Comparative Temperature-Dependent Development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) Preying on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae): Evaluation of a Linear and Various Nonlinear Models Using Specific Criteria

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ABSTRACT The effect of temperature on the development of the predators *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) was studied. The duration of the development of immature stages and the pre-oviposition period of the two predators, reared on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae) at eight constant temperatures (10, 15, 20, 25, 30, 32.5, 35, and 37.5 ± 1°C), have been recorded. The developmental zero (lower temperature threshold) was estimated to be 10.9 and 9.4°C, and the thermal constant was 490.5 and 614.3 DD for *N. includens* and *N. bisignatus*, respectively, using the linear model. Data were fitted to various nonlinear temperature-dependent models, and the thermal developmental thresholds (lower and upper), as well as the optimum temperature for development, have been estimated. Evaluation of the models took place, based on the following criteria: fit to data (residual sum of squares and coefficient of determination or coefficient of nonlinear regression), number and biological value of the fitted coefficients, number of measurable parameters, and accuracy on the estimation of the thresholds. Conclusively, linear and Lactin models are highly recommended for the description of temperature-dependent development of these two predators and possibly of other coccinellids.

KEY WORDS development, threshold, model, *Nephus bisignatus, Nephus includens*

TEMPERATURE IS THE MAIN abiotic factor influencing the biology, ecology, and population dynamics of pests and their natural enemies. In biological control, details concerning such responses are useful to select natural enemies that are best adapted to conditions favoring target pests (Jervis and Copland 1996, Obrycki and Kring 1998). Biological control, whether using introduction, conservation, or augmentation approaches, is facilitated when the climatic responses of biocontrol agents, especially to temperature, are known. The thermal thresholds for insect development can be estimated using several functional forms.

During the last two decades, numerous linear and nonlinear equations have been used to describe insect development rates and estimate various critical temperatures. The linear approximation enables the calculation of lower developmental threshold and thermal constant within a limited temperature range, usually 15–30°C (e.g., Campbell et al. 1974, Honěk 1999, Jarošik et al. 2002). To describe the developmental rate more realistically and over a wider temperature range, several nonlinear models have been applied (e.g., Stinner et al. 1974, Logan et al. 1976, Sharpe and DeMichele 1977, Lactin et al. 1995, Briere et al. 1999), providing value estimation for maximum and optimum temperatures for development. Estimation of thermal constant cannot be achieved by nonlinear models. They usually give good fit to most experimental data, and many of them incorporate physiological and biochemical constants (e.g., Logan et al. 1976, Schoolfield et al. 1981; Wagner et al. 1984, 1991).

Nephus bisignatus (Boheman) and *N. includens* (Kirsch) (Coleoptera: Coccinellidae) are species of the palearctic region and important indigenous predators of mealybugs (Homoptera: Pseudococcidae) in Greece (Argyriou 1968, Argyriou et al. 1976, Kontodimas 1997). Both species are among the less studied coccinellids, little is known about their biology, and no experimental data concerning the influence of temperature on their development are available.

Nephus bisignatus is distributed throughout in North Europe (South Norway, Finland, Sweden, Denmark, Netherlands, and Germany) (Pope 1973), but it has

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been also reported in Morocco, South France, Italy, and Portugal (Pope 1973, Francardi and Covassi 1992, Magro and Hemptinne 1999, Magro et al. 1999). It has been recently reported for the first time in Greece on *Thuja orientalis* L. (Cupressaceae) and *Pistacia lentiscus* L. (Anacardiaceae) infested by *Planococcus citri* (Kontodimas 1997). There are no data concerning any biological features of *N. bisignatus.*

Nephus includens has been reported in Greece, Turkey, Italy, Spain, and Portugal (Bodenheimer 1951, Viggiani 1974, Argyriou et al. 1976, Longo and Benfatto 1987, Suzer et al. 1992, Katsoyannos 1996, Magro and Hemptinne 1999, Magro et al. 1999). Tranfaglia and Viggiani (1972) found that the female laid 150.6 eggs and lived 74 d at 25–27°C preying on *P. citri.* Kontodimas (2003) studied the effect of temperature on many biological features of *N. includens.* The average total fecundity was 49.2, 97.8, 162.8, 108.5, 87.4, and 31.1 eggs/female at 15, 20, 25, 30, 32.5, and 35°C, respectively, whereas females lived 99.5, 84.7, 69.5, 61.1, 49.6, and 30.1 d, respectively, at the above-mentioned temperatures. The predator completes five generations in Greece, whereas *N. bisignatus* completes four. They both overwinter as adults and reach population peak during August and September (D.C.K., unpublished data).

The effect of temperature on the duration of immature stages and the pre-oviposition period of *N. bisignatus* and *N. includens* were studied here. The thermal thresholds were estimated using 1 linear and 13 nonlinear temperature-dependent models. Furthermore, the models were evaluated according to their fit to the data, the number and biological interpretation of the fitted coefficients, the number of the measurable parameters, and the accuracy on threshold estimation.

Materials and Methods

Rearing Methods and Experimental Conditions. *Nephus bisignatus* and *N. includens* were originally collected in 1997 from *Thuja orientalis* L. (Cupressaceae) in Attiki Co. (Central Greece), and *Citrus* sp. (Rutaceae) in Preveza Co. (Northwestern Greece), respectively, infested by *P. citri.* The same mealybug was used as prey for predator rearing in the laboratory. Citrus mealybug was reared on potato sprouts (*Solanum tuberosum*) and pumpkins (*Cucurbita pepo* and *C. maxima*) at 25 ± 1°C, L:D 16:8 h photoperiod, and 65 ± 2% RH, in large plastic boxes (30 by 40 by 15 cm) tightly covered with mesh (hole: 0.3 by 0.4 cm). Both predators were reared in large cylindrical plexiglas cages (50 cm height by 30 cm diameter) containing an abundance of prey under controlled conditions (10, 15, 20, 25, 30, 32.5, 35, and 37.5 ± 1°C; 65 ± 2% RH; L:D 16:8 h). Additionally, male-female pairs of each coccinellid were kept separately in plastic petri dishes (9 cm diameter by 1.6 cm height) with abundance of prey in the same conditions as above. The eggs for development measurements were collected from these pairs. All experiments and rearings were conducted in incubators (model MLR-3500T, 3500HT; Sanyo, Kifissia, Greece).

Development and Survivorship of Immatures. Newly laid eggs were placed individually in plastic petri dishes and transferred to incubators. On hatching, coccinellid larvae were constantly supplied with an excess of *P. citri* of various stages. Progress in development and survival was assessed every 12 h. In case of immature mortality, the dead individual was removed and replaced by another of the same age, taken from laboratory rearing of the same temperature. Thereby, 25 individuals of each species completed their development to adult emergence.

Pre-ovipositional Period. The pre-ovipositional period (time interval required for ovary maturation and initiation of mature egg production) was measured for newly emerged females ($N = 25$) of both species. Each female was isolated with a male in plastic petri dishes with an excess of prey. Observations for initiation of egg laying were made every 12 h.

Biological Cycle. The total time for completion of the biological cycle (time elapsed from egg stage until adult oviposition) was estimated by adding the duration of immature stages with the respective pre-ovipositional period.

Statistical Methods. Data were submitted to analysis of variance (ANOVA) at $\alpha = 0.05$. Means were separated by using the Tukey–Kramer honestly significant difference (HSD) test (Sokal and Rohlf 1995). Data were also submitted to two-way ANOVA at $\alpha = 0.05$ for the significance of the main effects (species, temperature) and interactions. Statistical analysis was performed by using the JMP statistical package (v. 4.02; SAS Institute 1989).

Mathematical Models. Standard thermal indices were calculated, where appropriate, for each of 14 developmental models.

- The lower developmental threshold ($t_{\min}$).
- The minimum temperature at which the rate of development is zero or there is no measurable development. It may be estimated by some nonlinear and by linear models as the intercept value of the temperature axis. The SE of $t_{\min}$, when calculated from linear models, is:

$$\mathrm{SE}_{t_{\min}} = \frac{\bar{r}}{b}\sqrt{\frac{s^2}{N \cdot \bar{r}^2} + \left[\frac{\mathrm{SE_b}}{b}\right]^2}$$

where s^2 is the residual mean square of r, $\bar{r}$ is the sample mean, and N is the sample size (Campbell et al. 1974).

- The upper developmental threshold ($t_{\max}$).
- The maximum temperature at which the rate of development is zero or life cannot be maintained for a prolonged period. This is estimated by most nonlinear models. The SE of $t_{\max}$ was calculated from the nonlinear regression.
- The optimum temperature for development (t_{opt}).
- The temperature at which the rate of development is maximum. It may be estimated directly by the equations of some nonlinear models, or as the pa-

rameter value for which their first derivatives equals zero. The SE of t_{opt} was calculated from the nonlinear regression.

- The thermal constant (K).
- The amount of thermal energy (day-degrees) needed to complete development. The thermal constant K can be estimated only by the linear equation as the reciprocal of the slope b, $K = 1/b$. The SE of K is (Campbell et al. 1974):

$$\mathrm{SE}_K = \frac{\mathrm{SE}_b}{b^2}$$

Model Evaluation. Fourteen (1 linear and 13 nonlinear) models that describe the effect of temperature on the development of insects were estimated (Table 1). The model evaluation involved *a priori* (the already known model properties) and *a posteriori* features (the fit of the model to experimental data and accuracy on the estimation of critical temperatures).

A priori evaluation was based on the following criteria:

- Number of fitted coefficients (NFCs).
- The number of fitted coefficients (a, b, c, d, f, g, ρ, λ, and others) that are not directly calculated but estimated as coefficients of nonlinear regression. Model application is facilitated when estimation of few coefficients is required. Most models include more than three fitted coefficients. The Sharpe and DeMichele equation requires the estimation of the most (six), whereas the fewest coefficients were for the Sigmoid, Equation 16, and Briere (three), as well as the two-parameter linear model (Table 1).
- Biological interpretation of fitted coefficients (BIs).
- Some models are favored because they not only describe but also attempt to explain the relationship between temperature and development in terms of physiological and biochemical mechanisms. The value of fitted coefficients are often strongly related to such biological processes.
- Number of measurable parameters (MPs).
- With this term, the critical temperatures (t_{opt}, t_{max}, t_{min}) and thermal constant (K) are defined. The model should allow the estimation of as many MPs as possible. Most models enable the estimation of two or more parameters. The only models that estimate all three are the Analytis, Equation 16, Lactin, and Briere (Table 1). The Logan-6, Logan-10, third order Polynomial, and Holling-III do not estimate the lower developmental threshold, because they are asymptotic to the left of the temperature axis. The Janisch and the Stinner equations are asymptotic to the temperature axis and cannot estimate t_{min} and t_{max}, just t_{opt}. The Sharpe and DeMichele and the Gauss equations are also asymptotic to the temperature axis, but because of the rapid decline of the curve, the value of t_{max} can be calculated graphically. The linear model does not provide either t_{opt} or t_{max}. The sigmoid equation fails to estimate any of the three parameters, because it is asymptotic to the left of the temperature axis.

General Applicability. This criterion was met by models that were adopted in many studies for description of temperature-dependent insect development. Most commonly used models are the linear, Logan-6, Logan-10, Sharpe and DeMichelle, Gauss, Polynomial, and Lactin (Table 1).

A posteriori evaluation was based on:

- Fit to data.
- Two statistics were used to evaluate goodness-of-fit. The coefficient of determination (for linear model) or the coefficient of nonlinear regression (for nonlinear models; R^2) and the residual sum of squares (RSS). The higher the values of R^2 and lower of RSS, the better the fit is.
- Accuracy.
- Evaluation of accuracy at estimation of critical temperatures was based on their comparison with experimental data. The lower developmental threshold should lie within 10 (lethal temperature for both species; Table 2) and 15°C to be accurate. Similarly, the true value of t_{max} is located between 35 and 37.5°C for *N. includens* and 32.5 and 35°C for *N. bisignatus*, given that 37.5 and 35°C were lethal for *N. includens* and *N. bisignatus*, respectively (Table 2). The optimum temperature for development should be close to 30–32.5 or 32.5–35°C, where maximum developmental rate was measured for *N. bisignatus* and *N. includens*, respectively (Table 2).

In the linear regression, the last data value, which deviated from the straight line, was omitted. The omission was necessary for the correct calculation of the parameters t_{min} and K (De Clerq and Degheele 1992). Furthermore, Equations 1 and 3 were considered as equivalent, and parameters K and t_{min} were estimated from the linear regression (Table 1). In other studies, these equations have been considered as different models, and the parameters K and t_{min} have been estimated from the nonlinear regression of Equation 1 (Johnson et al. 1979, Fornasari 1995, Muniz and Nombela 2001).

The nonlinear regression was analyzed with the Marquardt algorithm (Marquardt 1963) using the JMP (v. 4.02; SAS Institute 1989) and SPSS (v. 9.0; SPSS 1999) statistical programs.

Results

Development Time. The development time, the pre-oviposition period, and the duration of biological cycle of both predators at eight constant temperatures are presented in Table 2. None of the species succeeded in completing development at 10 and 37.5° C, while *N. bisignatus* did not complete it at 35°C as well. The rate of development was positively correlated with temperature until the upper limit of 32.5 and 30°C for *N. bisignatus* and *N. includens*, respectively. As far as pre-ovipositional period is concerned, the ovaries of *N. includens* showed a higher maturation rate because they start ovipositing ≈1–2 d earlier than *N. bisignatus*.

Table 1. Mathematical models that were used to describe the effect of temperature on the development of *N. bisignatus* and *N. includens*

Equation	Model	Reference
$D = K/(\text{temp} - t_{\text{min}}) \quad (1)$	Linear or thermal summation	Uvarov 1931, Wigglesworth 1953, Campbell et al. 1974, Campbell and Mackauer 1975, Obrycki and Tauber 1982, Logan 1988, De Clerq and Degheele 1992, Lamb 1992, Worner 1992, Formassari 1995, Lactin and Johnson 1995, Briere and Pracros 1998, Royer et al. 1999, Stathas 2000, Muniz and Nombela 2001, Roy et al. 2002, and others
$K = D \times (\text{temp} - t_{\text{min}}) \quad (2)$		
$\frac{1}{D} = \frac{1}{K} \times \text{temp} - \frac{t_{\text{min}}}{K} \quad (3)$		
$r = b \times \text{temp} + a \quad (4)$		
$1/D = C/1 + e^{(\text{a} + \text{b} \times \text{temp})} \quad (5)$	Sigmoid or logistic	Davidson 1942, 1944; Wigglesworth 1953, Analytis 1974
$D = \frac{D_{\text{min}}}{2} \times [e^{\text{k} \times (\text{temp} - \text{t}_{\text{p}})} + e^{-\lambda \times (\text{temp} - \text{t}_{\text{p}})}] \quad (6)$	Janisch (Analytis modification)	Janisch 1932, Analytis 1981
$\frac{1}{D} = \left\{\frac{D_{\text{min}}}{2} \times [e^{\text{k} \times (\text{temp} - \text{t}_{\text{p}})} + e^{-\lambda \times (\text{temp} - \text{t}_{\text{p}})}]\right\}^{-1} \quad (7)$		
$\frac{1}{D} = \frac{C}{1 + e^{(\text{a} + \text{b} \times \text{temp})}} \text{ if temp} \leq t_{\text{opt}}$	Stinner	Stinner et al. 1974, Smith and Ward 1995, Logan 1988
$\frac{1}{D} = \frac{C}{1 + e^{[\text{a} + \text{b} \times (2 \times \text{t}_{\text{opt}} - \text{temp})]}} \text{ if temp} > t_{\text{opt}} \quad (8)$		
$\frac{1}{D} = \psi \times \left[e^{\rho \times \text{temp}} - e^{\left(\text{p} \times \text{t}_{\text{max}} - \frac{\text{t}_{\text{max}} - \text{temp}}{\Delta}\right)}\right] \quad (9)$	Logan-6	Logan et al. 1976, Logan 1988, Gould and Elkinton 1990, Morales-Ramos and Cate 1993, Got et al. 1996, Briere and Pracros 1998, Briere et al. 1998, Hentz et al. 1998, Sigsgaard 2000, Tobin et al. 2001, Roy et al. 2002, and others
$\frac{1}{D} = \alpha \times \left[\frac{1}{1 + k \times e^{-\rho \times \text{temp}}} e^{\left(\frac{t_{\text{max}} - \text{temp}}{\Delta}\right)}\right] \quad (10)$	Logan-10	
$\frac{1}{D} = \text{temp} \times \frac{e^{\left(\phi \frac{\Delta H_{\text{A}}^{\neq}}{R \times \text{temp}}\right)}}{1 + e^{\left(\frac{\Delta S_{\text{L}}}{R} - \frac{\Delta \text{H}_{\text{L}}}{R \times \text{temp}}\right)} + e^{\left(\frac{\Delta S_{\text{H}}}{R} - \frac{\Delta \text{H}_{\text{H}}}{R \times \text{temp}}\right)}} \quad (11)$	Sharpe and DeMichele	Sharpe and De Michele 1977, Sharpe et al. 1977, Schoolfield et al 1981, Hilbert and Logan 1983, Lamb et al. 1984, Wagner et al. 1984, Worner 1992, Roy et al. 2002
$\frac{1}{D} = \text{temp} \times \frac{e^{\left(a - \frac{b}{\text{temp}}\right)}}{1 + e^{\left(c - \frac{d}{\text{temp}}\right)} + e^{\left(f - \frac{g}{\text{temp}}\right)}} \quad (12)$		
$\frac{1}{D} = a \times (\text{temp} - t_{\text{min}})^{\text{n}} \times (t_{\text{max}} - \text{temp})^{\text{m}} \quad (13)$	Analytis	Analytis 1977, 1979, 1980, 1981
$\frac{1}{D} = r_{\text{m}} \times e\left[-\frac{1}{2} \times \left(\frac{\text{temp} - t_{\text{opt}}}{\text{t}_{\text{s}}}\right)\right] \text{if temp} \leq t_{\text{opt}}$	Gauss (or Taylor) -non symetric	Taylor 1981, 1982; Lamb et al. 1984, Lamb et al. 1992, Roy et al. 2002
$\frac{1}{D} = r_m \times e\left[-\frac{1}{2} \times \left(\frac{\text{temp} - t_{\text{opt}}}{t_{\text{si}}}\right)\right] \text{if temp} > t_{\text{opt}} \quad (14)$		
$\frac{1}{D} = a \times \text{temp}^3 + b \times \text{temp}^2 + c \times \text{temp} + d \quad (15)$	Polynomial 3rd order (Harcourt Equation)	Harcourt and Yee 1982, Lamb et al. 1984, Briere and Pracros 1998
$\frac{1}{D} = a \times (\text{temp} - t_{\text{min}})^2 \times (t_{\text{max}} - \text{temp}) \quad (16)$	Equation (16)	Present Study
$\frac{1}{D} = r_{\text{m}} \times \left[\frac{\text{temp}^2}{\text{temp}^2 + x^2} e^{\left(\frac{t_{\text{m}} - \text{temp}}{\Delta}\right)}\right] \quad (17)$	Holling Type III (Hilbert and Logan modification)	Holling 1965, Hilbert and Logan 1983, Smith and Ward 1995, Roy et al. 2002
$\frac{1}{D} = e^{\rho \times \text{temp}} - e^{\left(\rho \times t_m \frac{t_{\text{m}} - \text{temp}}{\Delta}\right)} + \lambda \quad (18)$	Lactin	Lactin et al. 1995, Lactin and Johnson 1995, Briere and Pracros 1998, Royer et al. 1999, Muniz and Nombela 2001, Tobin et al. 2001, Roy et al. 2002
$\frac{1}{D} = a \times \text{temp} \times (\text{temp} - t_{\text{min}}) \times \sqrt{t_{\text{max}} - \text{temp}} \quad (19)$	Briere	Briere et al. 1999, Roy et al. 2002

Table 2. Duration (mean ± SE) of development, pre-oviposition period, and biological cycle of *N. includens* and *N. bisignatus* at various constant temperatures (number in brackets is the sample size, number in parentheses is the percentage mortality during each instar)

Temperature/ Species (°C)		Developmental stage							Pre-oviposition period (adult–egg)	Biological cycle (egg–egg)
		Egg	Larval instar				Prepupa	Pupa		
			First	Second	Third	Fourth				
10	*Ni*^{a},*Nb*^{b}	—	—	—	—	—	—	—	—	—
15	*Ni*	26.84 ± 1.28a [33] (24.24)	8.18 ± 0.24a [30] (16.67)	6.36 ± 0.34a [31] (19.35)	7.26 ± 0.36a [29] (13.79)	15.12 ± 0.79a [28] (10.71)	6.08 ± 0.66a [26] (3.85)	24.14 ± 1.13a [27] (7.41)	20.34 ± 0.59a	114.32 ± 1.61a
	Nb	27.02 ± 1.08a [32] (21.87)	8.52 ± 0.57a [30] (16.67)	6.58 ± 0.43a [29] (13.79)	7.90 ± 0.60a [29] (13.79)	13.28 ± 0.78a [27] (7.41)	5.16 ± 0.51a [27] (7.41)	22.76 ± 1.20a [26] (3.85)	21.76 ± 0.90b^c	112.98 ± 2.51b^c
20	*Ni*	13.18 ± 1.07a [29] (13.79)	4.82 ± 0.24 [26] (3.85)	3.78 ± 0.25a [27] (7.41)	4.04 ± 0.20a [26] (3.85)	5.84 ± 0.31a [26] (3.85)	2.96 ± 0.35a [26] (3.85)	11.72 ± 1.08a [27] (7.41)	9.48 ± 0.37a	55.82 ± 1.10a
	Nb	14.02 ± 0.99a [30] (16.67)	5.08 ± 0.37a [27] (7.41)	3.92 ± 0.37a [26] (3.85)	4.94 ± 0.58b^c [26] (3.85)	6.38 ± 0.65b^c [26] (3.85)	2.88 ± 0.44a [26] (3.85)	10.82 ± 0.89a [27] (7.41)	10.02 ± 0.59^c	58.06 ± 2.90b^c
25	*Ni*	8.28 ± 0.36a [27] (7.41)	2.56 ± 0.22a [27] (7.41)	2.08 ± 0.19a [27] (7.41)	2.34 ± 0.24a [26] (3.85)	4.10 ± 0.33a [25] (0.00)	1.64 ± 0.45a [26] (3.85)	8.12 ± 0.30a [26] (3.85)	5.78 ± 0.38a	34.90 ± 0.46a
	Nb	9.10 ± 0.48b [28] (10.71)	3.36 ± 0.40b [27] (7.41)	2.48 ± 0.42bc [27] (7.41)	3.34 ± 0.55b [27] (7.41)	4.26 ± 0.44a [26] (3.85)	1.76 ± 0.25a [26] (3.85)	7.28 ± 0.66b [27] (7.41)	6.48 ± 0.76^c	38.06 ± 2.25b
30	*Ni*	5.38 ± 0.30a [28] (10.71)	2.04 ± 0.14a [28] (10.71)	1.58 ± 0.19a [26] (3.85)	1.88 ± 0.22a [26] (3.85)	3.46 ± 0.29a [26] (0.00)	1.32 ± 0.35a [26] (3.85)	5.28 ± 0.38a [28] (10.71)	4.56 ± 0.17a	25.50 ± 0.66a
	Nb	7.10 ± 0.58b [30] (16.67)	2.92 ± 0.47b [28] (10.71)	2.10 ± 0.41b [27] (7.41)	2.68 ± 0.66b [27] (7.41)	3.56 ± 0.46a [28] (10.71)	1.50 ± 0.25a [26] (3.85)	5.22 ± 0.60a [29] (13.79)	5.24 ± 0.46b^c	30.32 ± 2.14b
32.5	*Ni*	4.98 ± 0.39a [29] (13.79)	1.84 ± 0.24a [28] (10.71)	1.52 ± 0.34a [28] (10.71)	1.68 ± 0.35a [27] (7.41)	3.04 ± 0.32a [26] (3.85)	1.18 ± 0.24a [26] (3.85)	4.44 ± 0.58a [27] (7.41)	4.12 ± 0.46a	22.80 ± 1.53a
	Nb	8.04 ± 0.75b [34] (26.47)	3.08 ± 0.43b [30] (16.67)	2.32 ± 0.035b [31] (19.35)	3.14 ± 0.70b [30] (16.67)	4.06 ± 71b [29] (13.79)	1.78 ± 0.33b [28] (10.71)	5.62 ± 0.92b [30] (16.67)	6.26 ± 0.63b	34.30 ± 1.84b
35	*Ni*	5.68 ± 0.89 [36] (30.56)	2.42 ± 0.66 [32] (21.87)	1.68 ± 0.56 [31] (19.35)	1.74 ± 0.29 [31] (19.35)	3.32 ± 0.48 [30] (16.67)	1.52 ± 0.51 [29] (13.79)	5.06 ± 0.55 [32] (21.87)	4.42 ± 0.31	25.84 ± 1.57
	Nb	—	—	—	—	—	—	—	—	—
37.5	*Ni, Nb*	—	—	—	—	—	—	—	—	—

The means in the same temperature and column followed by the same letter are statistically equivalent, Tukey–Kramer HSD Test, $\alpha = 0.05$.

[a] *Ni: Nephus includens.*

[b] *Nb: Nephus bisignatus.*

[c] Difference is marginally significant ($0.02 \leq P \leq 0.05$).

Differences in the total time of the biological cycle were only marginally significant, biologically meaningless, at temperatures ≤20°C. At higher temperatures, *N. includens* completed development faster. The $t_{\min}$, $t_{\max}$, and t_{opt} for the biological cycle of the two predators (Table 3) showed that *N. bisignatus* had generally lower temperatures than *N. includens.*

A two-way ANOVA for duration of development with species and temperature as factors revealed significant interaction of the two factors ($\text{df} = 5, 264$; $P < 0.0001$).

Model Evaluation. All fitted and some measurable parameters were estimated from the regression, whereas some other measurable parameters were calculated as a result of the solution of the equations or their first derivatives. The values of fitted coefficients and measurable parameters of the models are included in Tables 3 and 4. In Table 4, there is also a synoptic presentation of how each model met the criteria of the evaluation.

R^2 and RSS. The value of R^2 varied between 0.9689–0.9999 and 0.9738–0.9999 for *N. bisignatus* and *N. includens,* respectively. The RSS had similar trends. The highest values of R^2 and the lowest RSS were obtained by the Stinner, Logan-10, Sharpe and DeMichele, Analytis, and Lactin equations (Table 4).

The curves of the influence of temperature on the biological cycle of each species for each model are depicted in Fig. 1.

Discussion

Nephus includens has a shorter biological cycle than *N. bisignatus.* However, the latter species is more tolerant at lower temperatures, having $t_{\min} \approx 2$–3°C lower than the former. This corresponds to the known distribution of *N. bisignatus* in Northern Europe (Norway, Finland, Sweden, Denmark, Netherlands, and Germany) (Pope 1973, Francardi and Covassi 1992), and *N. includens* is exclusively in countries with a warmer climate (Turkey, Spain, Italy, and Portugal) (Bodenheimer 1951, Tranfaglia and Viggiani 1972, Viggiani 1974, Longo and Benfatto 1987, Suzer et al. 1992, Magro et al. 1999, Magro and Hemptinne 1999). The comparison of the thermal constants leads us to conclude that *N. includens* can complete more generations per year than *N. bisignatus* in temperate climatic conditions. In fact in Greece, they complete five and four generations annually, respectively (D.C.K., unpublished data).

Our results also support the conclusion that *N. bisignatus* is much more tolerant to cold than its conspecific. Both predators are more tolerant at low temperatures than *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae), a cosmopolitan predator of *P. citri,* given that its lower developmental threshold for total development is 13.7°C (Babu and Azam 1988). In contrast, the respective threshold of another pseudococcid predator *Nephus reunioni* is 10.9°C (Izhevsky and Orlinsky 1988), almost identical to

Table 3. Values ± SE of the fitted coefficients and measurable parameters of 14 developmental rate models for describing total development of *N. bisignatus* and *N. includens*

Model	*N. includens*	*N. bisignatus*
Linear or thermal summation		
b	0.0020 ± 0.0000	0.0016 ± 0.0000
a	−0.0222 ± 0.0008	−0.0153 ± 0.0016
K	490.4846 ± 7.6984	614.2506 ± 25.6566
t_{min}	10.9309 ± 0.2137	9.3857 ± 0.5488
Sigmoid or logistic		
a	4.9185 ± 1.1162	4.8463 ± 1.4640
b	−0.2280 ± 0.0598	−0.2525 ± 0.0836
C	0.0438 ± 0.0043	0.0324 ± 0.0029
Janisch (analysis modification)		
D_{min}	24.3383 ± 2.1273	31.9226 ± 2.2067
k	0.1943 ± 0.1155	0.2182 ± 0.0918
λ	0.1111 ± 0.0226	0.1147 ± 0.0185
t_{opt}	34.0646 ± 2.1500	31.4750 ± 1.4904
Stinner		
a	4.1518 ± 0.1967	4.0354 ± 0.1221
b	−0.1687 ± 0.0135	−0.1826 ± 0.0093
C	0.0553 ± 0.0039	0.0419 ± 0.0020
t_{opt}	32.3856 ± 0.0039	29.5866 ± 0.1454
Logan-6		
ψ	0.0504 ± 0.0000	0.0089 ± 0.0000
ρ	0.1611 ± 0.0063	0.1653 ± 0.0051
t_{max}	38.7675 ± 0.3874	35.9410 ± 0.2641
Δ	6.1762 ± 0.2374	5.8911 ± 0.1629
t_{opt}	32.6	30.0
Logan-10		
α	0.0542 ± 0.0022	0.0389 ± 0.0002
ρ	0.1730 ± 0.0098	0.1948 ± 0.0019
t_{max}	35.0677 ± 0.0027	32.7502 ± 0.0018
Δ	0.0358 ± 0.0000	0.1320 ± 0.0000
κ	66.8770 ± 10.2312	62.6158 ± 1.8103
t_{opt}	34.8	32.1
Sharpe and DeMichele		
a	−5.6900 ± 0.0215	−5.9991 ± 0.0296
b	26.4591 ± 0.3839	21.3241 ± 0.6394
c	3.0189 ± 0.5054	15.8018 ± 0.9209
d	170.2647 ± 19.3200	540.7930 ± 30.6777
f	7770.7458 ± 0.0253	21698.5226 ± 0.0000
g	272021 ± 0.0000	754716.4226 ± 0.0000
t_{opt}	34.9	30.0
t_{max}	~35.1 (graphical estimation)	~34.8 (graphical estimation)
Analytis		
a	0.0004 ± 0.0002	0.0001 ± 0.0000
t_{min}	7.9601 ± 1.1380	4.9125 ± 0.0000
t_{max}	35.0276 ± 0.0445	33.0781 ± 0.0000
n	1.3945 ± 0.1485	1.7766 ± 0.0000
m	0.0577 ± 0.0216	0.1740 ± 0.0000
t_{opt}	34.0	30.6
Gauss (or Taylor equation)—nonsymmetric		
r_m	0.0441 ± 0.0005	0.0338 ± 0.0001
t_{opt}	34.9999 ± 0.0000	32.4999 ± 0.0000
t_s	11.0220 ± 0.1996	10.7097 ± 0.0551
t_{st}	−0.000021 ± 0.000000	0.000023 ± 0.000000
t_{max}	~35.1 (graphical estimation)	~32.6 (graphical estimation)
Polynomial third order (Harcourt Equation)		
a	−0.0001 ± 0.0000	−0.0001 ± 0.0000
b	0.0007 ± 0.0003	0.0007 ± 0.0003
c	−0.0143 ± 0.0075	−0.0142 ± 0.0081
d	0.0952 ± 0.0582	0.0911 ± 0.0596
t_{opt}	32.6	29.7
t_{max}	42.8	38.8
Equation 16		
a	0.0001 ± 0.0000	0.0001 ± 0.0000
t_{min}	8.5021 ± 0.8673	7.4083 ± 0.7733
t_{max}	45.4570 ± 0.0876	41.6658 ± 0.0840
t_{opt}	33.2	30.3

(continued on next page)

Table 3. Continued

Model	*N. includens*	*N. bisignatus*
Holling type III (Hilbert and Logan modification)		
r_m	0.4335 ± 0.3561	0.1477 ± 0.0696
x	95.9281 ± 43.0784	55.2850 ± 16.0371
T_m	35.4846 ± 0.0969	32.6883 ± 0.0229
Δ	0.1358 ± 0.0000	0.0666 ± 0.0000
t_{opt}	33.3	30.3
t_{max}	37.4	35.3
Lactin		
ρ	0.0019 ± 0.0000	0.0017 ± 0.0000
T_m	38.2976 ± 2.1509	39.6875 ± 1.1931
Δ	0.7152 ± 0.4728	1.5488 ± 0.2730
λ	−1.0214 ± 0.0010	−1.0168 ± 0.0010
t_{min}	10.9	9.9
t_{max}	36.1	34.7
t_{opt}	33.6	30.5
Briere		
a	0.0000 ± 0.0000	0.0000 ± 0.0000
t_{min}	10.3132 ± 1.5379	9.1307 ± 1.4075
t_{max}	39.5970 ± 1.1878	36.2159 ± 0.8231
t_{opt}	32.1	30.1

N. includens lower developmental threshold. No other experimental data about critical temperatures of citrus mealybug predators are available in the literature.

The developmental zero and the thermal constant have been estimated by the linear equation (or thermal summation) in numerous studies (Table 1). Inherent deficiencies of the model are as follows: First, the assumed relationship holds only for a medium range of temperatures (usually 15–30°C) (Campbell et al. 1974, Gilbert et al. 1976, Syrett and Penman 1981). Second, the estimated threshold is an extrapolation of the linear portion of the relationship into a region where the relationship is unlikely to be linear (Jervis and Copland 1996). For these reasons, the lower developmental threshold and the thermal constant may be underestimated at temperatures close to the lower threshold (Howe 1967). Despite these disadvantages, the linear model has been used widely, because it requires minimal data for formulation, it is very easy to calculate and apply, and usually yields approximately correct values with negligible differences in accuracy from more complex models (e.g., Eckenrode and Chapman 1972, AliNiazee 1976, Butts and McEwen 1981, Obrycki and Tauber 1981). Moreover, it is the simplest and easiest method for estimation of the thermal constant (K) (Worner 1992).

All nonlinear models were fitted very well to the data of the current study, as indicated by the high values of R^2. However, crucial differences among them have been observed, especially in the estimated values of $t_{min,}$ t_{max}, and t_{opt}.

The sigmoid equation did not estimate any of the measurable parameters. Although the equation corresponds well with the observed data over much of the temperature range, the curve fails to follow the decline in developmental rate that should occur within

Table 4. Evaluation of 14 equations for describing the effect of temperature on the development of *N. bisignatus* and *N. includens* based on specific criteria

Model	*N. includens*		*N. bisignatus*		MP	NFC	BI	Acc			G
	R^2	*RSS* $(\times 10^{-6})$	R^2	*RSS* $(\times 10^{-6})$				t_{min}	t_{opt}	t_{max}	A
Linear	0.9930	62.71	0.9965	1.152	1	2	+	+	•	•	+
Sigmoid or logistic	0.9738	25.0403	0.9689	11.8658	0	3	+	•	•	•	−
Janisch	0.9936	6.0737	0.9972	1.0711	1	4	+	•	+	•	−
Stinner	0.9995	0.4490	0.9999	0.0033	1	4	+	•	−	•	+
Logan-6	0.9963	3.5663	0.9983	0.6503	2	4	+	•	+	−	+
Logan-10	0.9995	0.4490	0.9999	0.0033	2	5	+	•	+	+	+
Sharpe and DeMichele	0.9999	0.0022	0.9998	0.8661	2	6	+	•	+	+	+
Analytis	0.9999	0.0425	0.9999	0.0019	3	5	+	−	+	+	−
Gauss (or Taylor)	0.9973	12.1271	0.9977	4.6852	2	4	+	•	+	+	+
Polynomial third order	0.9905	9.0519	0.9942	2.2244	2	4	−	•	−	−	+
Equation 16	0.9816	17.5749	0.9838	6.2032	3	3	+	−	+	−	−
Holling type III	0.9973	2.5796	0.9985	5.7955	2	4	+	•	+	−	−
Lactin	0.9995	0.4865	0.9997	1.0767	3	4	+	+	+	+	+
Briere	0.9875	11.9025	0.9916	3.2149	3	3	+	+	+	−	−

+, yes; −, no; •, not estimated; R^2, coefficient of determination (linear), coefficient of nonlinear regression (nonlinear); RSS, residual sum of squares; MP, number of measurable parameters; NFC, number of fitted coefficients; BI, the fitted coefficients have biological interpretation; GA, general application of the model to many insect species (obtained from the literature); Acc., accuracy of the estimated values of the thresholds.

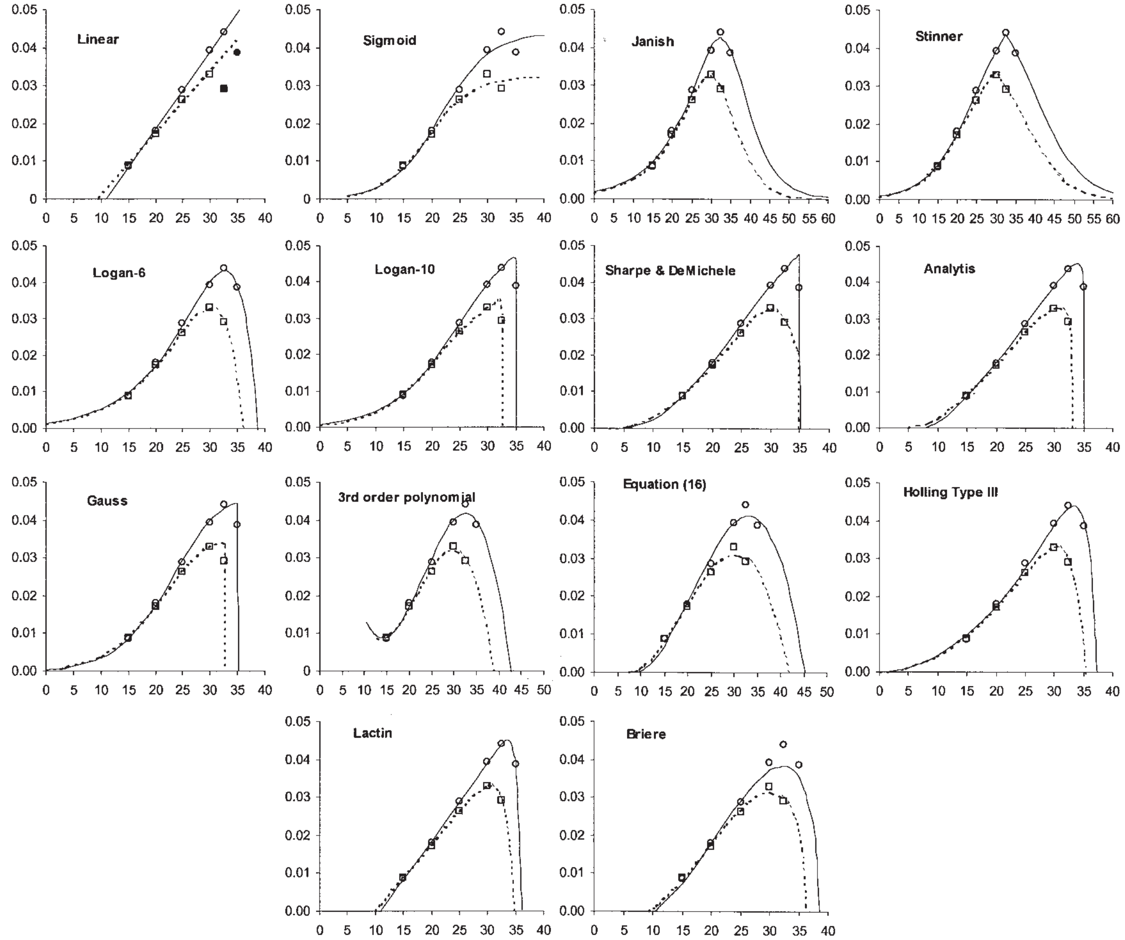

Fig. 1. Fitting of equations of Table 1 on data of Table 2 for the total biological cycle of *N. includens* (solid line) and *N. bisignatus* (dotted line). In all charts, the ordinate is the rate of development (1/D, in days^{-1}), and the abscissa is the temperature (in °C). In the linear regression, the last data values have been omitted because of deviation from the straight line.

a few degrees of the upper threshold. Similar conclusions have been reported by Stinner et al. (1974) and Lamb and Loschiavo (1981).

Estimation of t_{opt} by the Janisch equation is in accordance with experimental data of the current study. The Janisch equation has been used with variable success (e.g., Huffaker 1944, Quednav 1957) and has been criticized for inadequate fit and computational difficulties (Messenger and Flitters 1958). The Stinner equation, which produces a curve similar to the Sigmoid but decreases above t_{opt}, seems to underestimate slightly this critical temperature. It also has drawbacks at higher temperatures because of unrealistic symmetry about optimum temperature; this has been pointed out by Logan et al. (1976) and proven by the current study, as well.

The Logan-6 and Holling III equations seem to overestimate $t_{\max}$, because neither species completed development at 37.5 and 35°C, values lower than the calculated $t_{\max}$. In contrast, the Logan-10 equation provided more realistic estimates. All three models did provide accurate values for t_{opt}. Nevertheless, the biological interpretation of all fitted coefficients of the Logan-6 equation is remarkable (Logan et al. 1976) and should be regarded as a major advantage when evaluating this model. Moreover, it is one of the most commonly used models for description of temperature-dependent development of insects and other arthropods.

As far as Sharpe and DeMichele and Gauss equations are concerned, estimation of t_{opt} is achieved by the solution of the first derivative, whereas $t_{\max}$ is calculated graphically from the rapid decline of the right descending branch. A disadvantage of the Sharpe and DeMichele equation is the large number of fitted coefficients. However, it remains a biologically meaningful model adopted by many authors (Table 1) and modified by Schoolfield et al. (1981) and Wagner et al. (1984).

The estimation of the third order polynomial for t_{opt} is slightly lower than the observed values, but the overestimation of t_{max} is noteworthy. The model cannot estimate t_{min} because there is no intersection with the temperature axis. Moreover, the curve obtained below 15°C is unrealistic, given that the rate of development increases even though the insect is in a temperature range where almost no development occurs. Under- and overestimation of t_{opt} and t_{max}, respectively, by this model has been observed in other studies (Lamb et al. 1984, Briere and Pracros 1998).

To overcome this deficiency, another third order polynomial (Equation 16) was tested. It is the same as the Analytis equation when $n = 2$ and $m = 1$. This equation estimated the three essential parameters, t_{min}, t_{max}, and t_{opt}, doing well for t_{opt}, overestimating t_{max}, and underestimating t_{min} compared with most other models.

The Analytis equation provided realistic values for t_{opt} and t_{max} but underestimated the value of t_{min}. This model does not have general application because it has been used only by Analytis (1977, 1979, 1980, 1981). The current study is the first to evaluate it for insect development. The Briere equation estimated the values of t_{opt} and t_{min} satisfactorily. However, noteworthy overestimation of t_{max} occurred. However, the Lactin model calculated all the thermal thresholds very well.

To conclude, the Lactin model was the only model that met all the criteria. This equation has been proposed by Lactin et al. (1995), who made two major modifications on the Logan-6 model, omitting a redundant parameter (ψ) and incorporating another one (λ), to force the curve to intercept the y axis and thus allow estimation of lower developmental threshold. It has also described successfully the influence of temperature on the development of many arthropods (see Table 1).

However, it should be noticed that the linear equation was not only very well-fitted to experimental data, but the easiest to calculate. Moreover, it is the only equation that enables the calculation of the thermal constant. These two models (linear and Lactin) are recommended as the most efficient for the description of temperature-dependent development of *N. includens* and *N. bisignatus,* and possibly of other coccinellids.

References Cited

AliNiazee, M. T. 1976. Thermal unit requirements for determining adult emergence of the western cherry fruit fly (Diptera: Tephritidae) in the Willamette valley of Oregon. Environ. Entomol. 5: 397–402.

Analytis, S. 1974. Der einsatz von wachstumsfunktionen zur analyse der befallskurven von pflanzenkrankheiten. Phytopath. Z. 81: 133–144.

Analytis, S. 1977. Über die relation zwischen biologischer entwicklung und temperatur bei phytopathogenen Pilzen. Phytopath. Z. 90: 64–76.

Analytis, S. 1979. Study on relationships between temperature and development times in phytopathogenic fungus: a mathematical model. Agric. Res. (Athens). 3: 5–30.

Analytis, S. 1980. Obtaining of sub-models for modeling the entire life cycle of a pathogen.. Z. Pflanzenkr. Pflanzenschutz. 87: 371–382.

Analytis, S. 1981. Relationship between temperature and development times in phytopathogenic fungus and in plant pests: a mathematical model. Agric. Res. (Athens). 5: 133–159.

Argyriou, L. C. 1968. Contribution to the biological control of citrus scales. PhD Thesis, Agricultural University of Athens, Athens, Greece.

Argyriou, L. C., H. G. Stavraki, and P. A. Mourikis. 1976. A list of recorded entomophagous insects of Greece. Benaki Phytopathological Institute, Kifissia, Greece.

Babu, T. R., and K. M. Azam. 1988. Effect of low holding temperature during pupal instar on adult emergence, pre-oviposition and fecundity of *Cryptolaemus montrouzieri* Mulsant (Coccinellidae: Coleoptera). Insect Sci. Appl. 9: 175–177.

Bodenheimer, F. S. 1951. Citrus entomology in the Middle East. W. Junk, The Hague, Netherlands.

Briere, J. F., and P. Pracros. 1998. Comparison of temperature-dependent growth models with the development of *Lobesia botrana* (Lepidoptera: Tortricidae). Environ. Entomol. 27: 94–101.

Briere, J. F., P. Pracos, J. Stockel, and P. Blaise. 1998. Modeling development rate for predicting *Lobesia botrana* (Den. and Schiff.) population dynamics. Bull. OILB/IOBC. 21: 51–52.

Briere, J. F., P. Pracros, A. Y. le Roux, and J. S. Pierre. 1999. A novel rate model of temperature-dependent development for arthropods. Environ. Entomol. 28: 22–29.

Butts, R. A., and F. L. McEwen. 1981. Seasonal populations of the diamondback moth: *Plutella xylostella* (Lepidoptera: Plutellidae), in relation to day-degree accumulation. Can. Entomol. 113: 127–131.

Campbell, A., and M. Mackauer. 1975. Thermal constants for development of the pea aphid (Homoptera: Aphididae) and some of its parasites. Can. Entomol. 107: 419–423.

Campbell, A., B. D. Frazer, N. Gilbert, A. P. Gutierrez, and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11: 431–438.

Davidson, J. 1942. On the speed of development of insect eggs at constant temperatures. Aust. J. Exp. Biol. Med. Sci. 20: 233–239.

Davidson, J. 1944. On the relationship between temperature and the rate of development of insects at constant temperatures. J. Anim. Ecol. 13: 26–38.

De Clerq, P., and D. Degheele. 1992. Development and survival of *Podisus maculiventris* (Say) and *Podisus sagitta* (Fab.) (Het.: Pentatomidae) at various constant temperatures. Can. Entomol. 124: 125–133.

Eckenrode, C. J., and R. K. Chapman. 1972. Seasonal adult cabbage maggot populations in the field in relation to thermal-unit accumulation. Ann. Entomol. Soc. Am. 65: 151–156.

Fornasari, L. 1995. Temperature effects and embryonic development of *Aphthona abdominalis* (Col.: Chrysomelidae), a natural enemy of *Euphorbia esula* (Euphorbiales: Euphorbiaceae). Environ. Entomol. 24: 720–723.

Francardi, V., and M. Covassi. 1992. Note bio-ecologishe sul *Planococcus novae* (Nasonov) dannoso a *Juniperus* spp. in Toscana (Homoptera: Pseudococcidae). Redia 75: 1–20.

Gilbert, N., A. P. Gutierrez, B. D. Frazer, and R. E. Jones. 1976. Ecological relationships. W. H. Freeman and Co., Reading, United Kingdom.

Got, B., J. M. Labatte, and S. Piry. 1996. European corn borer (Lepidoptera: Pyralidae) development model. Environ. Entomol. 25: 310–320.

Gould, J. R., and J. S. Elkinton. 1990. Temperature-dependent growth of *Cotesia melanoscela* (Hymenoptera: Braconidae) a parasitoid of the gypsy moth (Lepidoptera: Lymantriidae). Environ. Entomol. 19: 859–865.

Harcourt, D. C., and J. M. Yee. 1982. Polynomial algorithm for predicting the duration of insect life stages. Environ. Entomol. 11: 581–584.

Hentz, G. M., P. C. Ellsworth, S. E. Naranjo, and T. F. Watson. 1998. Development, longevity, and fecundity of *Chelonus sp. nr. curvimaculatus* (Hymenoptera: Braconidae), an egg-larval parasitoid of pink bollworm (Lepidoptera: Gelechiidae). Environ. Entomol. 27: 443–449.

Hilbert, D. W., and J. A. Logan. 1983. Empirical model of nymphal development for the migratory grasshopper, *Melanoplus saguinipes* (Orthoptera: Acrididae). Environ. Entomol. 12: 1–5.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 45: 1–60.

Honěk, A. 1999. Constraints on thermal requirements for insect development. Entomol. Sci. 2: 615–621.

Howe, R. W. 1967. Temperature effects on embryonic development in insects. Annu. Rev. Entomol. 10: 15–42.

Huffaker, C. B. 1944. The temperature relations of the immature stages of the malarial mosquito *Anopheles quadrimaculatus* Say, with a comparison of the developmental power of constant and variable temperatures in insect metabolism. Ann. Entomol. Soc. Am. 37: 1–27.

Izhevsky, S. S., and A. D. Orlinsky. 1988. Life history of the imported *Scymnus* (*Nephus*) *reunioni* (Col.: Coccinellidae) predator of mealybugs. Entomophaga. 33: 101–114.

Janisch, E. 1932. The influence of temperature on the life-history of insects. Trans. Entomol. Soc. Lond. 80: 137–168.

Jarošik, V., A. Honěk, and A.F.G. Dixon. 2002. Developmental rate isomorphy in insects and mites. Am. Nat. 160: 497–510.

Jervis, M. A., and M.J.W. Copland. 1996. The life cycle, pp. 63–161. *In:* M. A. Jervis and N. Kidd (eds.), Insect natural enemies—practical approaches to their study and evaluation. Chapman & Hall, London, United Kingdom.

Johnson, E. F., R. Trottier, and J. E. Laing. 1979. Degree-day relationships to the development of *Lithocolletis blancardella* (Lepidoptera: Gracillariidae) and its parasite *Apanteles ornigis* (Hymenoptera: Braconidae). Can. Entomol. 111: 1177–1184.

Katsoyannos, P. 1996. Integrated insect pest management for citrus in northern Mediterranean countries. Benaki Phytopathological Institute, Kifissia, Greece.

Kontodimas, D. C. 1997. First record of the predatory insect *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) in Greece. Ann. Inst. Phytopathol. 18: 61–63.

Kontodimas, D. C. 2003. Study on fecundity of the pseudococcids' predator *Nephus includens* (Kirsch) (Coleoptera: Coccinellidae), p. 56. *In* Abstracts of "Integrated Protection and Production in Viticulture", European Meeting of the IOBC/WPRS Working Group "Integrated Control in Viticulture", March 18–22, 2003, Volos, Greece.

Lactin, D. J., and D. L. Johnson. 1995. Temperature-dependent feeding rates of *Melanophus sanguinipes* nymphs (Orthoptera: Acrididae) in laboratory trials. Environ. Entomol. 24: 1291–1296.

Lactin, D. J., N. J. Holliday, D. L. Johnson, and R. Craigen. 1995. Improved rate model of temperature-dependent development by arthropods. Environ. Entomol. 24: 68–75.

Lamb, R. J. 1992. Developmental rate of *Acyrthosiphon pisum* (Homoptera: Aphididae) at low temperatures: implications for estimating rate parameters for insects. Environ. Entomol. 21: 10–19.

Lamb, R. J., and S. R. Loschiavo. 1981. Diet, temperature, and the logistic model of developmental rate for *Tribolium confusum* (Coleoptera: Tenebrionidae). Can. Entomol. 113: 813–818.

Lamb, R. J., G. H. Gerber, and G. F. Atkinson. 1984. Comparison of developmental rate curves applied to egg hatching data of *Entomoscelis americana* Brown (Col: Chrysomelidae) Environ. Entomol. 13: 868–872.

Logan, J. A. 1988. Toward an expert system for development of pest simulation models. Environ. Entomol. 17: 359–376.

Logan, J. A., D. J. Wollkind, S. C. Hoyt, and L. K. Tanigoshi. 1976. An analytical model for description of temperature dependent rate phenomena in arthropods. Environ. Entomol. 5: 1133–1140.

Longo, S., and Benfatto, D. 1987. Coleotteri entomofagi presenti sugli agrumi in Italia. Inform. Fitopat. 37: 21–30.

Magro, A., and J. L. Hemptinne. 1999. The pool of coccinellids (Coleoptera: Coccinellidae) to control coccids (Homoptera: Coccoidea) in portuguese citrus groves. Bol. San. Veg. Plagas. 25: 311–320.

Magro, A., J. Araujo, and J. L. Hemptinne. 1999. Coccinellids (Coleoptera: Coccinellidae) in citrus groves in Portugal: listing and analysis of geographical distribution. Bol. San. Veg. Plagas. 25: 335–345.

Marquardt, D. V. 1963. An algorithm for least squares estimation of nonlinear parameters. J. Soc. Ind. Appl. Math. 11: 431–441.

Messenger, P. S., and N. E. Flitters. 1958. Effect of constant temperature environments on the egg stage of three species of Hawaiian fruit flies. Ann. Entomol. Soc. Am. 51: 109–119.

Morales-Ramos, J. A., and J. R. Cate. 1993. Temperature-dependent developmental rates of *Catolacus grandis* (Hymenoptera: Pteromalidae). Environ. Entomol. 22: 226–233.

Muniz, M., and Nombela, G. 2001. Differential variation in development of the B- and Q-Biotypes of *Bemisia tabaci* (Homoptera: Aleyrodidae) on sweet pepper at constant temperatures. Environ. Entomol. 30: 720–727.

Obrycki, J. J., and M. J. Tauber. 1981. Phenology of three coccinellid species: thermal requirements for development. Ann. Entomol. Soc. Am. 74: 31–36.

Obrycki, J. J., and M. J. Tauber. 1982. Thermal requirements for development of *Hippodamia convergens* (Coleoptera: Coccinellidae). Ann. Entomol. Soc. Am. 75: 678–683.

Obrycki, J. J., and T. J. Kring. 1998. Predaceous Coccinellidae in biological control. Annu. Rev. Entomol. 43: 295–321.

Pope, R. D. 1973. The species of *Scymnus* (s. str.), *Scymnus* (Pullus) and *Nephus* (Col., Coccinellidae) occurring in the British Isles. Entomol. Mon. Mag. 109: 3–39.

Quednav, W. 1957. Über den einfluss von temperatur und luftfeuchtigkeit auf den eiparasiten *Trichogramma cacoeciae* Marchal. Mitt. Biol. Bundesanst. Land Forstwirtch Berl. Dahlem. 90: 1–63.

Roy, M., J. Brodeur, and C. Cloutier. 2002. Relationship between temperature and developmental rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdaniali* (Acarina: Tetranychidae). Environ. Entomol. 31: 177–187.

Royer, T. A., J. V. Edelson, and M. K. Harris. 1999. Temperature related, stage-specific development and fecundity of colonizing and root-feeding morphs of *Pemphigus populitransversus* (Homoptera: Aphididae) on brassica. Environ. Entomol. 28: 265–271.

SAS Institute. 1989. JMP: a guide to statistical and data analysis, version 4.02. SAS Institute, Cary, NC.

Schoolfield, R. M., P.J.H. Sharpe, and C. E. Magnuson. 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. J. Theor. Biol. 88: 719–731.

Sharpe, P.J.H., and D. W. DeMichele. 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 66: 649–670.

Sharpe, P.J.H., G. L. Curry, D. W. DeMichele, and C. L. Cole. 1977. Distribution models of organism development times. J. Theor. Biol. 66: 1–38.

Sigsgaard, L. 2000. The temperature-dependent duration of development and parasitism of three cereal aphid parasitoids, Aphidius ervi, *A. rhopalosiphi,* and *Praon volucre.* Entomol. Exp. Appl. 95: 173–184.

Smith, M. A., and S. A. Ward. 1995. Temperature effects on larval and pupal development, adult emergence, and survival of the pea weevil (Coleoptera: Chrysomelidae). Environ. Entomol. 24: 623–634.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed. Freedman, San Francisco, CA.

SPSS. 1999. SPSS base 9.0 user's guide. SPSS, Chicago, IL.

Stathas, G. J. 2000. The effect of temperature on the development of the predator *Rhyzobius lophanthae* and its phenology in Greece. BioControl. 45: 439–451.

Stinner, R. E., A. P. Gutierez, and G. D. Butler, Jr. 1974. An algorithm for temperature-dependent growth rate simulation. Can. Entomol. 106: 519–524.

Suzer, T., M. Aytas, and R. Yumruktepe. 1992. Chemical experiment on citrus whitefly (*Dialeurodes citri* Ashmead), citrus red mite (*Panonychus citri* McGregor) and citrus rust mite (*Phyllocoptruta oleivora* Ashmead) in the Mediterranean region. Zir. Muc. Arast. Yill. 22–23: 61–63.

Syrett, P., and D. R. Penman. 1981. Developmental threshold temperatures for the brown lacewing, *Micromus tasmaniae* (Neuroptera: Hemerobiidae). New Zealand J. Zool. 8: 281–283.

Taylor, F. 1981. Ecology and evolution of physiological time in insects. Am. Nat. 117: 1–23.

Taylor, F. 1982. Sensitivity of physiological time in arthropods to variation of its parameters. Environ. Entomol. 11: 573–577.

Tobin, P. C., S. Nagarkatti, and M. C. Saunders. 2001. Modeling development in grape berry moth (Lepidoptera: Tortricidae). Environ. Entomol. 30: 692–699.

Tranfaglia, A., and G. Viggiani. 1972. Dati biologici sullo *Scymnus includens* Kirsch (Coleoptera: Coccinellidae). Boll. Lab. Entomol. Agrar. Filippo-Silvestri. 30: 9–18.

Uvarov, B. P. 1931. Insects and climate. Trans. Entomol. Soc. Lond. 79: 1–247.

Viggiani, G. 1974. Recherches sur les cochenilles des agrumes. IOBC/WPRS Bulletin. 3: 117–120.

Wagner, T. L., H. I. Wu, P.J.H. Sharpe, R. M. Schoolfield, and R. N. Coulson. 1984. Modeling insect development rates: a literature review and application of a biophysical model. Ann. Entomol. Soc. Am. 77: 208–225.

Wagner, T. L., R. L. Olson, and J. L. Willers. 1991. Modeling arthropod development time. J. Agric. Entomol. 8: 251–270.

Wigglesworth, V. B. 1953. The principles of insects physiology, fifth ed. Methuen, London, United Kingdom.

Worner, S. P. 1992. Performance of phenological models under variable temperature regimes: consequences of the Kaufman or rate summation effect. Environ. Entomol. 21: 689–699.

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