin-2	D	9.459	1.937	47.282	6.758	8.305	5.756	12.478	
	Δ	1.047	4.307	0.717	1.403	0.920	0.069	0.095	
	P	0.013	0.018	0.021	0.020	0.007	0.007	0.003	
	Λ	- 1.139	- 1.211	- 1.284	- 1.251	- 1.085	- 1.086	- 1.036	
Lactin-2	T_l (°C)	35.209	42.200	33.886	35.519	35.320	32.280	32.439	
	t_{min} (°C)	9.899	10.895	11.905	11.399	11.109	11.615	11.30	
	t_{max} (°C)	33.819	37.663	33.142	34.040	33.581	32.141	32.177	
	t_{opt} (°C)	30.69	30.22	30.90	30.34	30.90	31.75	31.72	
	Logan-6	ψ	0.012	0.084	0.025	0.051	0.010	0.006	0.002
		P	0.141	0.165	0.108	0.193	0.179	0.114	0.149
t_{max} (°C)		35.863	35.944	32.710	35.095	35.632	34.679	35.703	
Δ		4.451	5.877	0.606	5.023	5.219	2.120	4.169	
Logan-10	t_{opt} (°C)	30.29	29.97	30.94	29.99	30.23	30.71	30.46	
	A	0.430	0.393	3.031	0.693	0.198	0.252	0.085	
	P	0.179	0.254	0.121	0.199	0.197	0.158	0.181	
	t_{max} (°C)	32.186	35.472	32.164	34.220	32.167	32.236	32.198	
	Δ	0.084	1.146	0.063	1.252	0.078	0.103	0.090	
	K	61.799	156.773	146.967	117.827	92.036	73.437	79.579	
Polynomial 3rd order	t_{opt} (°C)	31.66	30.75	31.75	30.27	31.68	31.64	31.67	
	A	$- 9.37 \times 10^{-5}$	$- 8.87 \times 10^{-5}$	$- 2.00 \times 10^{-4}$	$- 2.00 \times 10^{-4}$	$- 4.53 \times 10^{-5}$	$- 2.71 \times 10^{-5}$	$- 1.58 \times 10^{-5}$	
	b	0.006	0.005	0.013	0.013	0.003	0.002	0.001	
	C	- 0.116	- 0.089	- 0.254	- 0.258	- 0.055	- 0.032	- 0.019	
	D	0.743	0.488	1.682	1.648	0.340	0.192	0.119	
	t_{max} (°C)	40.566	40.364	41.155	38.757	40.396	44.737	41.573	
t_{opt} (°C)	30.79	30.100	31.75	30.09	30.74	33.32	31.46		

$$AIC = n \ln \left(\frac{SSE}{n} \right) + 2\rho$$

where n is the number of observations (in this study, the number of examined temperatures), ρ is the number of model parameters also including intercept, and SSE is the sum of squared errors.

4- The adjusted coefficient of determination: this index is shown by R^2_{adj} . This index deducts the effect of parameter numbers from the value of determination coefficient, so higher values of R^2_{adj} shows the better fit of data with the model (Rezaei and Soltani 1998). R^2_{adj} and AIC are parameter-independent indices of evaluation, therefore are more accurate, but R^2 and RSS are parameter-dependent. R^2_{adj} is calculated by the following formula:

$$R_{\text{adj}}^2 = 1 - \left(\frac{n-1}{n-p} \right) (1 - R^2)$$

where n is the number of observations, p is the number of model parameters, and R^2 is determination coefficient.

All nonlinear models and parameter estimation was statistically analyzed using the SPSS.V.16.0 software.

Biological indices

A good model should be able to estimate t_{opt} , t_{max} , and t_{min} or at least t_{opt} and t_{min} . Models, with better estimation of biological indices and their predicted values, closer to the values obtained in laboratory tests are more appropriate to predict insect development at different temperatures. In order to select the best describing model for temperature development of *C. carnea*, first, statistical parameters were calculated, and then, results were evaluated in terms of biological standards, considering that biological parameters are much more important.

Results and discussion

Developmental time

In this research, relationship between temperature and developmental rate of *C. carnea* was studied. Increasing temperature showed an inverse effect on developmental time of *C. carnea*, and increasing temperature led to decreasing its developmental time. Mean developmental times of the lacewing immature stages are shown in Table 2. Based on these findings, it was concluded that the total developmental time varied from a maximum of 79.71 days at 15 °C through a minimum of 15.73 days at 30 °C. Based on ANOVA, incubation period ($F = 19$, 019.30, $df = 5$, $P < 0.001$), 1st instar larvae ($F = 10$, 591.93, $df = 5$, $P < 0.001$), 2nd instar larvae ($F = 9135.29$, $df = 5$, $P < 0.001$), 3rd instar larvae ($F = 6989.31$, $df = 5$, $P < 0.001$), total larval period ($F = 44,234.98$, $df = 5$, $P < 0.001$), pupal period ($F = 64,071.34$, $df = 5$, $P < 0.001$), and total immature stages ($F = 217,654.73$, $df = 5$, $P < 0.001$) of *C. carnea* were significantly different among examined temperatures. Means were compared using Tukey range test at 5% probability level (Table 2).

Model evaluation

Maximum total developmental time (79.714 ± 0.052 days) was recorded at 15 °C, while the minimum (15.730 ± 0.057 days) was found at 30 °C. This relationship was not linear and accordingly nonlinear models could present better description for temperature-dependent developmental rate of *C. carnea*. Hence, nonlinear models were fitted well to the data (Table 3). Accordingly, these models all fitted and some measurable

parameters were estimated from the regression, whereas some other measurable parameters were calculated because of the solution of the equations or their first derivatives. The values of fitted coefficients and measurable parameters of the model are presented in Table 4. In Table 5, there is a synoptic presentation of how each model met criteria of the evaluation.

Many references confirmed nonlinear relationship between temperature and developmental rate of different insect's species, e.g., Kontodimas et al. (2004), Arbab et al. (2006), Ranjbar Aghdam et al. (2009), and Saljoqi et al. (2015). Based on Saljoqi et al. (2015), the total developmental times *C. carnea* fed on cabbage aphid, *Brevicoryne brassicae* (Linnaeus), were 26.5, 23.1, 21.4, and 19.8 days at temperatures 20, 24, 28, and 32 °C, respectively. Obtained results showed a little difference than Saljoqi et al. (2015) results. This difference may be due to using different hosts, environmental factors, and/or different populations (Gilbert and Raworth 1996, Roy et al. 2002 and Roy et al. 2003, and Kayahan et al. 2014). Maximum and minimum developmental times of all immature stages of *C. carnea* were recorded at 15 and 30 °C, respectively. In contrast, increasing temperature to 32 °C increased developmental time. This subject is more responsible for curvilinear relationship between temperature and developmental rate of *C. carnea* at higher temperatures. Butler and Ritchie (1970) previously suggested using prediction models, to show the rate of development in relation to temperature. Moreover, Nadeem et al. (2012) reported *C. carnea* larval duration of 20.4 ± 0.12 , 12.9 ± 0.21 , 11.0 ± 0.14 , 10.2 ± 0.11 , and 10.0 ± 0.10 (days) at 20, 28, 31, and 35 (± 1)°C, respectively.

Statistical criteria

All evaluated nonlinear models were fitted well to the data (Table 3). Nevertheless, crucial differences among

Table 5 Estimated values of the lower temperature threshold (t_{min}), optimal temperature (t_{opt}), and upper temperature threshold (t_{max}) for different immature stages of the common green lacewing, *Chrysoperla carnea*, using Lactin-2 nonlinear model

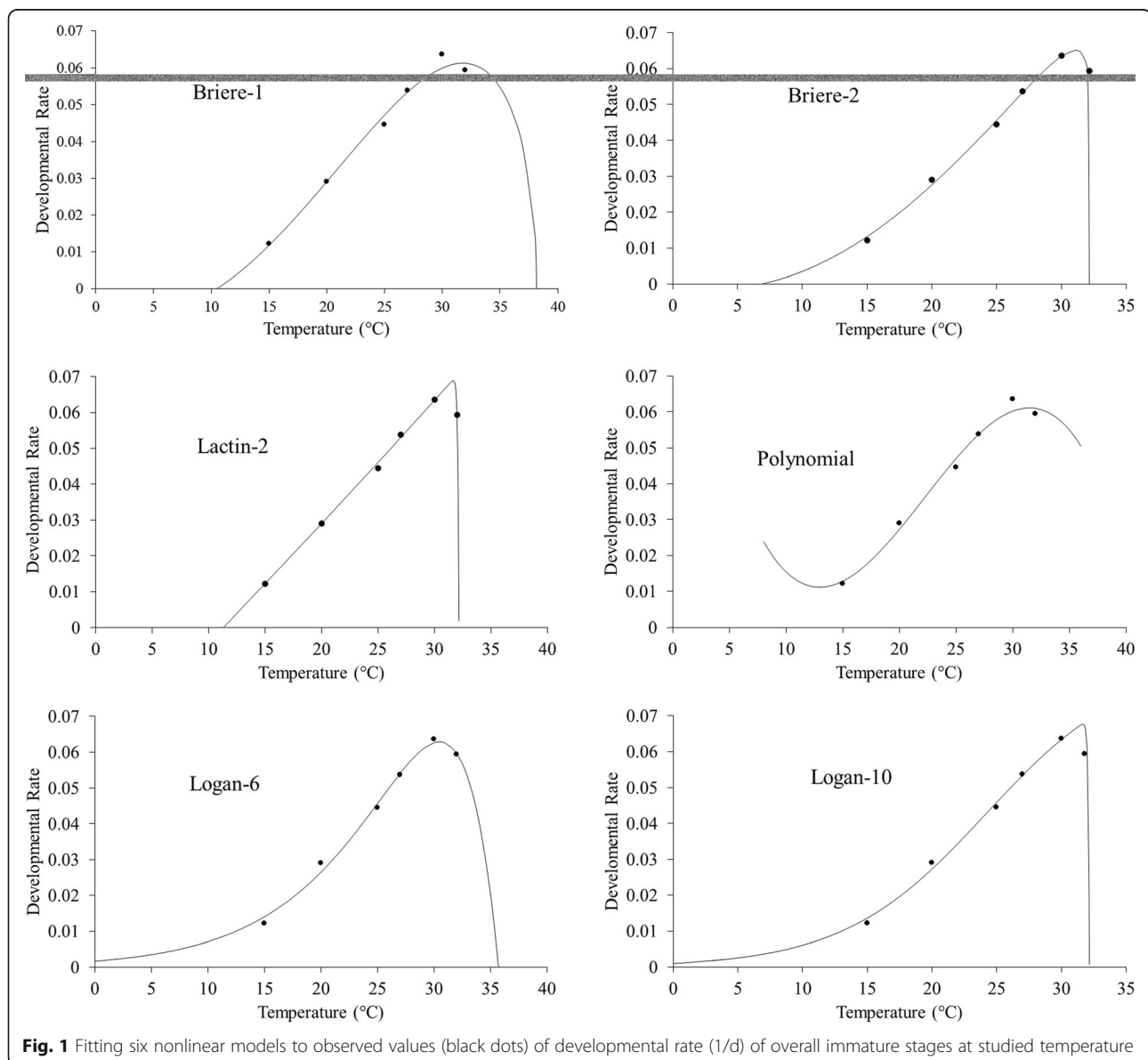
Life stage	$t_{\text{min}} \pm \text{SE}$ (°C)	t_{opt} (°C) ^a	$t_{\text{max}} \pm \text{SE}$ (°C)
Egg	9.899 ± 1.134	30.69	33.819 ± 0.967
1st larval instar	10.895 ± 0.932	30.22	37.663 ± 0.833
2nd larval instar	11.905 ± 1.508	30.90	33.142 ± 1.785
3rd larval instar	11.399 ± 2.235	30.34	34.040 ± 1.214
Larval period	11.109 ± 0.809	30.90	33.581 ± 2.691
Pupal period	11.615 ± 1.908	31.75	32.141 ± 1.053
Total immature stages	11.300 ± 1.556	31.72	32.177 ± 1.466

^aDue to estimation of this parameter by using graphical method, calculation of SE was impossible.

them were observed, especially in the estimated values of t_{min} , t_{opt} and t_{max} . Considering the values of statistical criteria, Lactin-2 showed the best fit to data among evaluated models (Table 3). The best model for estimating lower and upper temperature thresholds of *C. carnea* development was Lactin-2. As presented in Table 3, Lactin-2 model compared to the others was the best model to estimate the lower and upper temperature thresholds in most cases due to having the highest value of adjusted determination coefficient and lowest value of Akaike information criterion. Lactin-2 model was also used to estimate temperature indices of different stages of development because of better conditions than the other models regarding biological indices. Lower temperature threshold, the optimum temperature of

development, and the upper temperature threshold were estimated by Lactin-2 model (Tables 4 and 5, Fig. 1).

In the present study, Lactin-2 showed the best fit on observations among evaluated nonlinear models, considering statistical criteria and biological significance. Similarly, Fantinou et al. (2003) estimated the lower temperature thresholds for developmental stages of egg, larva, and pupa of sugarcane stem borer, *Sesamia nonagrioides* Lefebvre, by using Lactin-2 model. Moreover, Kontodimas et al. (2004) estimated the lower temperature thresholds of 2 species of ladybirds, *Nephus includens* and *N. bisignatus*, by using Lactin-2 nonlinear model. All of these references showed the abilities of Lactin-2 for modeling of temperature-dependent developments of the insects and mites. [Figueira et al. \(2000\)](#)



calculated the lower temperature threshold of the green lacewing, *C. externa*, for different immature stages using a linear model, which was close to the estimates of this study. Kazemi and Mehrnejad (2011) reported that the lower temperature thresholds of different immature stages of the lacewing, *C. lucasina*, using a conventional linear model, were very close to the estimates of the present study. Results of the experimental observations showed that the optimum temperature for development stages of *C. carnea* was around 30 to 32 °C (Table 5).

Conclusion

This study seemed to be the first attempt to determine the optimal temperature for development of *C. carnea*. The results showed that the predator could be used well for biological control aims within the mentioned thermal tolerance.

Abbreviations

R^2 : Coefficient of determination; R^2_{adj} : Adjusted coefficient of determination; RSS: Residual sum of squares; AIC: Akaike information criterion; L: Light; D: Dark; SSE: Sum of squared errors; t_{min} : Lower temperature threshold (here for development); t_{opt} : Optimal temperature (here for development); t_{max} : Upper temperature threshold (here for development)

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Authors' contributions

ZN conducted the study under the supervision of HRA. HRA supervised the work, analyzed the data, and prepared the manuscript. Both of the authors have read and approved the manuscript.

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Competing interests

The authors declare no conflict of interest.

Author details

¹Iranian Research Institute of Plant Protection, Agricultural, Research, Education and Extension Organization (ARREO), Tehran, Iran. ²Department of Plant Protection, College of Agricultural Science, University of Shahed, Tehran, Iran.

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