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Models to describe the thermal development rates of *Cycloneda sanguinea* L. (Coleoptera: Coccinelidae)



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ABSTRACT

Precise estimates of the lower (T_{min}) and higher (T_{max}) thermal thresholds as well as the temperature range that provides optimum performance (T_{opt}) enable to obtain the desired number of individuals in conservation systems, rearing and release of natural enemies. In this study, the relationship between the development rates of *Cycloneda sanguinea* L. (Coleoptera: Coccinelidae) and temperature was described using non-linear models developed by Analytis, Brière, Lactin, Lamb, Logan and Sharpe & DeMichele. There were differences between the models, considering the estimates of the parameters T_{min} , T_{max} , and T_{opt} . All of the tested models were able to describe non-linear responses involving the development rates of *C. sanguinea* at constant temperatures. Lactin and Lamb gave the highest z weight for egg, while Analytis, Sharpe & DeMichele and Brière gave the highest values for larvae and pupae. The more realistic T_{opt} estimated by the models varied from 29° to 31°C for egg, 27–28 °C for larvae and 28–29 °C for pupae. The Logan, Lactin and Analytis models estimated the T_{max} for egg, larvae and pupae to be approximately 34 °C, while the T_{min} estimated by the Analytis model was 16 °C for larvae and pupae. The information generated by our research will contribute towards improving the rearing and release of *C. sanguinea* in biological control programs, accurately controlling the rate of development in laboratory conditions or even scheduling the most favourable this species' release.

1. Introduction

Pest control using beneficial insects such as coccinellids has been demonstrated as a valuable method in the rational use of agricultural inputs and in producing agricultural crops within an agroecological approach (Almeida, 2001). *Cycloneda sanguinea* (Linnaeus) (Coleoptera: Coccinellidae) is one of the most abundant aphidophagous species among coccinellids in Brazilian agro-ecosystems (Faria et al., 2006). They are active predators during both the larval and adult stages, and prefer feeding on aphids and mealybugs, but may also feed on eggs, caterpillars, mites and 26 other small arthropods (Casari and Ide, 2012). Most ladybugs are generalist predators and are considered one of the best predators of aphids (Evans, 2008).

The duration of the ladybug development cycle may be influenced by the size of the species and thermal conditions. Insects and other organisms depend on temperature for development. Therefore, knowledge about the biological aspects of an insect is of fundamental importance in developing efficient management strategies and the economic production of predators in the laboratory (Parra et al., 2002). The development rate is the inverse of development time. These rates are used for linear and non-linear models when data are reached on everyday terms, wherein complete development is considered when the sum of the growth rates equals 1 ((Malaquias et al., 2014a; Aghdam et al., 2009). Therefore, in these models, the integral function of the rate of development of an organism over time can be used to simulate and predict the development of an organism exposed to different temperatures (Arbab et al., 2006).

Studies of variations in the rate of insect development allow an integrated view of the biological characteristics and adequate environmental conditions for the development of both pest insects, natural enemies, and their interactions. The development rate of a predator insect is often estimated using models based on degree days to estimate the lower developmental thermal threshold values or base temperature (Tb) and the thermal constant (K). However, existing linear models are not able to estimate the maximum thresholds of development curves because the models are derived from the linear equation (Haddad et al.,

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1999). Non-linear models have proven to be more suitable for these rate estimates, because they are more realistic and provide estimates of the optimum and maximum temperatures (Kontodimas et al., 2004) for the development of insects. Therefore, models provide a better description of curvilinear paths permitted due to algebraic structure and the combination of their constants, such as those observed for development estimates (Malaquias et al., 2014b).

In the current paper, we are testing 6 different models developed by Analytis, Brière, Lactin, Lamb, Logan and Sharpe & DeMichele, with the objective to predict the development rates of C. sanguinea. The first reason to use these six models is the good description of the non-linear responses involving the important prey development rates of C. sanguinea, such as Hyadaphis foeniculi (Hemiptera: Aphididae) (Malaquias et al., 2014b). The second fact that motivated the choice of these multiple models is that the activity and denaturation of enzymes are usually associated with temperature; this has been considered in some thermal models (Shi and Ge, 2010; Shi et al., 2011), and may be easily estimated using non-linear models such as Sharpe & DeMichele's biophysical model (Malaquias et al., 2014b). In addition, although the linear relationship is not often attempted, some non-linear models constructed to estimate development rates also include this linear relationship, especially at intermediate temperatures (Shi and Ge, 2010). In this context, one of the hypotheses of this study is that models such as that of Sharpe & DeMichele are effective in providing accurate estimates of the development rates of C. sanguinea. This hypothesis is based on the fact that this model is one of the most robust for the description of non-linear responses involving rates of insect development at constant extreme temperatures (high and low) through the incorporation of biophysical parameters, as well as to describe a linear relationship at intermediate temperatures (Wagner et al., 1984). A second hypothesis of this study is that there are more suitable models to describe the development of larvae and others that are applicable to pupae.

Despite the importance of *C. sanguinea* in regulating populations of pest insects in Nearctic and Neotropical regions (Milléo et al., 2014), information about the thermal performance of this coccinellidae is considered incipient. Understanding how abiotic factors affect the population dynamics of ladybugs are of foremost importance for the development of appropriate tactics to control pests such as aphids, to assist in the development of forecasts of insects in the field, to determine the best time to release them, or to run ecological practices that allow conservation of the predator in agroecosystems. In this context, here, we described the relationship between *C. sanguinea* development rates as a function of temperature using non-linear functions to estimate the parameters T_{min} , T_{max} , and T_{opt} in a precise way.

2. Material and methods

2.1. Bioassay

The research was carried out under laboratory conditions. Insects were reared at the Insect Ecology and Forestry Entomology Laboratory of the Department of Entomology and Acarology (LEA) of the Luiz de Queiroz College of Agriculture (ESALQ) at the University of São Paulo Paulo (USP), Piracicaba, São Paulo, Brazil. Adults of C. sanguinea were collected in cotton plants in the experimental area from LEA. Insectrearing stocks were kept in a climate-controlled chamber at 25 °C with a relative humidity of $65 \pm 10\%$ and a 12-h photophase. Specimens of C. sanguinea were transported to the laboratory for the establishment of rearing at LEA. In both rearing and experiments, all stages of the predator (egg, larva or pupae) were individualised in 9 cm Petri dishes until adult emergence. Into each Petri, a cotton swab moistened with a honey-water solution (50%) was placed, and specimens were fed daily ad libitum with frozen eggs of Ephestia kuehniella (Zeller) (Lepidoptera: Pyralidae) (Milléo et al., 2014). Specimens were maintained in BODtype chambers at constant temperatures of 16, 19, 22, 25, 28, 31 and 34 °C, under a 12-h photophase and relative humidity of 70 \pm 10%. The

development of all stages was evaluated at 24-h intervals, and the duration data of each stage was recorded, considering the time interval from embryonic development to the emergence of adults. The experimental design was a randomised block design. For each temperature, four groups of 30 insects (120 insects in total) were used, totalling 120 insects per temperature.

2.2. Models

The models developed by Analytis, Brière, Lactin, Lamb, Logan and Sharpe & DeMichele were fitted to the experimental data obtained in the present study.

With the Logan and Lactin models, it is possible to estimate the constant that defines the development rate at the optimum temperature. The rate of development can be estimated by the function developed by Logan using the following equation:

$$r(T) = \psi. \left[e^{\rho.T} - e^{\left(\rho.TL - \frac{TL - T}{\Delta T}\right)} \right]$$
(1)

The parameter ψ is the maximum development rate, ρ is a constant defining the development rate at the optimal temperature, T_L is the maximum lethal temperature in degrees Celsius, and ΔT is the temperature variation in which the physiological collapse (due to thermal degradation) becomes a dominant influence (Logan et al., 1976).

As a result of modification of the non-linear model proposed by Logan et al. (1976) in the equation below, Lactin excludes ψ and incorporates γ , which in turn enables the curve to intercept the abscissa, thereby permitting an estimation of the base temperature (Lactin et al., 1995).

$$r(T) = e^{\rho \cdot T} - e^{\left(\rho \cdot TL - \frac{TL - T}{\Delta T}\right)} + \gamma$$
⁽²⁾

The biophysical model of Sharpe & DeMichele (Sharpe and DeMichele, 1977; Schoolfield et al., 1981) considers several biophysical parameters associated with the thermal performance of the insect. For the present study, an adaptation of the Sharpe & DeMichele model was adopted, as expressed in the following function (Arbab et al., 2006).

$$r(T) = T. \frac{e\left(a - \frac{b}{T}\right)}{1 + e\left(c - \frac{d}{T}\right) + e\left(f - \frac{g}{T}\right)}$$
(3)

Where T is the temperature in degrees Kelvin, and a, b, c, d, f and g are empirical constants.

The thermal thresholds are estimated by the T_{min} and T_{max} parameters in the Analytis model, which correspond to the minimum and maximum thermal thresholds, respectively (Analytis, 1977). Given that a, n and m are constants in this model, the development rate can be estimated by the Analytis model using the following formula:

$$r(T) = a. (T - T_{min})^n . (T_{max} - T)^m$$
(4)

In the Lamb model, the parameters T_oL and T_oH make the intercept curve, where T_oL is used when $T < T_m$, and T_oH is a parameter that makes the intercept curve when $T > T_m$; R_m and T_m , expressed in the model by Lamb are given by the Taylor (Lamb, 1992) equation, so the development rate for this model is estimated by:

$$\frac{r(T) = R_m \cdot e\left[-\frac{1}{2}\left(\frac{T - T_m}{T_{\sigma L}}\right)^2\right] if T \le T_m}{r(T) = R_m - e\left[-\frac{1}{2}\left(\frac{T - T_m}{T_{\sigma H}}\right)^2\right] if T > T_m}$$
(5)

Finally, considering the Brière model, the lower thermal threshold (T_o) and upper thermal threshold (T_L) , together with the constant *a* (Brière and Pracros (1998) can be estimated by the following equation:

$$r(T) = a. T. (T - T_0). \sqrt{T_L - T}$$
 (6)

2.3. Statistical analysis

The parameters of the linear models were estimated using the NLIN Procedure of the SAS (method = Marquardt) (SAS, 2000). The residual sum of squares (*RSS*), coefficient of determination (R^2), adjusted coefficient of determination ($R^2 adj$). R^2 and $R^2 adj$ measured the strength of the relationship between the models and the development rate. High Rsquared values do not necessarily show the goodness-of-fit of the models; for instance, we also used Akaike information criterion (*AIC*), Bayesian information criterion (*BIC*) and corrected Akaike information criterion (*AICC*) as indicators for comparing fitted non-linear models. In general, models with the lowest values of *AIC*, *BIC* and *AICC* are the best. In this study, the *z*-weight was also used as a reference indicator (Shi and Ge, 2010). Models with the highest *z*-weight are the best. *AIC*, *BIC* and *AICC* were calculated with the following formulas:

$$L = -\frac{N}{2}ln\left(\frac{RSS}{N}\right) \tag{7}$$

$$AIC = -2L + 2K \tag{8}$$

$$BIC = -2L + Kln(N) \tag{9}$$

$$AICC = \frac{-2L + 2KN}{(N - K - 1)}$$
(10)

K is the number of parameters including the error, while *L* indicates the maximised log-likelihood value. *L* can be obtained from *N* and *RSS*, which correspond to the sample number and residual sum of squares, respectively.

Given the candidate models, it was possible to select the best ones by comparing the values of their z-weight (Shi and Ge, 2010); this integrates the aforementioned indicators to select the best model:

$$z_i = \frac{D_i}{\sum_{j=1}^{S} D_j} \tag{11}$$

Where Di is the weighted average of the standardized indicators, i = 1, 2, 3, ..., *S* and Di can be calculated using the following formula:

$$D_{i} = \frac{1}{5} \left(\frac{|R_{i}^{2} - min(R^{2})|}{max(R^{2}) - min(R^{2})} + \frac{|R_{adj,i}^{2} - min(R_{adj}^{2})|}{max(R_{adj}^{2}) - min(R_{adj}^{2})} \right. \\ \left. + \frac{|AIC_{i} - max(AIC)|}{max(AIC) - min(AIC)} + \frac{|BIC_{i} - max(BIC)|}{max(BIC) - min(BIC)} \right. \\ \left. + \frac{|AICC_{i} - max(AICC)|}{max(AICC) - min(AICC)} \right)$$
(12)

where $\max(x)$ and $\min(x)$ represent, respectively, the maximum and minimum values of x in all of the S candidate models; x_i denotes the value x of the candidate model and i = 1, 2, 3, ..., S (Shi and Ge, 2010).

3. Results

There was no predator development at the evaluated temperatures of 16 and 34 °C; however, temperatures between 19 and 31 °C allowed the development of all instars of *C. sanguinea*. The highest observed development rates with the original data were found at 31 °C for eggs (Figs. 1–6), 28 °C for larvae (Figs. 1–6) and in the range between 28 and 31 °C for pupae (Figs. 1–6).

The values predicted for the optimal temperature of development (T_{opt}) were 31 °C for eggs, 28 °C for larvae and 29 °C for pupae using the model of Sharpe and DeMichele. However, the Lactin overestimated the T_{opt} by predicting values superior to 33 °C for all stages. The T_{opt} estimated by the Analytis and Brière models were close to 29 °C for eggs and 28 °C for larvae and pupae (Table 1).

A comparison of the models revealed some variation in the estimates of the lower and upper thermal limits. The upper thermal limit (T_{max}), estimated by Logan and Analytis was approximately 34 °C for all



Fig. 1. Fitting Logan's model to the observed values of development rates (day⁻¹) of the eggs, larvae and pupae stages of *Cycloneda sanguinea* as a function of temperature (°C). Observed (dots) and predicted data (lines). R_{adj}^2 : adjusted coefficient of determination.



Fig. 2. Fitting Lactin's model to the observed values of development rates (day^{-1}) of eggs, larvae and pupae stages of *Cycloneda sanguinea* as a function of temperature (°C). Observed (dots) and predicted data (lines). R_{adj}^2 : adjusted coefficient of determination.

stages (Table 1). The Brière function predicted a low thermal limit (T_{min}) between 15 and 16 °C for all stages. The T_{min} values estimated by Analytis and Lactin-2 were 16 °C and below 14 °C, respectively, for all stages (Table 1). As for the lower thermal threshold, we observed high variability in the estimate of Brière functions, according to the values of the confidence intervals.

Higher values of R^2 and R_{adj}^2 (> 0.8500) and lower values of *AIC*, *AICC* and *BIC* were observed in the models of Lactin and Lamb for egg, and Analytis, Brière and Sharpe & DeMichele for larvae and pupae (Table 2). The calculated *z*-weight showed that Lactin and Lamb were



Fig. 3. Fitting Sharpe & DeMichele's model to the observed values of development rates (day⁻¹) of eggs, larvae and pupae stages of Cycloneda sanguinea as a function of temperature (°C). Observed (dots) and predicted data (lines). R_{adi}²: adjusted coefficient of determination.



Fig. 4. Fitting Analytis' model to the observed values of development rates (day⁻¹) of eggs, larvae and pupae stages of Cycloneda sanguinea as a function of temperature (°C). Observed (dots) and predicted data (lines). R²_{adj}: adjusted coefficient of determination.

the best models to describe the embryonic development rates of predators at different temperatures (Fig. 7). The advantage of the use of these models in relation to the others can be compared based on the zweight values shown in Fig. 7. Analysis of the larval and pupal stages revealed that the lower variability measured by the values of R^2 and R_{adi}^2 could be obtained using the models of Analytis, Sharpe and De-Michele and Brière (Table 2). The high z-weight values reinforce the appropriate adjustment of these models for estimates of the rates of development of the larval and pupal stages of C. sanguinea (Fig. 7).



Fig. 5. Fitting Lamb's model to the observed values of development rates (day⁻¹) of eggs, larvae and pupae stages of Cycloneda sanguinea as a function of temperature (°C). Observed (dots) and predicted data (lines). R²_{adj}: adjusted coefficient of determination.



- Observed data larvae a
- Observed data pupae

Fig. 6. Fitting Lamb's model to the observed values of development rates (day⁻¹) of eggs, larvae and pupae stages of Cycloneda sanguinea as a function of temperature (°C). Observed (dots) and predicted data (lines). R²_{adj}: adjusted coefficient of determination.

4. Discussion

The closest development rates to those observed experimentally in the larval and pupal stages were estimated by the Analytis, Brière and Sharpe & DeMichele models. For eggs this result was found using the Lactin and Lamb models. High R^2 values were obtained for all stages for the models used, and the R^2 values were close to or greater than 0.90 for the above-mentioned models. A goodness-of-fit using the Sharpe & DeMichele (Ramalho et al., 2009; Medeiros et al., 2004) and Brière models (Duarte and Polania, 2009) was found in other studies. The

Table 1

Values of fitted coefficients (IC 95%) and measureable parameters of thermal development rate models for describing embryonic, larvae and pupae stages of Cycloneda sanguinea.

Model	Parameter	Egg	Larvae	Рирае
Logan (1)	Ψ	0.0225	-0.0383	0.0300
	$T_L(=t_{max})$	34.0001 (33.6375-34.3627)	33.9121 (32.67-35.15)	33.9556 (33.0794–34.8318)
	ΔT	0.8589	05.01	0.47212
	ρ	0.1012	0.2015	0.2079
	t _{opt}	31.7100	28.9000	29.0800
Lactin (2)	ρ	0.0183	0.0051	0.0107
	$T_L (= t_{max})$	34.0544 (34.04-34.06)	34.1464 (34.09-34.19)	34.1456 (34.09-34.19)
	ΔT	0.0472	0.0653	0.0922
	X	-1.2735	-1.0637	-1.1405
	t _{min}	13.2200	12.1200	12.2900
	topt	33.4300	33.7100	33.5100
Sharpe & DeMichele (3)	a	-1434.4000	- 255.4000	-416.9000
	b	-435811.0000	- 75253.9000	-124756.0000
	с	-1455.8000	- 291.0000	-447.5000
	d	-444262.0000	- 88269.2000	-136088.0000
	f	99.9000	99.9999	99.9900
	g	169583.00000	169583.0000	169583.0000
	t _{opt}	31.1000	28.2900	29.3600
Analytis (4)	a	0.0132	0.00659	0.0111
	t _{min}	16.0000 (15.77-16.13)	16.0000 (15.88–16.11)	16.0000 (15.97–16.02)
	t _{max}	34.0000 (33.99-34.00)	34.0000 (33.99-34.00)	34.0000 (33.99-34.00)
	n	1.1021	0.8172	0.9200
	m	0.4000	0.3696	0.3999
	t _{opt}	29.12	28.2900	28.3800
Lamb (5)	T_m	32.0000	31.0000	31.0000
	T _{oL}	8.7102	8.5404	8.3135
	R_m	0.4407	0.1022	0.2346
	T _{oH}	1.5000	1.4025	1.7589
Brière (6)	$T_o(=t_{min})$	15.1459 (10.30–19.99)	15.9278 (14.25-17.60)	15.5417 (13.55–17.53)
	$T_L (= t_{max})$	34.0000 (34.00-34.00)	31.8656 (31.14-32.59)	32.5777 (31.25-33.89)
	t _{opt}	29.1400	27.6600	28.2100
	a	0.000480	0.000167	0.000322

Sharpe & DeMichele models were more realistic in estimating the T_{opt} for larval and pupal stages. This temperature range is similar to that found in other species of ladybugs (Butcher et al., 1971). The optimum temperature values (T_{opt}) estimated by the Lactin models for the embryonic, larval and pupal stages, were unrealistic because they are close to the lethal temperature (33 °C).

In the case of Brière model, the minimum temperature estimated was approximately 16 °C for all stages of *C. sanguinea*, which was also consistent with the value predicted by the Analytis model. The Lactin model estimated a lower temperature threshold (T_{min}), which was below 14 °C for all development stages of *C. sanguinea*. In most cases,

the Lactin model accurately predicted the development rate of insects, especially when temperatures were close to the minimum (Lactin et al., 1995). The Lactin model best described the T_{min} of another Coccinellidae, *Stethorus punctillum* Weise (Coleoptera: Coccinellidae) (Roy et al., 2002). The Lactin model may be superior for estimating temperature thresholds compared to other non-linear models for some species of ladybugs (Kontodimas et al., 2004; Roy et al., 2002). On the other hand, models such as Brière (Papanikolaou, 2013) are also considered good tools for estimating the optimal temperature and upper temperature threshold. However, there are cases that cannot provide realistic estimates of T_{min} (Roy et al., 2002). For example, the Brière

Table 2

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Reg	ression	anaiv	ISIS OF	models	descripting	της επέςτα	it temp	eranıre (n the	aever	nment	time to	or a	eserining	emory	vonic.	larvae a	וח הח	inae sta	JUDES OF 1	vcioneaa	sanonnea
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Model	Stage	R^2	R_{adj}^2	AIC	BIC	AICC	P > F
Logan	Egg	0.8922	0.8787	-190.5541	-197.2219	-242.5234	0.0180
	Larvae	0.8658	0.8491	-263.3843	-270.0521	-335.2164	0.0256
	Pupae	0.9223	0.9125	-234.7919	-241.4597	-298.826	0.0107
Lactin	Egg	0.9339	0.9257	-204.2614	-210.9292	-259.9691	0.0043
	Larvae	0.7392	0.7066	-244.7699	-251.4377	-311.5253	0.0500
	Pupae	0.8450	0.8257	-215.4779	-222.1457	-274.2447	0.0240
Sharpe & DeMichele	Egg	0.8947	0.8707	-187.2068	-197.87463	-262.0895	0.0025
	Larvae	0.9300	0.9141	-277.60076	-288.2685	-388.6410	0.0098
	Pupae	0.9277	0.9112	-232.8044	-243.4722	-325.9262	0.0096
Analytis	Egg	0.8927	0.8841	-192.6834	-197.3512	-234.5711	0.0014
-	Larvae	0.9309	0.9254	-283.9698	-288.6376	-345.7024	0.0006
	Pupae	0.9981	0.9979	-340.2691	-344.9369	-414.2407	< 0.0001
Lamb	Egg	0.9051	0.8975	-196.1276	-200.7953	-238.7640	0.0017
	Larvae	0.8250	0.8110	-257.9446	-262.6124	-314.0195	0.0394
	Pupae	0.9050	0.8974	-231.1903	-235.8581	-281.4490	0.0144
Brière	Egg	0.8922	0.8836	-192.5541	-197.2219	-234.4137	0.0026
	Larvae	0.9874	0.9864	-331.6521	-336.3199	-403.7504	0.0005
	Pupae	0.9872	0.9862	-287.3396	-292.0074	- 349.8047	0.0005

 R^2 = coefficient of determination; R_{adj}^2 = adjusted coefficient of determination; AIC = Akaike information criterion; BIC = Bayesian information criterion; AICC = corrected Akaike information criterion. P = probability. F = F-value.



Fig. 7. Goodness-of-fit evaluation of non-linear models based on z-values to describe the development rate of *Cycloneda sanguinea* at its egg, larvae and pupae stages. S&DM = Sharpe & DeMichele.

model failed to correctly estimate the T_{min} for *Bactericera cockerelli* (Hemiptera: Triozidae), although that model and the Lactin model accurately estimated the upper limit of development (Tran et al., 2012). In *Adalia bipunctata* L. (Coleoptera: Coccinellidae) that were fed an artificial diet, the lower limit for the egg stage was estimated to be 8.87 and 9.18 °C by the Brière and linear models, respectively; however, the Lactin model predicted a threshold of 14.79 °C (Jalali et al., 2010).

In addition to the values of non-linear regression coefficient (R^2), and adjusted R^2 , we considered the *AIC*, *AICC* and *BIC*, all of which have been considered in previous studies (Aghdam et al., 2009; Roy et al., 2002; Papanikolaou, 2002). The adjusted R^2 , *AIC*, *BIC* and *AICC* consider the complexity of a model by the addition of parameters (Shi and Ge, 2010). In a general analysis, the lower values of the information criteria and higher *z* weight values for the larval and pupal phases were observed in the Analytis, Brière and Sharpe & DeMichele models, while the best adjustments for the egg stage were revealed by the Lactin and Lamb models, reinforcing the second hypothesis presented in this work.

The confidence intervals associated with the parameters that estimate the thermal development thresholds for larval and pupal stages of *C. sanguinea* were analysed. Using analysis, it was possible to observe a greater variability in the confidence intervals estimated by the Brière model. However, such variability in the assessment criteria should be viewed cautiously because the estimation of confidence intervals incorporates all relevant components of variation and is often a more unstable and difficult step of the analysis. Furthermore, the different packages or procedures use different approaches, and almost all of this information involves an iterative process (Bolker et al., 2013).

The adoption of non-linear models such as Analytis, Brière and Sharpe & DeMichele are important tools for better understanding the relationship involving the temperature and development rates of both larval and pupal stages of C. sanguinea. Therefore, these models contribute towards obtaining the desired number of individuals to optimise the storage system for rearing and for predator release. The trajectories of the curves revealed by the Lactin and Lamb models show that the highest growth rates for eggs are seen at 31 °C. For larvae at temperature ranging from 19° to 27°C and 29–32 °C, the development rates are inferior in relation to the interval between 27 and 29 °C, while a higher pupal development rate can be obtained from 28 and 31 °C. In the pupal stage, there is a clear reduction in the development of C. sanguinea pupae between 28 and 31 °C. These results demonstrate the feasibility of non-linear models to estimate insect development rates; such models may be useful for predicting population peaks in agroecosystems (Lewis et al., 2015). Furthermore, the prediction of the total number of days required to reach the completion of development enable the improvement of different large-scale production processes. In addition, we would like to emphasise that a diet with eggs of *E. kuehniella* used in this study could have a detrimental effect on the performance of ladybugs. Therefore, we would encourage further studies on the use of different natural diets for the assessment of non-linear responses in relationships involving temperature and development rates. Another challenging subject of research is the combination of phenological and dynamic models based on thermal development rates of prey and *C. sanguinea* stages, making the prediction of outbreaks in field conditions easier.

5. Conclusions

- i. Based on the *z*-value for the evaluation of non-linear models, the models of Lactin and Lamb best describe the development rates of *C. sanguinea* embryonic stage, while the best goodness-of-fit to describe the larval and pupal thermal development rates was obtained with the Analytis, Brière and Sharpe & DeMichele models.
- ii. The T_{opt} estimated by the models for best fit was close to 31 °C for egg, and varied from 27° to 28°C for larvae and 28–29 °C for pupae.
- iii. For both stages of development, the more realistic estimates of minimum and maximum thermal limits were approximately 16 and 34 °C, respectively.

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